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Prey choice and habitat use of people exploiting intertidal resources

W.F. DE BOER[1, 2]*, A.-F. BLIJDENSTEIN[2] AND F. LONGAMANE[3]
[1]*Department of Biological Sciences, Eduardo Mondlane University, CP 257, Maputo, Mozambique,* [2]*Behavioural Biology, Biological Centre, Groningen University, PO Bag 14, 9750 AA, Haren, The Netherlands, and* [3]*Department of Forestry and Wildlife, CP 1406, Maputo, Mozambique*
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SUMMARY

The impact of human exploitation depends mostly on the size of the catch and the species targeted. The value of a species is an important explanatory variable in understanding human impact. Co-management of resources should take into account these different resource values, when evaluating exploitation strategies. The prey choice and foraging behaviour of women and children searching for crabs and shells on the intertidal area at Inhaca Island, South Mozambique, were investigated using optimal foraging theory. This theoretical framework offers the possibility to understand the reasoning of an exploitation strategy and the preference for certain prey species. The number of people was registered, catches were analysed, and timing and substrate choice were recorded. The value of species was estimated using contingency tables. Women were more efficient than children, as their catch was heavier, and the mean weight/animal was larger. The density of women and their timing were positively correlated to prey availability. During neap tide, they spread their visit over more of the low water period and collected crabs by digging in the mangrove forests. No digging occurred during spring tide when a larger area was exposed, the total abundance of species increased, and more species became available. Women then switched to a second strategy, targeting swimming crabs in the tidal channel. Mean neap and spring tide catches were equal (133 g ash-free dry weight per person), but spring catches comprised significantly fewer animals per catch (42 against 123 per person), and mean animal weight was larger (5.4 against 3.0 g ash-free dry-weight per person). Diet breadth was narrower during spring tide, and decreased significantly with increased catch weight. Species with profitabilities (energy intake/handling time) lower than the mean intake rate of 0.024–0.028 g ash-free dry weight s^{-1} were generally excluded from the diet. The prey preference was positively related to the relative value ranks of the prey species, as measured by ranking of species by women. Women maximized the cumulative relative value ranks during spring tide, instead of total weight. Using this analysis, differences in prey choice and spatial differences in exploitation can be understood as a strategy aimed at maximizing intake and the relative value of a prey species.

Keywords: diet choice, behaviour, efficiency, profitability, species composition, value

INTRODUCTION

Intertidal resources are widely exploited by the human population in southern Africa (Hockey & Bosman 1986; Hockey *et al.* 1988; Lasiak 1993; Siegfried *et al.* 1994; Dye *et al.* 1997), and other parts of the world (Virnstein 1977; Castilla 1993; Newton *et al.* 1993; Addessi 1994; Defeo & de Alava 1995). The management of these intertidal areas is an important issue in eastern Africa with the majority of the people living along the coast, mainly depending on the exploitation of natural resources (Coughanowr *et al.* 1995). The impact of human exploitation on the intertidal community is partly determined by the choice of their prey species. Kyle *et al.* (1997*a, b*) showed that in Natal exploitation was directed at only a couple of species. Catches in other areas comprised only a few species (Hockey & Bosman 1986; Castilla 1993; Lasiak 1993; Addessi 1994; Siegfried *et al.* 1994; Defeo & de Alava 1995). At Inhaca Island, South Mozambique, the catches are much more diverse, comprising 17 different species, including small shells, such as Moon shells *Polynices* spp. (de Boer & Longamane 1996). A first step towards an impact assessment of the people on the ecosystem structure is to analyse why certain species are exploited and others not, and to understand the temporal and regional scale of exploitation. We analysed the prey choice and foraging behaviour of people searching on the intertidal area at Inhaca using the optimal foraging theory (OFT). This modelling approach, which was originally developed to understand the diet breadth, patch use and other foraging decisions of animals (Stephen & Krebs 1986; Kamil *et al.* 1987; Krebs & Davies 1991) is also used in human behavioural studies (Winterhalder & Smith 1981; Bettinger 1991; Borgerhoff Mulder 1991; Smith & Winterhalder 1992). The main decisions to be made are: when to go, where to go, and what to eat? Are these prey species selected randomly, or is the

* Correspondence: Dr Fred de Boer, Tropical Nature Conservation and Vertebrate Ecology Group, Environmental Sciences, Wageningen University, Bornsesteeg 69, 6708 PD, Wageningen, The Netherlands Tel: +31 317 483174 Fax: +31 317 484845 e-mail: fred.deboer@staf.ton.wau.nl

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species composition of catch determined by intake optimization rules? According to the OFT we expected that people's prey choice, substrate choice and timing is determined by decisions aimed at maximizing energy intake. Understanding people's choices will improve our knowledge of the spatial and seasonal differences in human impacts. It is essential to comprehend the reasoning of people in order to propose or improve a management strategy for an area.

Diet choice

The diet breadth model (MacArthur & Pianka 1966; Winterhalder 1981; Hames & Vickers 1982; Bettinger 1991) predicts the diet composition in terms of the energy expenditure. The question is, how many different food items should be included in the diet? The model assumes that the predator knows the profitability (E_i/h_i) of the prey, determined by the energy content (E_i) per handling time (h_i) necessary to catch the prey. The mean expected energy intake during the foraging trip is calculated from the total energy intake (E) over the total combined handling (h) and searching time (s). New, less profitable species should be added to the diet as long as the profitability of this species is larger than the mean expected energy intake, thus:

$$E_i/h_i \geq E/(s+h) \quad (1)$$

The lower part of the equation $E/(s+h)$ is a threshold; dietary items with profitabilities lower than this value should not be included in the diet. One of the implications of this model is that a decreased searching time (s) will increase the threshold, so that less profitable prey species are dropped from the diet. The 14-day tidal cycle on Inhaca creates a pattern of 7 days with a small exposed intertidal area (neap tide), followed by 7 days of large exposure (spring tide), corresponding respectively to a small and large supply of potential prey species. This tidal fluctuation offers a unique natural experiment, by creating regular differences in prey abundance, as the substrate with the highest invertebrate abundance and highest species richness, the tidal channels, only becomes accessible during spring tide. The OFT predicts that if the expected total net energy gain increases due to a higher encounter rate in a rich environment (spring tide), the diet should only include the more profitable species. In a poor environment (neap tide), the diet should be broader, and also include the less profitable species as long as Equation (1) is satisfied. We sought to test this prediction, by comparing the composition of people's catches on spring and on neap tides. Total catch weight should be larger during spring tides if total weight is being maximized. Seasonality affects species availability too (de Boer 2001), and was therefore also included in the analysis. The model predicts that the food items will be included in the diet as long as their profitability is above the above mentioned threshold, regardless of the abundance of that specific prey species. We also aimed to test this expectation.

The OFT offers a good theoretical framework for the interpretation of diet differences under multiple choices, or carried out by different actors. Children and women carry out the exploitation of the intertidal fauna. The exploitation efficiency (intake rate, see below) of women is expected to be higher as they are more experienced (Bird & Bird 2000).

Time planning

A larger number of people are expected to collect during spring tide, assuming that prey abundance is then higher. People should also time their visit to the area in such a way that it corresponds with the highest potential exploitation rate. This should be precisely during the period of lowest water when the largest area of intertidal zone is exposed. During this short period of total exposure, intake should be maximal, which should affect species choice since people should concentrate on the most profitable diet and thus reduce the number of different species collected. Another of our objectives was to test this prediction.

Substrate choice

The exploitation by women on Inhaca (0.12 g ash-free dry weight [AFDW] m^{-2} yr^{-1}) is small compared to resource availability (6.4 g AFDW m^{-2}; de Boer 2001). Women are therefore not expected to deplete patches. Patch choice is determined by the profitability of the patch via the intake rate of the women. Women should concentrate on the most profitable patches in terms of energy intake over time, and only visit other less suitable patches if the intake rate in these patches is above the overall intake rate of all patches combined (MacArthur & Pianka 1966; Winterhalder 1981; Stephen & Krebs 1986). Similar models can therefore describe diet choice and patch choice. Several predictions can be made regarding patch use. Firstly, people should concentrate in the patch with the highest profitability. Secondly, we expect the number of women and the resource availability of the patch to be positively correlated; this is the so-called ideal free distribution (Begon *et al.* 1996). Thirdly, following the same reasoning as explained above under diet choice, during neap tide, when prey abundance is reduced, people should increase the number of patches in their itinerary. The testing of these predictions were additional objectives of our study.

Currency

The choice of the currency to be maximized is important. AFDW of the prey is a good estimator of the organic biomass of the prey and therefore related to the amount of metabolizable energy. The relatively easy to measure intake rate (g AFDW s^{-1}) will therefore be taken as the currency to be maximized. Prey species should be included or excluded depending or their profitability, regardless of their specific abundance. The number of animals collected per prey species depends on availability, once the species is included in the

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diet. Hence species are collected in relation to their encounter rate and no preference or avoidance is expected. Other factors, such as the monetary value of the prey, could influence prey choice. We aimed to investigate this further.

METHODS

Study site

The general ecology of Inhaca Island (E 26°07', S 32°56') is well described by Kalk (1995). Total annual rainfall is 880 mm and mean air temperature is 23°C. There is a hot, rainy summer (November–April), and a colder, drier winter (March–October).

It is mainly women and children who carry out intertidal shellfish harvesting around Maputo Bay. Women work in subsistence agriculture, which, due to the low fertility of the sandy soils, does not produce large crops. Men fish and take care of goats. Except for chickens and a few pigs, no other pastoral activities are practised on the island. Given the low occurrence of pastoral activities, shellfish collection is an important source of protein (Hockey *et al.* 1988; Siegfried *et al.* 1994).

The study was carried out in the Saco, an intertidal area in the southern bay of Inhaca. The area was subdivided into five different substrate types. Mudflats are the lower lying areas that are totally inundated during low water neap tide (LWNT). Sandbanks are slightly elevated areas containing coarser sand, some parts of which are exposed during high water neap tide (HWNT). Sandflats are intermediate in depth, consist of finer sands than the sandbanks and cover extensive areas. A large tidal channel is the main inlet and outlet of the water, and the bed of the channel is exposed only during LWNT, and is covered by old coral debris and rocks, with small patches of seagrass vegetation (*Halodule wrightii*). Mangrove forest fringes the area.

Data collection

Catch composition was studied each month from January 1995–September 1996. A total of 450 catches of women and children returning from the Saco, comprising 33 166 different organisms, were recorded. All organisms were measured and weighed. Subsamples were taken to calculate the relation between fresh weight (FW), dry weight (DW) and AFDW for the different species. Drying was done at 95°C for three days, and incinerating at 550°C for 2 hours, after which ash-weight remained constant.

The distribution of people over the substrates was registered during low water on 57 days from January 1994 to November 1996. The OFT makes important distinctions between handling time and searching time. Foraging behaviour was therefore recorded using a Psion hand-held computer loaded with the Observer software package V 3.0 (Noldus 1994). Between December 1997 and March 1998, 57 foraging trips of five women were recorded. Each foraging trip comprised the activities of one woman during one low water period, starting from the moment she left her house until she returned. The behaviour, substrate choice, and prey choice were therefore registered. Behaviour was classified as walking (not searching), searching, digging, digging with stick or axe, feeling, washing, talking or other behaviour. Substrate choice, tide (neap or spring), the water level above the substrate, and the tidal phase (-3, -2, -1, 1, 2, 3, 4 hours after the time of low water) were registered. Prey choice was recorded with reference to species and size. Prey size (mm) was later substituted by g AFDW, using species specific size-weight conversion algorithms derived from animals collected especially for this purpose (totalling 3000).

In order to study prey preference and the currency being maximized, thirty women were each asked to value different species by filling in a matrix (Guijt & Neefjes 1991; de Boer & Baquete 1998). The matrices comprised photographs of a standard amount of the most collected species and several different columns for different variables: taste, preparation time (as an indication of post-harvesting costs; Bird 1997), abundance in the field, ease of collection, monetary value, and relative importance within their own household. People valued each variable per resource by placing between 0 and 10 matchsticks in the corresponding cell. The mean number of matchsticks/cell was the relative value rank.

Statistical analysis

The FW/AFDW ratio from the subsamples was used to calculate the organic weight of the catches. Differences in size, weight or number of species in the catch were compared by an analysis of variance (ANOVA), after normalization of variances through logarithmic or square root transformation if necessary. Women's catches were classified in three different size categories: namely small, medium and large, according to the total weight of the catch. The cut-off point of these classes was set to equalize sample sizes. Factors in the ANOVA were tide (spring or neap), age (women or children), substrate type, and catch-size category. Diet breadth was calculated using Hurlbert's (*B'a*) and Smith's (*FT*) indices, both scaled to the availability of the resources (Krebs 1989), using data from of de Boer (2001). Species richness of catches was based on the indices of Margalef, Shannon–Wiener, and Hill, using Primer software (Clarke & Warwick 1994). Similarity in species composition of catches from different categories was calculated using Bray-Curtis similarity coefficients on 4th root transformed biomass data. Differences in species similarity were tested with an analysis of similarity (ANOSIM, with nul hypothesis of equal distribution of species in catches) and similarity percentage analysis (SIMPER), using Primer.

Prey choice and foraging behaviour data registered on the Psion computer were analysed using the Observer V 3.0 software (Noldus 1994). The matrices were analysed using χ^2-test with a null hypothesis of equal preference. Confidence limits of the relative value ranks were calculated for each

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species (Wonnacott & Wonnacott 1990). The observed number of value ranks was compared with the expected number; the observed/expected ratio was expected to equal 1 under the assumption of no preference. A multiple comparison among species was possible by comparing overlap of ratio confidence intervals (Siegel & Castellan 1988). Prey preference was calculated by comparing the catch composition with prey availability (both calculated in AFDW) using the rank preference ratio (Krebs 1989), after which the ratios were correlated (Spearman r_s) with the relative value ranks and other variables that could influence preference.

RESULTS

Timing

The daily number of foraging women, children and men was not normally distributed during low tide. The median number of people found searching for invertebrates during spring tides was 4.5, against 8.0 for neap tides; however, this difference was not significantly different (Mann-Whitney $U = 333$, $n = 57$, $p > 0.05$).

People timed their visits in such a way that they coincided with the period of greatest exposure (Fig. 1*a*, *b*). The mean foraging trip duration was not significantly different between spring and neap tides, but the timing and substrate choice were different between the two tides (Fig. 1*b*, Fig. 2), as most women timed their spring visits to coincide with lowest water. At neap tide, women arrived earlier, and left later. The activity of the women was different when spring and neap tides were compared (Fig. 3). Looking at the total percentage of time dedicated to certain activities, less time was spent handling, and more time was spent searching and walking at spring tide. More animals were collected per searching hour at lowest water (Fig. 1*c*), mean intake rate ($E/(s+h)$) increasing with the lowering of the water table (Fig. 1*d*; Linear regression: $F_{1,5} = 11.524$, $p < 0.02$, $R^2 = 0.64$). High intake rate was related to high species diversity (Fig. 1*d*, *e*; linear regression $F_{1,9} = 6.428$, $p < 0.05$, $R^2 = 0.42$). Thus, contrary to expectation, catches were more diverse during periods of highest intake.

The density of people searching for invertebrates was highest from November to February, but no clear seasonal pattern was apparent from the monthly registrations (Fig. 4).

Substrate choice

Women preferred the channel during spring tides, and concentrated on the mangrove fringe and channel at neap tides (Fig. 2, Fig 5). So the change in timing is accompanied by a change in substrate choice, and by a change in activity. Mangrove crabs hide in the mud and must be dug out with an axe, which took 5.2% of the women's total time during neap tide; women did not dig during spring tides. Variances of the samples were large and no indication could be found of women concentrating on the more profitable substrates during spring tide as compared to neap tide.

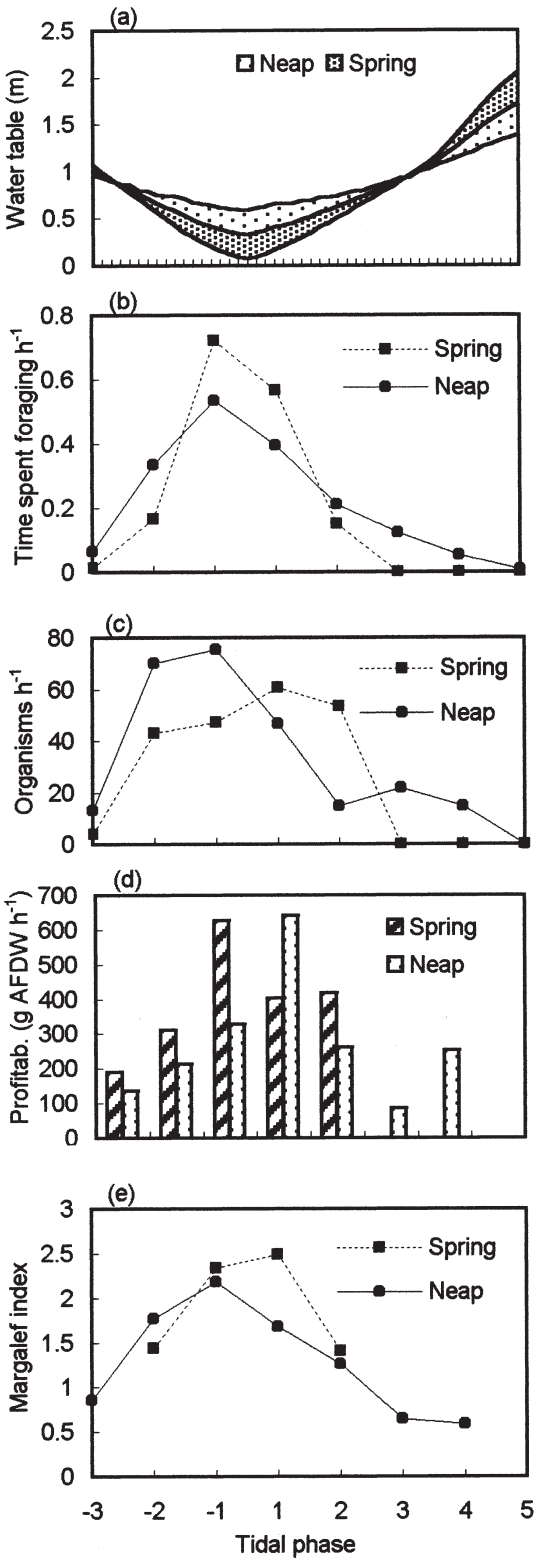


Figure 1 Changes of foraging behaviour during low water, from -3 hours before to +5 hours after low water; (*a*) neap and spring tidal ranges during low water; (*b*) average time spent foraging per hour during foraging trip; (*c*) number of animals collected per foraging hour; (*d*) mean profitability in g AFDW per foraging hour; and (*e*) Margalef index of diversity of the catches obtained per foraging hour for low tides.

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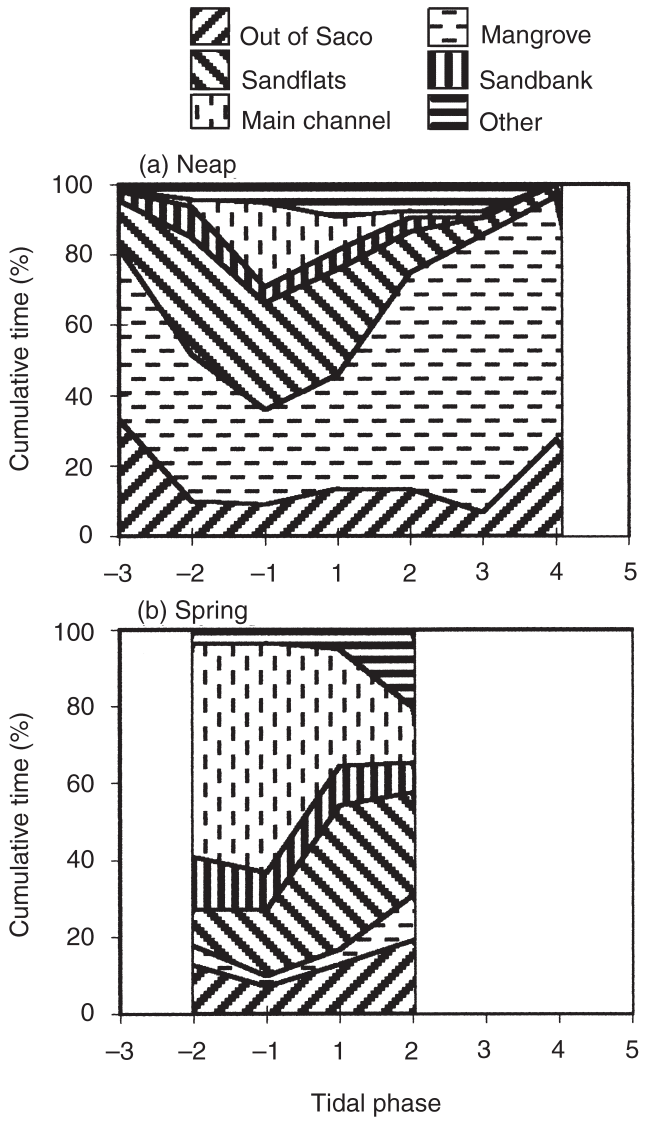


Figure 2 Cumulative percentage of time spent by women per substrate (out of Saco [the area passed when travelling between house and the Saco], the mangrove fringe, the sandflats, the sandbanks, the main tidal channel and unidentified other substrates) for (*a*) neap and (*b*) spring tides.

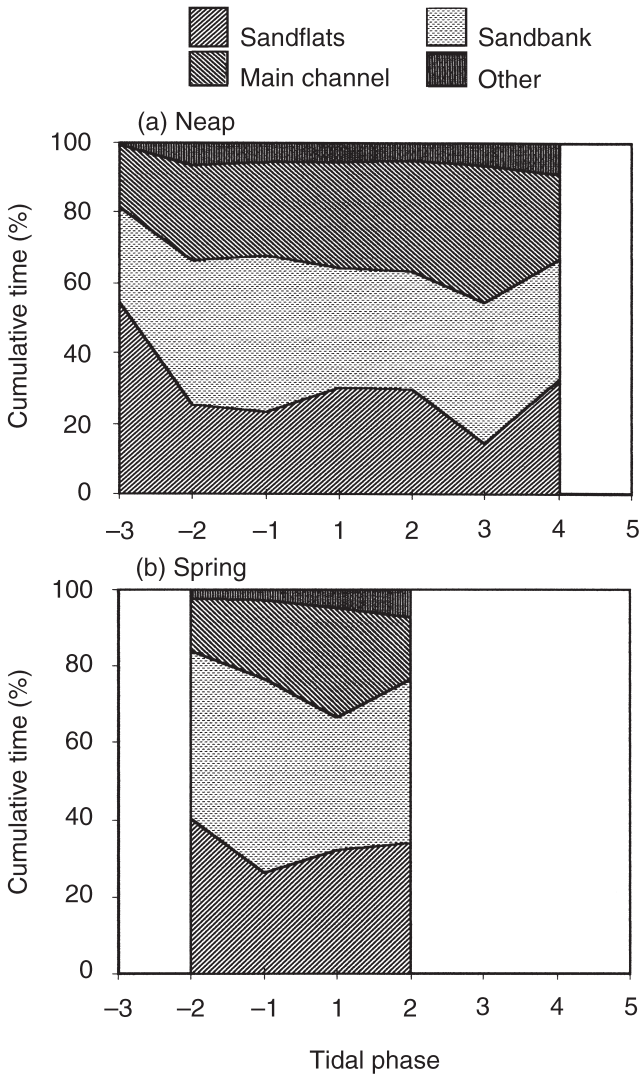


Figure 3 Cumulative percentage of time spent by women in activity (walking [no searching], searching, handling prey items, and other activities [such as talking]) for (*a*) neap and (*b*) spring tides.

Women were not distributed over the substrates at random. A positive relation existed between prey availability per substrate type (g AFDW in 10 × 10 m squares searched by women in summer and winter) and the mean density of searching people (Fig. 6; $F_{1,8} = 8.229$, $p < 0.02$, adjusted-$R^2 = 0.45$).

The total foraging time of women increased with the profitability of the patch, the latter expressed as the intake per foraging time (handling and search time combined; Fig. 7). The greatest outlier, where a relatively large amount of time was spent with a relatively low intake, was the mangrove area (indicated by *M* in Fig. 7). Profitability increased with total foraging time ($F_8 = 7.955$, $p < 0.03$, $R^2 = 0.47$), when this point was excluded from the regression.

Catch composition

The mean catch, measured in AFDW, was largest in July–August (Fig. 4*b*), when more swimming crabs (*Portunus pelagicus*) and bivalves (the only catches of the oyster *Saccostrea cucullata*) were taken. Throughout the year crabs were the most important prey species, especially *P. pelagicus*, which comprised 32.4% of the abundance in the women's catches during spring tide, and 62.3% of the weight (Table 1). The only seasonal difference was the increased contribution of bivalves from July to October. People regarded this colder period as a better season for bivalve exploitation and this is supported by an increased catch of the oyster *S. cucullata*. Bivalves contain more flesh at this time.

Women switched between different prey species. Prey switching occurred during the low water period, as the higher-lying mangrove areas were being exposed first and

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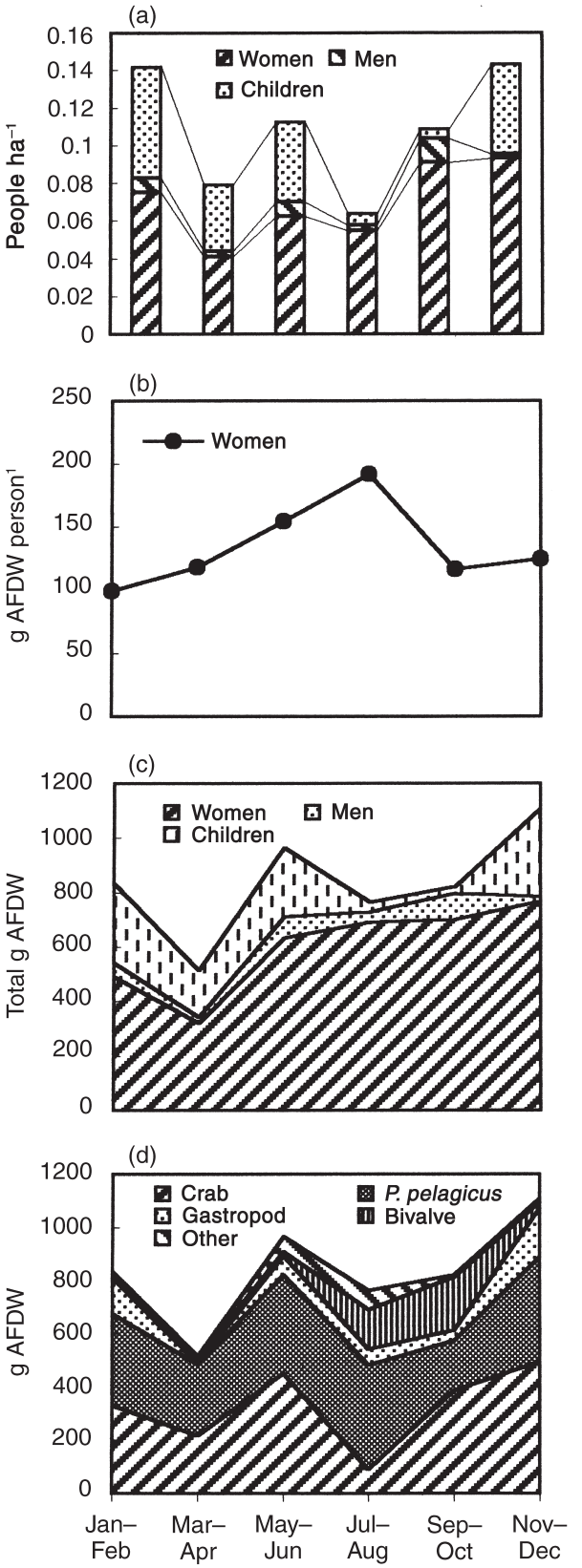


Figure 4 The bimonthly fluctuations of (*a*) the people density on the mudflats of the Saco at Inhaca; (*b*) the mean catch per woman; (*c*) the cumulative total g AFDW collected by children, women and men; and (*d*) the bimonthly total offtake per taxonomic group.

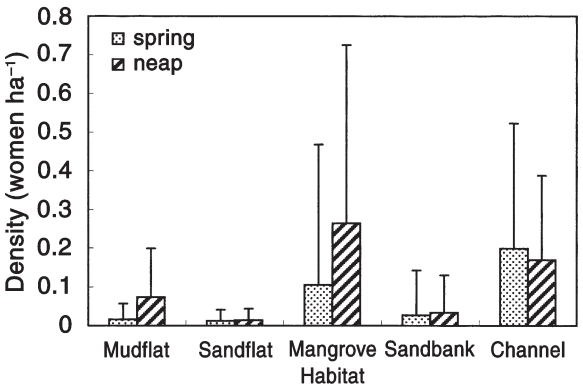


Figure 5 Mean density (±1 SD) of women over the substrates in the Saco for neap and spring tides, as calculated from the monthly counts at low water ($n = 31$ for neap tides and $n = 26$ for spring tides).

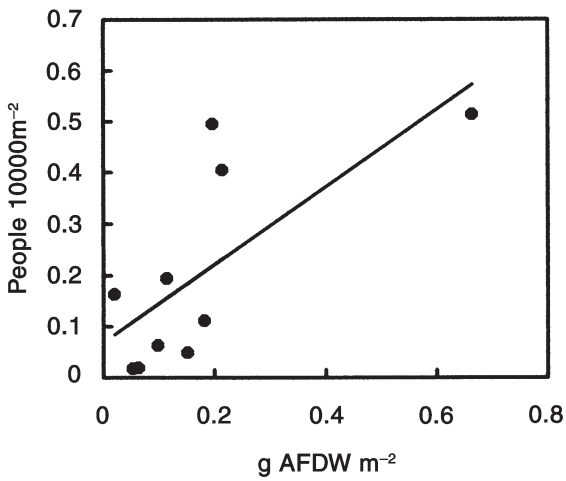


Figure 6 The relation between the total AFDW of benthic organisms and the density of people searching in the same substrates (from de Boer 2001). Line illustrates least-squares regression.

people collected *S. serrata* (Fig. 8). Later, when the main channel was exposed at low water, women switched to *P. pelagicus* in the channel, which comprised 41% of the catch in weight. At the end of low water, women switched again to *S. serrata* and other species.

The total AFDW harvest from the area per taxonomic group could be calculated on the basis of the people densities, their mean catch, the species composition of the catch, correcting for adult-child differences (Fig. 4*c*). The catch of *P. pelagicus* and other crabs was by far the most important, and comprised 60–98% of the total catch in weight (Fig. 4*d*).

Catches varied from 40–17 000 g FW during the study period. Catches were easily carried since 96% of them were < 3 kg. The mean catch of women (133.6±158.4 g AFDW) was significantly larger than that of children (85.9±62.2 g

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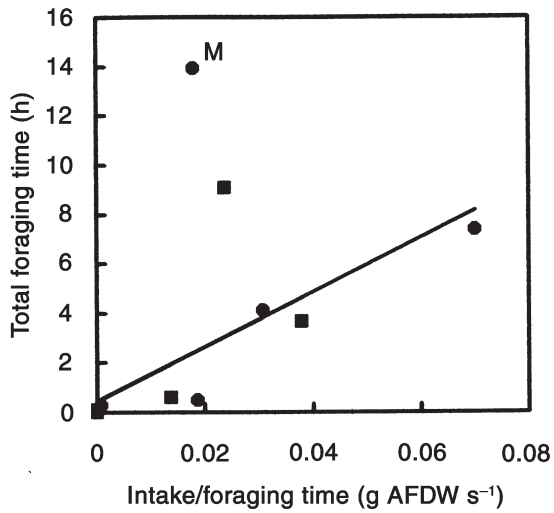


Figure 7 Plot of foraging time per substrate against profitability of the substrate (neap tides = circles; spring tides = squares). M = the mangrove during neap tides. Line illustrates least-squares regression.

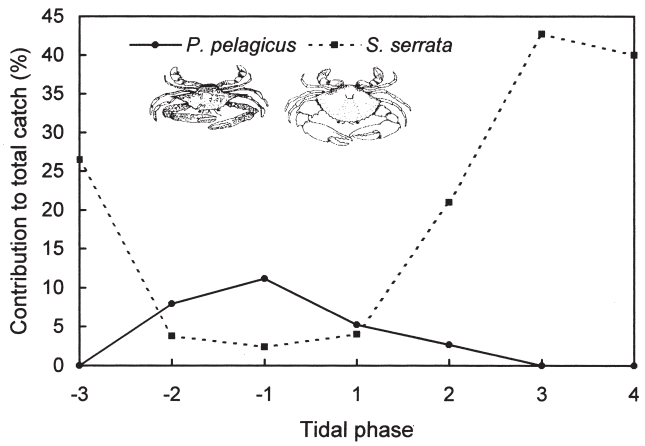


Figure 8 The fluctuating prey choice of women collecting the two crabs *P. pelagicus* and *S. serrata* in relation to the tidal phase.

AFDW; $F_{1,424} = 27.492$, $p < 0.0001$). The total number of organisms collected was equal for women and children, totalling 111.5±126.3 organisms catch^{-1}. The number of species comprising the catch was slightly lower for women (3.8±2.3 species) compared to children (4.3±2.5 species), but this was not significant ($F_{1,424} = 3.428$, $p = 0.06$). The mean weight of organisms collected was significantly larger for women (4.3±4.1 g AFDW) than for children (3.2±3.0 g AFDW; $F_{1,424} = 7.250$, $p < 0.01$). Apparently women were more efficient, because they specialized in more profitable species, and their total catch was heavier.

Neap or spring tide significantly altered the catch for women but not so for children. The mean animal weight was larger for women during spring tides than neap tides (5.4±4.1 g AFDW and 3.0±3.8 g AFDW, respectively; $F_{1,232} = 33.049$, $p < 0.00001$), but the number of animals collected decreased, from 123 during neaps to 42 during spring tides ($F_{1,232} = 28.206$, $p < 0.00001$). The consequence of this larger weight but smaller number of animals was that the mean weight of the catch was equal between neap and spring tide (133.6±158.4 g AFDW).

Diet breadth changed over tides, it was smaller at spring tides, and *B'a* and *FT* were significantly reduced, from 0.046 to 0.012 for *B'a*, and 0.22 to 0.12 for the *FT* ($F_{1,232} > 28$, $p < 0.00001$ for both comparisons). Despite the low number of animals collected at spring tide, the mean number of species comprising the catch was significantly larger at spring tides (4.4 as against 3.2 for neap tide; $F_{1,232} = 18.888$, $p < 0.0001$). The Margalef, Shannon and Hill's indices were all larger at spring tide ($F_{1,232} > 11.470$, $p < 0.001$). This higher species richness was not accompanied by increased abundance of all species in the catch. During spring tide women concentrated on *P. pelagicus* and the mean catch per species was highly skewed in favour of the dominant species in the catch (Table 1). Only three species contributed more then 5% to the total AFDW, whereas this was six during neap tide. The skewness of the percentages of the catch in AFDW (Table 1) was 6.6 for spring tides and only 2.4 for neap tides; kurtosis was also much higher for spring catches (45.4 against 5.1).

The species composition of women's catches during spring tide was significantly different from the one during neap tide (ANOSIM, $R = 0.256$, $p < 0.01$). Spring catches were characterized by the presence of *P. pelagicus*, contributing 32.4% of total animals in the catch and 62.3% in terms of total weight. In neap catches *S. serrata*, and *S. cucullatta* were the heaviest species, whilst the crabs *Dotilla fenestrata*, *Macrophthalmus grandieri*, *Uca* spp., and the gastropod *Terebralia palustris* were more important in terms of number (Table 1). Half (50%) of the total dissimilarity between the catches of the two tides was attributed to 11 different species, with *P. pelagicus*, *T. palustris* and the fiddler crab *Uca lactea* explaining the first 18%.

Catches were classified in different size categories. Large catches had a significantly lower richness, lower evenness and higher dominance than medium and small catches ($r_s > 0.22$, $n = 234$, $p < 0.0001$ for all comparisons). A significant negative relation existed between the total weight of the women's catches and the diet breadth. Both Hulbert's diet breadth *B'a* and Smith's measure of diet breadth *FT* decreased with increasing catch weight ($n = 234$, r_s respectively -0.201 and -0.239, with $p < 0.005$ and $p < 0.001$). This means that women with large catches were more selective than those with smaller catches. There were significant differences between the species composition of large and small catches (ANOSIM $R = 0.367$, $p < 0.01$). Large catches were characterized by a relatively larger weight of *S. cuccullata*, *T. palustris*, *P. pelagicus* and *Polynices tumidus*. Small catches had relatively more *Uca vocans* and *M. grandidieri*, but none of the species explained more than 6% of the dissimilarity between the two categories.

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Table 1 The composition of the catch of women and children searching for intertidal shellfish in the Saco at Inhaca. Percentages are given for the total number of animals for every species in the catch (N-animal), and total AFDW of animals (AFDW), together with the subtotal per taxonomic group (– = not collected).

Species	*Women spring*		*Women neap*		*Children spring and neap*	
	N-animal %	*AFDW %*	*N-animal %*	*AFDW %*	*N-animal %*	*AFDW %*
Crab						
Portunus pelagicus	32.38	62.34	2.77	13.13	11.67	40.94
Portunus sanguinolentus	0.39	0.39	0.18	0.37	0.48	0.79
Thalamita crenata	4.11	4.40	1.36	3.08	2.78	6.52
Thalamita danae	0.02	0.00	0.02	0.01	0.06	0.12
Calappa hepatica	5.07	7.14	2.28	3.29	3.02	10.11
Dotilla fenestrata	9.66	0.52	19.54	4.83	38.36	3.97
Scylla serrata	6.58	5.84	4.70	20.18	2.97	7.63
Matuta lunaris	0.41	0.51	0.02	0.02	0.38	1.25
Eurycarcinus natalensis	0.85	0.40	0.99	0.77	0.29	0.98
Xanthidae	0.11	0.05	0.11	0.09	0.27	0.33
Pilumnus verspertilio	0.37	0.10	0.02	0.21	0.06	0.12
Macrophthalmus grandidieri	10.88	1.63	20.74	5.83	14.68	4.88
Uca vocans	3.29	0.44	3.21	1.52	1.60	0.88
Uca gaimardi	–	–	0.28	0.07	0.04	0.01
Uca inversa inversa	1.12	0.23	0.02	0.01	0.34	0.26
Uca lactea annulipes	5.17	0.73	11.64	6.65	7.28	3.99
Ocypode sp.	0.02	0.02	0.90	1.41	0.07	0.21
Ocypode ceratophthalmus	–	–	–	–	0.05	0.10
Ocypode kuhli	–	–	–	–	0.23	0.43
Crab-unidentified	0.25	0.08	–	–	0.02	0.04
Total crab	80.67	84.81	68.77	61.47	84.64	83.53
Shrimp						
Penaeus semisulcatus	–	–	–	–	0.00	0.01
Penaeus canaliculatus	0.02	0.00	0.02	0.01	0.01	0.00
Penaeus japonicus	–	–	–	–	0.00	0.00
Total shrimp	0.02	0.00	0.02	0.01	0.03	0.03
Bivalve	–	–	–	–	–	–
Anadara antiquata	0.50	1.25	0.09	0.61	0.19	1.24
Gafrarium divaricatum	0.05	0.11	0.03	0.35	–	–
Modiolus philippinarum	0.30	0.49	0.02	0.14	0.07	0.18
Trachycardium flavum	0.48	1.20	0.02	0.03	0.09	0.36
Chlamys sp.	0.04	0.04	–	–	–	–
Pinctada nigra	0.23	0.39	–	–	0.09	0.17
Mactra sp.	–	–	–	–	0.00	0.01
Gafrarium pectinatum	0.11	0.14	–	–	0.02	0.07
Callista florida	–	–	–	–	0.00	0.04
Venus verrucosa	–	–	–	–	0.00	0.00
Saccostrea cucullata	–	–	7.87	20.52	0.92	2.12
Bivalve unidentified	–	–	0.13	0.46	0.08	0.25
Total bivalve	1.71	3.61	8.15	22.11	1.47	4.44
Gastropods						
Conus betulinus	0.52	1.24	0.03	0.26	0.17	0.82
Conus sp.	0.04	0.03	–	–	–	–
Volema pyrum	1.35	1.03	0.48	1.42	1.78	3.05
Terebralia palustris	–	–	8.97	8.65	1.07	0.83
Strombus gibberulus	0.23	0.22	0.03	0.16	0.05	0.17
Cypraea lamarcki	0.11	0.04	–	–	0.01	0.05
Murex brevispina	0.04	0.03	–	–	–	–
Rapana rapiformis	0.05	0.05	–	–	–	–
Polynices tumidus	12.93	1.97	12.26	4.77	9.93	4.13
Polynices didyma	0.02	0.02	–	–	–	–
Natica gualteriana	–	–	–	–	0.01	0.00
Total gastropods	15.27	4.62	21.77	15.26	13.03	9.05

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Table 1 continued.

Species	*Women spring*		*Women neap*		*Children spring and neap*	
	N-animal %	*AFDW %*	*N-animal %*	*AFDW %*	*N-animal %*	*AFDW %*
Fish						
Trachinotus blochii	0.04	0.29	–	–	–	–
Platycephalus indicus	0.27	1.22	–	–	0.02	0.22
Lutjanus sp.	–	–	–	–	0.00	0.00
Mugil cephalus	0.05	0.17	–	–	0.00	0.01
Torpedo sinuspersici	0.02	0.83	–	–	–	–
Lactoria diaphana	0.02	0.06	–	–	–	–
Terapon jarbua	0.04	0.03	–	–	–	–
Solea bleekeri	1.58	2.54	0.06	0.23	0.56	1.86
Sillago sihama	0.04	0.04	–	–	0.04	0.06
Epinephelus aeruleopunctatus	0.02	0.34	–	–	–	–
Epinephelus andersoni	0.04	0.17	–	–	–	–
Epinephelus sp.	0.02	0.36	–	–	–	–
Total fish	2.12	6.05	0.06	0.23	0.63	2.16
Other						
Holothuria scabra	–	–	0.00	0.39	–	–
Opisthobranchia-unidentified	–	–	–	–	0.00	0.00
Philine aperta	–	–	–	–	0.00	0.02
Loligo indica	0.04	0.26	–	–	–	–
Octopus granulatus	0.07	0.34	–	–	–	–
Not identified	0.11	0.30	1.22	0.54	0.18	0.77
Total other	0.21	0.90	1.23	0.93	0.20	0.79
Mean catch weight, g AFDW (±SD)		133±94		136±213		89±63
Mean number of animals catch^{-1} (±SD)	42±64		123±173		71±134	
Total sample size (catches)	131	131	103	103	192	192

Prey profitability

Larger species such as *Scylla serrata*, *Thalamita crenata,* and fish had larger weights, but were also more difficult to catch as the handling time increased (Table 2). The two crabs *Calappa hepatica* and *P. pelagicus* had the highest profitability and comprised 19% of those catches.

The intake was measured as the total AFDW over the total invested search and handling time combined. The mean intake was 0.024 g s^{-1} for neap tides and 0.028 g s^{-1} for spring tides. According to the optimal diet breadth model, this amount is the threshold value, and species with profitabilities below this value should be rejected. Table 2 shows that species numbered 14–20 had profitabilities lower than this threshold value, but they contributed only 1% to the diet in AFDW terms.

Currency

Women valued species on six categories, such as taste and monetary value. The relative value rank of 15 different species (comprising 91% of the total number and 83% of the weight of the catches) was significantly different for every value category ($\chi^2 > 50$, $df = 15$, $p < 0.001$ for all categories). The ratio of the observed/expected ranks and the 95% confidence limits showed that women valued species differently (Fig. 9). The crabs *S. serrata* and *P. pelagicus* were valued highest for taste, monetary value and their importance in the household. Bivalves also scored relatively highly for these three categories. Gastropod species were among the lowest valued species for these categories, but they were valued highest with respect to ease of collection and when preparation time was considered. Even within taxonomic groups, large differences occurred, such as the low relative value rank for taste, monetary value and household importance of the crabs *Uca* spp., *M. grandidieri* and *D. fenestrata*. These three crab species apparently had other benefits, such as their relatively high abundance. The species with the highest total rank were the crabs *S. serrata*, *P. pelagicus*, the gastropod *P. tumidus* (good taste, easy to collect and prepare) and the two bivalves *Anadara antiquata* and *Trachycardium flavum*.

C. hepatica, *P. tumidus*, *P. pelagicus*, and *S. cuccullata* had the highest rank preference ratios, and were collected much more than could be expected from their relative abundance. The rank preference ratio was significantly correlated with taste, importance of the species within their household, total relative rank values attributed, and total fresh weight per animal (Table 3). Other variables such as the monetary value and relative abundance also seemed important. Conspicuousness was calculated by attributing a different value to each species (1 = hidden in mud, 2 = swimming, 3 = surface dwelling). During neap tide, women were less influenced by the secondary characteristics of the species as

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Table 2 The profitability of species collected during the foraging trips. Species are ranked according to their different profitability (E_i/H_i).

Order	*Species*	*Sample size (n)*	*g AFDW (E_i)*	*H_i (s)*	*E_i/H_i (g s^{-1})*
1	*Calappa hepatica*	146	1.09686	3.3	0.33238
2	*Portunus pelagicus*	383	1.99233	7.3	0.27292
3	Fish (unidentified)	6	2.77231	14.0	0.19802
4	*Trachycardium flavum*	2	1.18210	6.5	0.18186
5	*Conus betulinus*	11	0.80238	4.5	0.17831
6	*Volema pyrum*	506	0.23985	1.6	0.14991
7	*Strombus gibberulus*	10	0.71704	5.0	0.14341
8	*Macrophthalmus grandidieri*	19	0.33169	2.4	0.13820
9	*Polynices tumidus*	1352	0.21602	1.6	0.13501
10	*Uca vocans*	973	0.78783	8.6	0.09161
11	*Scylla serrata*	210	4.11412	48.2	0.08536
12	*Thalamita crenata*	252	1.55288	27.4	0.05667
13	*Uca* sp.	650	0.56696	10.8	0.05250
14	*Uca lactea annulipes*	7	0.10438	5.4	0.01933
15	*Eurycarcinus natalensis*	185	0.19510	16.8	0.01161
16	*Anadara antiquata*	7	0.00090	4.7	0.00019
17	*Modiolus philippinarum*	2	0.00132	9.5	0.00014
18	*Tellina* sp.	1	0.00035	3.0	0.00012
19	*Saccostrea cuccullata*	2	0.00039	8.5	0.00005
20	*Solen cylindraceus*	1	0.00036	22.0	0.00002

no significant relationship existed between the preference ratio of neap catches and the variables in Table 3.

DISCUSSION

Timing and substrate choice

The results clearly indicated that the impact of human exploitation is not evenly distributed over the different substrates and over the low water period. The impact on the mangrove fauna could be considerably larger due to their exposure at neap tides, and their availability at low water when other substrates are still flooded. The lowest substrates, the tidal channels, are also preferred, due to the presence of swimming crabs. The latter substrate is probably less vulnerable due to their protection during neap tide when these areas are flooded and due to the possibility of colonization of prey species from deeper waters.

The density of people was not larger at spring tide when prey availability was expected to be larger. Two explanations could be given for this. First, searching for invertebrates in intertidal areas is regarded as a poor man's choice (Kyle *et al.* 1997*a*, *b*). Islanders are normally proud of not having to search for tiny shells or crabs. Intertidal harvesting in Natal decreased because of a fall in the level of unemployment (Kyle *et al.* 1997*a*, *b*). If no alternative exists, people will always be found in the intertidal area regardless of the fluctuations in prey abundance. This absence of other productive activities also explains the equal density of women over the year. The second explanation is that the opportunity costs are higher at spring tide, as line fishing in the tidal creeks is regarded as more lucrative during spring tide when fish concentrate in the few channels that still hold water. This could also explain the larger number of fishes in the spring-tide catches (Table 1).

The timing of the women clearly corresponded to the period with lowest water, and the highest prey abundance and intake rate. During spring tides women visited the area precisely during the period of lowest water, whilst during neap tide the trips started earlier or ended later. This change in timing is accompanied by a change in substrate choice. During spring tide women concentrated in the main channel where they collected *P. pelagicus*. During neap tide, when the favoured channel was inundated, the women concentrated in the mangroves where they collected *S. serrata*, *Eurycarcinus natalensis*, *Uca* spp., or *T. palustris*. Mangrove crabs must be dug out with an axe, thus explaining the high handling time per species (Table 2), the lower profitability, and the larger handling time during foraging during neaps (Fig. 3).

We assumed that prey availability would increase during spring tide. However, the water table increased more slowly during neap tide and did not attain the high water levels recorded at spring tide. Hence, the upper reaches of the mangrove forest were not flooded at neap tides and total inundation time of the mangrove forest was shortened. According to the women the water table is lower during neap tide in the mangroves, improving the accessibility of the crabs and facilitating digging. So the assumption that prey availability increased during spring tide was not totally correct. During spring tide, a larger area was exposed and the main channel was accessible offering the possibility to search for *P. pelagicus,* but foraging conditions in the mangrove area were impaired during spring tides. So in the mangroves only, neap tides offered slightly better foraging conditions due to the lowering of the water table.

In terms of substrate choice, the distribution of the people followed an ideal free distribution; women density and substrate profitability were positively correlated. The profitability of the different substrates was unequal. So why did

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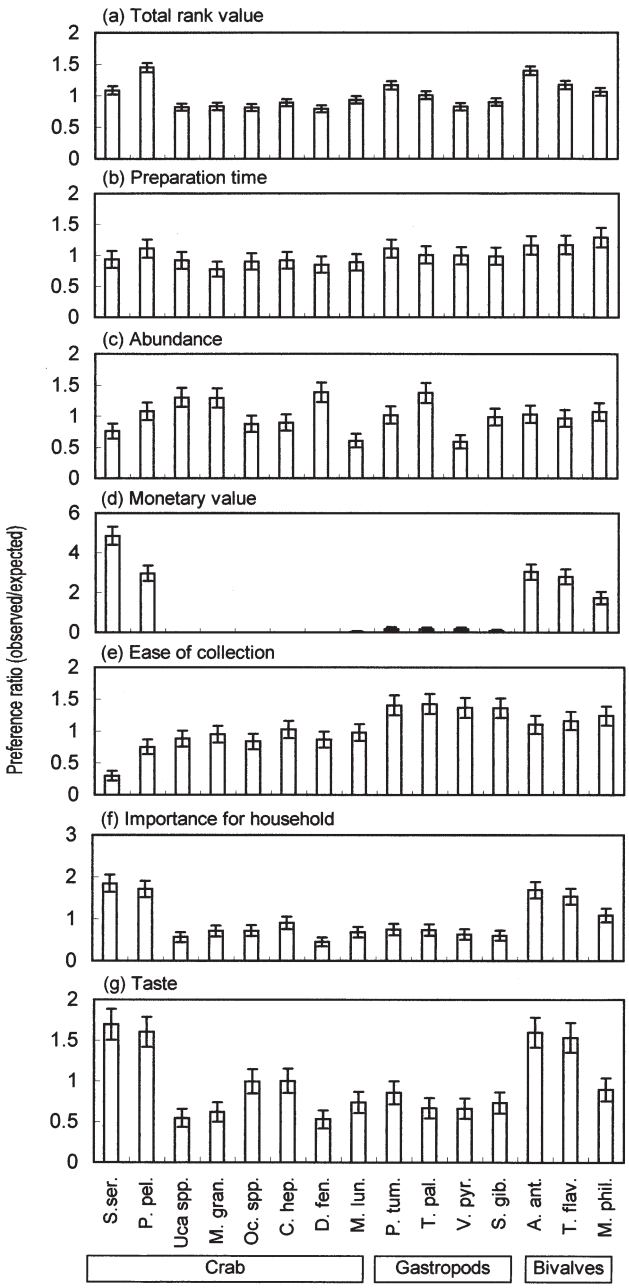


Figure 9 The mean relative value rank attributed to different species by women in a contingency table. Illustrated are the preference ratios, the observed/expected ratios (± 95% confidence limits) based on the average value per species for that specific category. A ratio of one indicates no preference, more than one indicates an increased preference in relation to the mean, less than one a significant negative preference. S. ser. = *Scylla serrata*; P. pel. = *Portunus pelagicus*; M. gran. = *Macrophthalmus grandidieri*; Oc. spp. = *Ocypode* spp.; C. hep. = *Calappa hepatica*; D. fen. = *Dotilla fenestrata*; M. lun. = *Matuta lunaris*; P. tum. = *Polynices tumidus*; T. pal. = *Terebralia palustris*; V. pyr. = *Volema pyrum*; S. glib. = *Strombus gibberulus*; A. ant. = *Anadara antiquata*; T. flav. = *Trachycardium flavum*; M. phil. = *Modiolus philippinarum*.

Table 3 Spearman rank correlation coefficient (r_s), and significance (p) of different variables in relation to the rank preference ratio of species. Profitability was taken from Table 2.

Variable	*n*	r_s	p
Taste	15	-3.41	0.00
Preparation time	15	-1.51	0.15
Relative abundance	15	1.94	0.07
Ease of collection	15	-0.34	0.71
Monetary value	15	-1.91	0.08
Household importance	15	-2.78	0.02
Total relative value ranks	15	-3.36	0.01
Profitability (E_i/H_i)	15	-0.50	0.63
Conspicuousness	44	-1.56	0.12
FW/AFDW ratio	44	-0.02	0.98
g AFDW animal^{-1}	24	0.49	0.63
g FW animal^{-1}	24	-2.05	0.05

women not only concentrate in the most profitable patch? Other constraints were probably important. Climatic conditions act as constraints on searching efficiency. Strong, mostly southerly winds caused waves in the channel on certain days. This decreased detection, and women had to leave for other, less favourable areas, when those conditions occurred. Even though the tidal channel was the most profitable substrate, children did not forage there in large numbers (57% of all women were counted in the channel against 37% of the children), because the water table in the channel and the skills needed to catch the fast-moving crabs probably reduced efficiency for children.

Prey choice and currency

Crabs were the main prey species over the whole study period, especially *P. pelagicus* collected in the tidal channels. Prey preference changed during the season and during the low water period. Prey switching (Winterhalder & Lu 1997) was observed when women changed their diet in winter and caught a large number of *S. cucullatta*. Prey switching was also observed during the low water period when the increase of *P. pelagicus* was negatively correlated with the abundance of *S. serrata* in the catch (Fig. 8). The latter change in species was related to the different substrate availability caused by exposure patterns. When the tidal channel became exposed they left the mangroves and concentrated on swimming crabs.

Women were better foragers than children, as their catches were heavier and contained more profitable species. This could be due to the greater experience of women, or to a lower prey encounter rate for children (Bird & Bird 2000).

The mean catch of women was 134 g AFDW, corresponding to 2827 kJ (1g AFDW = 21.1 kJ; Zwarts & Blomert 1990), which is one-third of the daily energy requirements for an adult (den Hartog *et al.* 1995). The fact that the catches were not considerably heavier at spring tide was unexpected, as we predicted that a larger exposed area during spring tide would increase prey availability and thereby catch weight. Searching was more costly at neap tide; as digging with axes

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took 5% of the total time. Net energy gain (energy collected/energy expenditure) would therefore have to been more profitable during spring tide. The spring and neap catches of women were similar in terms of weight but different in terms of species composition. Fewer animals were collected, mean animal weight was heavier, and diet breadth was reduced at spring tide. Hence, women were more selective, but this selectivity did not result in a larger mean catch weight. Perhaps other factors were more important, and it was not the weight of the catch that was maximized, but other catch variables such as taste, monetary value, or certain nutrients? One of the possible hypotheses is that protein intake is being maximized instead of energy intake (e.g. Byrne *et al.* 1993). The currency analysis showed that taste, household importance, FW per animal, total attributed values ranks, and monetary values explained the preferences for species. We checked whether spring catches would have a higher relative value ranking than the neap catches by multiplying each g AFDW with its total value rank (after standardization) for the five significant variables. The mean women's spring catch had 3754 value ranks, whilst the neap catch scored only 2264 value ranks. This larger total value rank at spring tide indicates that apparently other variables were being maximized, and organic weight was only one of the variables influencing prey choice. The mean catch of women comprised almost twice the daily adult protein requirements (using conversion factors from Zwarts & Blomert 1990; den Hartog *et al.* 1995), hence much more than the energetic value of the catch. More research is certainly needed to check whether perhaps certain nutrients were being maximized, such as calcium or proteins (Belovsky 1987; Hill 1988; Wynter 1990), or whether processing costs (Hill *et al.* 1987) are important in prey choice.

The optimal diet breadth theory was successful in explaining prey choice. The mean intake rate of 0.024 and 0.028 g s^{-1} for neap and spring tides were the threshold values that determined whether species were included or excluded from the diet. The rare events of species with low profitability being included could be linked with sampling behaviour (Stephens & Krebs 1986). The collection of unfavourable species (oysters, limpets and chitons) in Natal (Kyle *et al.* 1997*b*) was mainly reported during periods when women were waiting for the tide to uncover more favourable species or when the harvest of these species was low. Therefore, large catches of favourable prey species never occurred alongside large catches of less preferred species. Our dissimilarity analysis supports this. Small and large catches were significantly different in species composition. More profitable species (e.g. *P. pelagicus*) were characteristic of heavy catches, whilst less profitable species (e.g. *Uca* spp.) were more typical of light catches.

Species diversity

The species diversity of the catches changed with significant differences between children and women, neap and spring tides, between substrates and over tidal phases. Women were more effective foragers and only picked up larger animals. The diet breadth of women was reduced at spring tides, when they concentrated on only the most profitable species and the mean contribution of each species was thus more skewed. Selectivity of women was therefore greater during spring tides although they took many more species in the diet, albeit all with very low abundance. This difference in diet breadth was in agreement with our prediction.

We also expected smaller species diversity in the catch during spring tide, and on the most profitable substrates, such as documented in other studies (Winterhalder 1981; Hames & Vickers 1982; O'Connell & Hawkes 1984). The contrary was found, as spring catches were more diverse, catches in the channel were more diverse and diversity was highest with the greatest exposure. Three possible explanations for the absence of this pattern in our data can be given. First, the larger diversity on the richest substrates could be related to the fact that women were central place foragers (Bettinger 1991), optimizing the species composition of their foraging trip and not making different decisions in different substrates. They knew exactly what to expect. Hence the largest prey choice was made at the moment the species were expected to appear, on the richest substrate and the lowest water period. Choosing a more diverse diet in poor patches would decrease the time available for searching in more favourable patches, and therefore decrease overall expected energy intake. Women optimized overall prey choice of all substrates combined.

Yet a second explanation might be that the exploitation method was different between tides; only during neap tides did they use the axe, and handling time increased. The optimal foraging theory predicts a more specialized diet for a forager with larger handling costs. Hence, during spring tide two important changes occurred; the prey abundance increased (which should decrease the diet breadth), and the handling time decreased (which should increase the diet breadth). The latter factor could explain the higher diversity of spring catches.

A third explanation could be that neap and spring catches cannot be compared directly by one diet breadth model, because in the model they should be regarded as different situations. Species collected during spring tide could never be included in neap catches because they were not available. Spring catches were therefore richer than neap catches.

Exploitation strategy

The exploitation of the resources on the tidal mudflats by women and children was a multiple-stage decision-making process, several decisions being made with respect to the moment of searching, the substrate that is searched, collection method, and the prey species targeted (Fig. 10). Several different options could be chosen, with two different strategies being favoured, namely searching at neap tide for typical mangrove species, or searching at spring tide for P.

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pelagicus in the channel. Both strategies yielded the same catch in weight, but the spring tide was more favourable, as the cumulative relative value ranks are maximized.

Various assumptions of the OFT were violated in this case study (see Stephens & Krebs 1986). For instance, searching and handling were not mutually exclusive. Also, women did not have complete information regarding prey distribution. However, the OFT was successful in the interpretation of the substrate and prey choice of the women, and offered a sound scientific basis for the interpretation of natural resource exploitation. The diet breadth of the women at Inhaca was smaller during spring tides when prey availability increased and when the women specialized in *P. pelagicus*, such as was expected by the optimal diet breadth model. Women valued predatory crabs relatively high, which explained the preference for these animals, the catch composition, and the habitat choice and timing. The impact of this exploitation strategy (the removal of top-predators) on the intertidal community structure may have been larger than exploitation aimed at detritus-feeding gastropods. Human exploitation is a form of predation and can alter the intertidal community structure. However, little is known about how predation alters marine communities (Dayton 1984). Predation may change the size, biomass or abundance of a species, alter species richness or the energy flow of the community. Even relatively small catches, or catches of keystone species can modify the system (Castilla *et al*. 1994; Lasiak & Field 1995; Dye *et al*. 1997; Sharpe & Keough 1998). More research is necessary to evaluate the human impact in detail. However, the study showed that the OFT offers an excellent theoretic framework for the interpretation of human exploitation, as the reasoning behind the exploitation decisions becomes clear. The currency analyses showed that the relative value of each species explained prey preference, and thereby catch composition. The impact of new markets, improved conservation methods (freezers), or transport facilities would change the relative value of a species. This would first increase the relative value of mangrove, swimming crabs and some of the gastropods that could be sold. Due to the larger availability of the mangrove area, *S. serrata* will probably be the first species affected. This knowledge could be valuable in projects aimed at increasing the level of participation of local people in the co-management of resources. It illustrates the species with the highest relative value, species for which incentives for conservation initiatives will be highest. Moreover, the results indicate that certain substrate types and certain prey species are more preferred than others, and that these exploitation differences can be understood from differences in the costs-benefit equation.

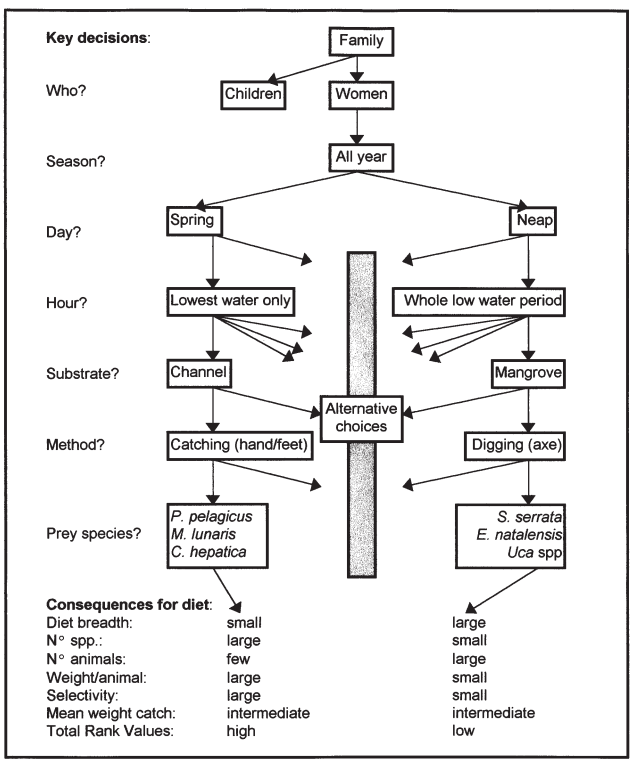


Figure 10 Diagram illustrating the different choices women have to make in order to optimize their catch when searching for invertebrates on the intertidal area of Inhaca.

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