Comparing recent and abandoned shell middens to detect the impact of human exploitation on the intertidal ecosystem

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Comparing recent and abandoned shell middens to detect the impact of human exploitation on the intertidal ecosystem

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Abstract

Abandoned and recent shell middens were compared from Inhaca island, Mozambique, to investigate the impact of human exploitation. The growing human population was expected to increase the exploitation pressure, decrease the mean shell size, and increase the species diversity. Moreover, exploitation-vulnerable species were expected to disappear from recent middens. 29252 shells were collected from 6 recent and 8 abandoned middens, comprising 78 species, the majority bivalves. *Pinctada nigra* was the most abundant. The mean shell size was significantly smaller in recent middens, and the conspicuous, surface-dwelling gastropod *Terebralia palustris* showed the largest size reduction. Size reduction was related with the life history of the species. Older, abandoned middens had a larger species richness, refuting the intermediate disturbance hypothesis. The species composition of recent and abandoned middens was relatively similar, which was probably caused by low human exploitation pressure and the substrate characteristics. The disappearance of the mussel *Perna perna* was thought to be related to overexploitation.

Introduction

Man has exploited intertidal resources in Africa for at least the last 100,000 years (Barradas, 1967; Parkington, 1976; Voigt, 1975; Volman, 1978; Morais, 1988; Thackeray, 1988; Siegfried et al., 1994; Griffiths & Branch, 1997). Shellfish gathering still contributes considerably to the present diet, especially in terms of protein (Bigalke, 1973; Bailey, 1978; Hockey et al., 1988; Lasiak, 1993; Siegfried et al., 1994; Kyle et al., 1997ab). The impact of people on the intertidal resources, and human diet choice can be studied by analysing shell remains in middens (Swadling, 1976; Bailey, 1978; Mellars, 1978; Anderson, 1981; Deith, 1986; Hockey & Bosman, 1986; Lasiak, 1991a).

The pressure on the intertidal resources has increased in Mozambique due to a rapidly growing human population (Lopes, 1985, 1991) and a concentration of people in coastal zones, partly in a reaction to the civil war (1978–1992). People living on Inhaca Island collect crabs, bivalves, and gastropods from intertidal areas during low tide (de Boer & Longamane, 1996). A higher exploitation level can lead to changes in the intertidal community, such as changes in organism size, and species composition (Siegfried, 1994). To determine the impact of human exploitation on the intertidal community, the contents of contemporary middens were compared with those of older, abandoned middens.

People prefer larger shells (de Boer & Longamane, 1996). The consequence of this selectivity can be a reduction of mean animal size (Branch, 1975; Blake, 1979; McLusky et al., 1983; Siegfried et al., 1985; Hockey & Bosman, 1986; Keough et al., 1993; Robertson, 1996; Dye et al., 1997; Fernandez & Castilla, 1997; Griffiths & Branch, 1997). It is therefore expected that the mean shell size is smaller in

recent middens, especially in those species which are the most conspicuous at low tide.

Exploitation of certain species could change the abundance and, likewise, the availability of species (Siegfried et al., 1985; Hockey & Bosman, 1986; Addessi, 1994; Branch & Moreno, 1994), and possibly change the community structure as a whole (Moreno et al., 1984; Durán & Castilla, 1989; Menge & Farrell, 1989; Lasiak & Field, 1995; Menge, 1995; Griffiths & Branch, 1997; Lasiak, 1998; Sharpe & Keough, 1998).

The impact of the exploitation does not depend only on the exploitation pressure, but also depends on the vulnerability of the species regarding exploitation. Griffiths & Branch (1997, see also Robertson, 1996) showed that a decrease of the mean size of a certain prey species can negatively effect fertility, because of the relatively larger contribution of larger shells to the total reproductive output of the species. Removing only the larger shells can therefore decerase the population size. Some species, such as Oysters (*Saccostrea* spp.), seem particularly vulnerable to exploitation (Catterall & Poiner, 1987), due to their inability to escape depredation and their large size at maturity. Also rarer species, or stressed species found at the limits of their distribution range, are expected to be more affected by exploitation (Catterall & Poiner, 1987; Swadling, 1976; Lasiak, 1991a). Species such as *Anadara* spp. and *Strombus* spp. which are abundant, able to hide in the mud, and have high growth rates are believed to be less vulnerable to depletion. Therefore, we predict that the difference in species composition between old and recent shell middens is a result of the disappearance of these exploitation-vulnerable species.

Human exploitation can be regarded as a disturbance factor for the ecosystem. Intermediate levels of disturbance could increase the species richness of the community (Hockey & Bosman, 1986) by creating patches with different stages of succession. The so-called Intermediate Disturbance Hypothesis (Connell, 1978) will be tested in this paper.

Study area

The general ecology of Inhaca Island (lat. 26°07′, long. 32°56′) is well described by Kalk (1995). 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). The present human population is estimated at 8000 inhabitants, living in three settlements: Ridjene, In-

guane, and Nhaquene (Figure 1). A conservative estimate of the population growth of 1% per year implies that the mean human population at Inhaca was <2000 between 1800–1900, suggesting that the exploitation pressure has more than doubled in the last century. Soil fertility is low and agricultural production is therefore reduced. Cattle are absent from the Island but some goats, pigs and chickens can be found. Thus, the local fisheries are of vital importance. Women and children are found in large numbers on the tidal flats during low tides searching for crabs and shellfish (de Boer & Longamane, 1996). There is no indication of a change in the exploitation methodology lately.

Materials and methods

An inventory of recent and old shell middens was made on Inhaca Island. The age of the abandoned middens was unknown, but an estimated age was obtained by interviewing people living in the vicinity. All abandoned middens could be traced back and were in use at least several generations ago. In order to decrease the influence of climate changes or fluctuations in sea level, middens older than approximately 200 years were excluded from the analysis. In order to avoid the problem of determining the middens' age, we classified the middens in only two groups: used ($n=6$), and abandoned middens ($n=8$; Figure 1). Five different surface samples were taken from each midden. One sample was collected from the middle of the midden. From this point four lines were drawn to North, East, South, and West boundary of the midden. Four samples were collected at the middle of each line. A steel quadrat of 0.5×0.5 m was inserted at each sample point, and the whole substrate, including shells, removed up to 0.3 m in depth. Samples were sieved over a 2 mm mesh and species were identified, and measured to the nearest mm using a digital vernier calliper connected to a computer. The five subsamples of each midden were lumped, to reduce the impact of differences originating from the spatial variation in the shell middens (see Lasiak, 1992). The resulting sample was compared among middens.

Analysis

Differences in size per species between recent and abandoned middens were analysed using one-way Anova, for those species with a sample size >10 per midden category. The assumptions of the Anova
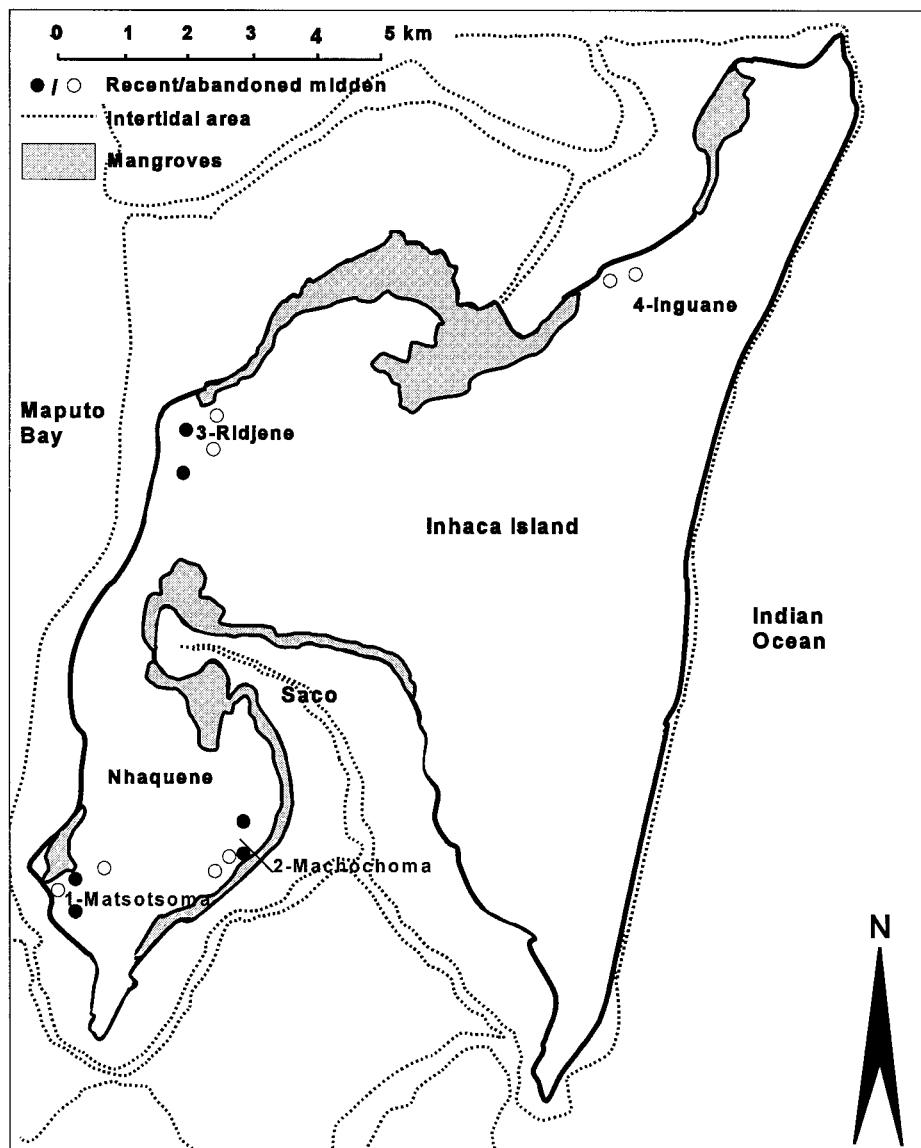
Figure 1. Inhaca Island with the three villages, the surrounding intertidal area, the mangrove forests and the location of the recent and abandoned middens.

were tested with a Kolmogorov-Smirnov test (test for normality, Zar, 1984) and a Levene test (test for homogeneity of variances, Levene, 1960). If possible, data were log-transformed to remove heterogeneity of variances and to correct for skewed distributions. Differences among samples which were not normal distributed or had heterogenic variances (even after transformation) were analysed using a Mann–Whitney U test (Zar, 1984). The hypothesis that the mean shell size of all species has decreased was tested by recoding the original data to z-scores (if neces-

sary after transformation for normality), lumping these scores of different species, adjusting sample size after randomization, and performing a non-parametric Kolmogorov–Smirnov test (Siegel & Castellan, 1988). Percentages were arcsine transformed prior to statistical analysis.

Using Primer software (Clarke & Warwick, 1994), species richness of middens was calculated using different indices for richness (Margalef and Shannon–Wiener), evenness, and dominance. Rarefaction of species richness was calculated from Krebs (1989).
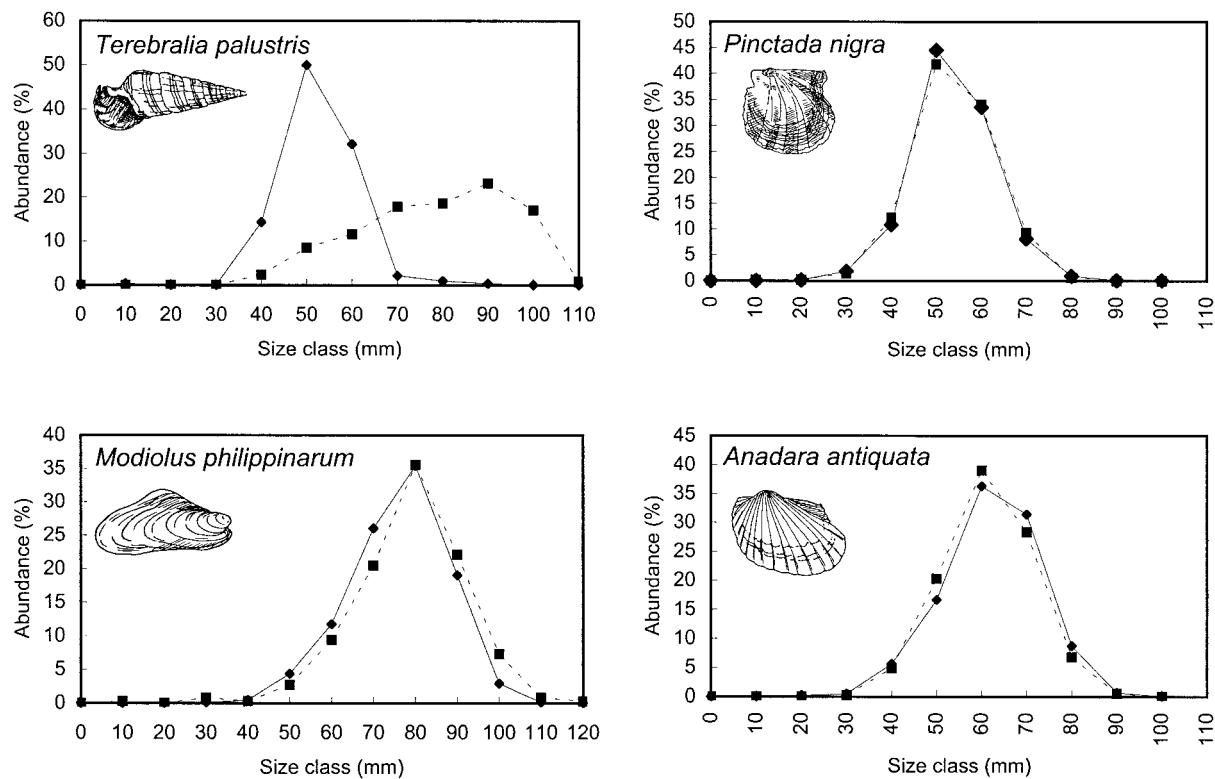
Figure 2. The size-frequency distribution of four abundant shell species as obtained from recent (solid line), and abandoned middens (broken line). Two species, *Terebralia palustris* ($n = 825$) and *Modiolus philippinarum* ($n = 1524$), showed a significant decrease in shell size (compare with Table 1). *Pinctada nigra* ($n = 9527$) had an equal size distribution, and the size of *Anadara antiquata* ($n = 2326$) was significantly larger in recent middens.
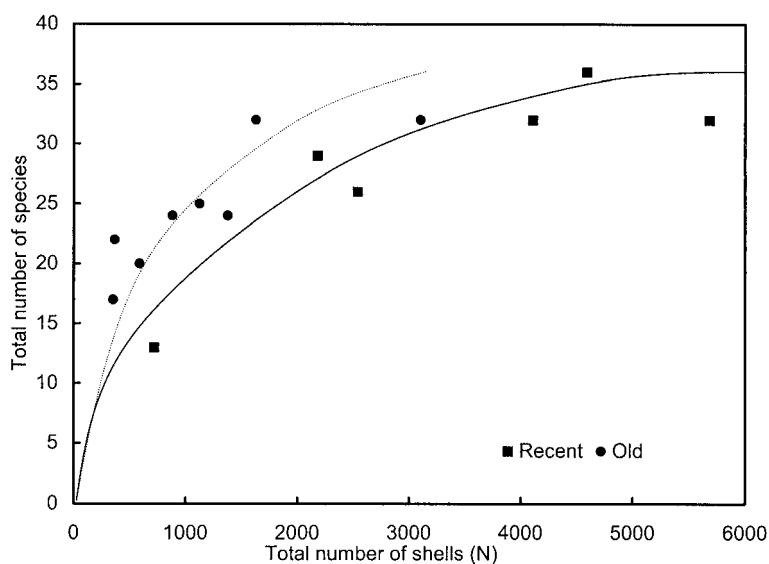

Figure 3. A species-effort curve for the old (broken line) and recent shell middens (solid line), with the total number of excavated shells per midden against the total number of identified species.

Table 1. Comparison of means and variances of shell sizes from recent and old middens. Species location in the substrate is given by s = surface dwelling, and b = buried. The mean length (mm), standard deviation (s.d.) and sample size (*n*), together with the results of the statistical comparison of the mean size between the two samples: the type of test used (Anova-F or Mann–Whitney U test), the value of the F or U test, and the level of significance (*p*). Also information is given about the distribution of the data (n = normal, nn = non-normal), the transformation used (− = no transformation, log = log transformation), and the heterogeneity of the two variances being compared (hetero = heterogenous, homo = homogenous)

Species	Substrate	Mean old	Mean recent	s.d. old	s.d. recent	*n* old	*n* recent	Normal	Transf.	Homo/ hetero	Test U/F	Value U/F	*p*
Anadara antiquata	b	56.3	57.2	9.7	10.4	971	1355	nn	−	homo	U	613037	<0.005
Anadara erythraeonensis	b	60.5	55.6	12.6	12.0	17	70	n	−	homo	F	2.249	ns
Barbatia foliata	b	38.7	37.4	9.0	8.8	64	114	n	log	homo	F	1.009	ns
Arca navicularis	b	41.5	37.3	12.3	11.0	24	53	n	log	homo	F	0.755	ns
Trachycardium flavum	b	50.3	50.5	7.4	6.7	321	718	nn	−	hetero	U	113756	ns
Mimachlamys senatoria	s	50.7	50.1	11.5	10.8	22	27	n	−	homo	F	0.029	ns
Chicoreus ramosus	s	127.0	103.8	38.8	46.1	11	12	n	−	homo	F	1.702	ns
Saccostrea cuccullata	s	31.1	30.2	9.7	7.2	1057	2136	nn	−	hetero	U	1095423	ns
Dotilla faba	b	20.4	20.4	3.0	2.3	65	68	n	−	homo	F	0.002	ns
Fasciolaria lugubris	b	107.4	99.7	15.7	34.1	27	22	n	−	hetero	U	295	ns
Gafrarium divaricatum	b	35.3	34.2	5.0	4.4	816	897	nn	−	homo	U	114581	<0.0001
Malleus regula	b	25.9	25.2	8.0	9.7	108	204	n	−	hetero	U	9864	ns
Modiolus philippinarum	b	73.4	71.1	13.2	11.6	371	1153	nn	−	hetero	U	182953	<0.0001
Pinctada nigra	b	48.8	48.8	8.8	8.6	3036	6491	nn	−	hetero	F	0.015	ns
Pitar abbreviatus	b	27.8	28.6	4.9	5.3	12	27	n	−	homo	F	0.188	ns
Polynices tumidus	s	26.8	23.6	5.5	6.8	384	840	n	−	hetero	U	115595	<0.0001
Polynices didyma	s	36.7	26.7	4.8	6.6	12	56	n	−	homo	F	24.721	<0.0001
Solen cylindraceus	b	42.3	43.2	8.6	5.0	37	398	n	−	hetero	U	7219	ns
Septifer bilocularis	b	29.9	32.4	8.3	6.9	141	237	n	−	homo	F	9.527	<0.0005
Strombus gibberulis	b	54.8	53.8	9.7	7.5	44	82	n	−	homo	F	0.394	ns
Terebralia palustris	s	73.4	47.7	16.3	7.6	258	567	nn	−	hetero	U	13980	<0.0001
Turbo coronatus	b	22.5	25.6	3.1	10.6	24	62	nn	−	hetero	U	736	ns
Volema pyrum	b	48.5	48.7	6.7	10.7	146	141	n	−	hetero	U	9618	ns

Similarity in species composition was calculated using Bray–Curtis similarity coefficients on square root transformed abundance data. Differences in species similarity were tested with an Anosim (analysis of similarity) and Simper procedure (similarity percentage analysis), using Primer. Sample ordination was carried out by a non-metric Multi-Dimensional Scaling (MDS), available in the same package. The MDS, Anosim and Simper analysis were only done on the three sites which had both recent and abandoned middens.

Results

The mean shell size was significantly smaller in recent middens compared to abandoned middens for *Gafrarium divaricatum*, *Modiolus philippinarum*, *Polynices*

didyma, *P. tumidus*, and *Terebralia palustris* (Table 1, Figure 2). *T. palustris* showed the largest reduction, 65%, of the mean shell length. The most abundant species, *Pinctada nigra*, did not change in size over time. Only two species, *Septifer bilocularis* and *Anadara antiquata*, showed a significant increase in shell size. The Kolmogorov–Smirnov tests on randomised *z*-scores proved that the mean size was significantly reduced in recent middens ($D_{max} = 0.054$, $p < 0.001$, $n = 7965$), with a mean z-score of -0.03 (s.d. relative to the mean) for contemporary middens, and $+0.07$ for the abandoned middens.

Using the (arcsine transformed) percentages of reduction per species (Table 2) from abandoned to recent middens, a two-way Anova could be carried out. The two independent factors were: location in the substrate (two categories: surface-dwelling and burrowers), and a binomial bed-forming variable. Species that are sur-

Table 2. The mean shell size reduction (%) for species according to their position in the substrate (surface-dwelling, or burrowers), and with regard to bed-forming. A negative reduction illustrates a species with a mean size larger in recent middens compared to older middens. Species taken frequently by the human population (de Boer et al., submitted) are indicated with an '*'

Species		Reduction %
Surface, non bed-forming		
Mimachlamys senatoria		1
Chicoreus ramosus		18
Polynices tumidus	*	12
Polynices didyma	*	27
Terebralia palustris		35
Surface, bed-forming		
Saccostrea cuccullata		3
Burrowers, non bed-forming		
Anadara antiquata	*	−2
Anadara erythraeonensis		8
Barbatia foliata		3
Arca navicularis		10
Trachycardium flavum	*	0
Dotilla faba		0
Fasciolaria lugubris		7
Gafrarium divaricatum		3
Malleus regula		3
Pitar abbreviatus		−3
Solen cylindraceus		−2
Septifer bilocularis		−8
Strombus gibberulis		2
Turbo coronatus		−14
Volema pyrum		0
Burrowers, bed-forming		
Modiolus philippinarum		3
Modiolus sp.		−9
Pinctada nigra		0

face dwellers, and form shell-beds are expected to suffer more from human exploitation. The effect of location in the substrate was confirmed ($F_{1,20} = 5.190$, $p < 0.05$); species living above the substrate had a significantly lower mean shell size in recent middens, with a mean reduction per species of 16.1%. Burrowers had a mean shell size in recent middens equal to abandoned middens (mean reduction 0.0%). No effect of bed-forming was detected.

The only true subtidal species in the middens was *Turbo laetus.* Due to the low number of subtidal species no effect of tidal habitat (intertidal/subtidal) was found. Moreover, the mean shell size did not influence the reduction of the shell; and larger shells did not have a larger reduction. Species that were preferred relatively more (*A. antiquata*, *Polynices* spp., *Trachycardium flavum* and *M. philippinarum*, de Boer et al., subm.) also did not suffer greater reduction than less preferred species.

In total, 19252 shells were identified, comprising 78 species (Table 3). Bivalves comprised 92% of the shells from the recent middens and 83% from the abandoned middens. The most abundant bivalve species were *P. nigra* (30–24% in recent and abandoned middens respectively), *A. antiquata* (15–16%), *Saccostrea cuccullata* (18–14%), *M. philippinarum* (6–13%), *T. flavum* (10–5%), and *G. divaricatum* (4–5%). *P. tumidus* (4–7%) and *T. palustris* (2–5%) were the only two gastropod species contributing >1% to the total. Species which were absent in recent middens but were found in older middens all contributed <1% to the total of these middens. *Perna perna* and *Thais savignyi* were the only two species present in older middens with 0.5–1.0%, but not found in recent middens.

All species which showed a significant size reduction and which contributed >1% to the total, also showed a decrease in abundance from older to recent middens. The species with a larger size in recent middens, *A. antiquata* and *S. occularis*, were also less abundant in recent middens. The four species with a considerably (>1%) larger contribution in total abundance in recent middens (*P. nigra*, *S. cuccullata*, *Solen cylindraceus*, and *T. flavum*), did not suffer any significant size reduction (compare Table 1 and 3).

The total number of species/midden varied from 13–36 species, but this was mainly influenced by the different sample size which varied from 354–5684 shells/midden. Abandoned middens had relatively more species than recent middens (Figure 3). Of the eight abandoned midden samples, only one sample had the same number of species as recent middens with an equal or larger samples size. Hence, species richness was larger in abandoned middens (Sign test, $p < 0.05$). The sample size was significantly larger for recent middens ($F_{1,12} = 8.366$, $p < 0.02$), but none of the species richness indices (Table 4) were significantly different when recent and abandoned middens were compared. The expected number of species per midden was calculated through rarefaction for the

Table 3. The species composition of the new (*n*=6) and old (*n*=8) shell middens of Inhaca. The frequency with which the species occurred in the middens over the total investigated middens (n/t) is also given. $-$ = not present

Species	New mean %	Old mean %	New freq n/t	Old freq n/t	Species	New mean %	Old mean %	New freq n/t	Old freq n/t
BIVALVES					*Cymatium muricinum*	0.04	0.01	0.2	0.1
Anadara antiquata	14.83	16.19	1.0	1.0	*Cymatium pileare*	0.01	0.03	0.2	0.1
Anadara erythraeonensis	0.30	0.15	0.3	0.1	*Cypraea annulus*	0.02	0.27	0.3	0.3
Anomia achaeus	0.02	0.00	0.3	0.1	*Cypraea erosa*	0.01	0.00	0.2	0.1
Arca navicularis	0.39	0.31	0.8	0.8	*Cypraea lamarcki*	0.01	$-$	0.2	$-$
Barbatia foliata	0.31	0.47	0.8	0.6	*Cypraea* sp1	$-$	0.00	$-$	0.1
Beguina gubernaculum	$-$	0.00	$-$	0.1	*Cypraea* sp2	$-$	0.01	$-$	0.1
Brachydontes semistriatus	$-$	0.19	$-$	0.1	*Cypraea vitellus*	0.00	$-$	0.2	$-$
Circe scripta	0.02	0.09	0.2	0.5	*Diodora ruppelli*	0.01	$-$	0.2	$-$
Codakia tigerina	0.03	0.06	0.3	0.3	*Fasciolaria lugubris*	0.10	0.08	0.7	0.6
Donax faba	0.30	0.78	0.5	0.5	*Fasciolaria trapezium*	$-$	0.04	$-$	0.3
Dosinia hepatica	$-$	0.08	$-$	0.1	*Granata sulcifera*	0.03	$-$	0.7	$-$
Fulvia papyracea	$-$	0.03	$-$	0.3	*Hydatina* sp.	$-$	0.01	$-$	0.1
Gafrarium divaricatum	4.24	5.07	1.0	0.9	*Jujubinus suarezensis*	0.02	$-$	0.2	$-$
Hyotissa numisma	0.01	0.14	0.2	0.1	*Mancinella echinulata*	$-$	0.01	$-$	0.1
Isognomon ephippium	0.49	0.10	0.5	0.3	*Murex brevispina*	0.09	0.05	0.8	0.4
Lithophaga nasuta	$-$	0.01	$-$	0.1	*Nassarius coronatus*	0.01	0.04	0.3	0.3
Lutraria australis	0.01	$-$	0.2	$-$	*Nerita albicilla*	0.01	0.03	0.5	0.4
Mactrotoma ovalina	$-$	0.01	$-$	0.1	*Nerita polita*	$-$	0.04	$-$	0.1
Malleus regula	0.94	0.57	0.8	0.5	*Polynices didyma*	0.24	0.10	0.5	0.4
Mimachlamys senatoria	0.18	0.21	0.8	0.6	*Polynices tumidus*	3.81	6.96	1.0	1.0
Modiolus philippinarum	6.26	12.96	1.0	1.0	*Priotrochus obscurus*	$-$	0.08	$-$	0.1
Musculus sp.	$-$	0.04	$-$	0.1	*Pteria tortirostris*	0.01	$-$	0.2	$-$
Perna perna	$-$	0.66	$-$	0.4	*Rapana rapiformis*	0.02	0.06	0.5	0.4
Pinctada nigra	29.93	23.76	1.0	1.0	*Sinum haliotoideum*	0.04	0.02	0.5	0.1
Pitar abbreviatus	0.16	0.14	0.8	0.5	*Strombus decorus*	0.02	0.04	0.3	0.4
Protapes sp.	$-$	0.01	$-$	0.1	*Strombus gibberulus*	0.55	0.75	1.0	0.9
Saccostrea cuccullata	18.31	13.68	1.0	1.0	*Terebralia palustris*	2.08	5.27	0.8	0.8
Septifer bilocularis	1.21	1.56	0.8	0.9	*Thais bufo*	$-$	0.01	$-$	0.1
Solen cylindraceus	3.06	0.15	0.2	0.1	*Thais savignyi*	$-$	0.56	$-$	0.3
Tapes deshayessi	0.02	0.02	0.5	0.3	*Thais* sp.	0.01	$-$	0.3	$-$
Tellina capsoïdes	$-$	0.01	$-$	0.1	*Tonna cepa*	0.00	$-$	0.2	$-$
Trachycardium assimile	0.01	$-$	0.2	$-$	*Trochus nigropunctatus*	0.01	0.04	0.2	0.3
Trachycardium flavum	10.45	5.03	1.0	1.0	*Turbo coronatus*	0.41	0.36	0.5	0.4
Trisodos tortuosa	$-$	0.02	$-$	0.1	*Turbo laetus*	$-$	0.01	$-$	0.1
Unidentified sp2	0.15	0.04	0.7	0.4	*Vexillum intermedia*	0.01	$-$	0.2	$-$
GASTROPODS					*Volema pyrum*	0.71	2.34	1.0	1.0
Chicoreus ramosus	0.05	0.08	0.7	0.4	Unidentified sp1	$-$	0.08	$-$	0.3
Clypeomorus batillariaeformis	0.00	$-$	0.2	$-$	Total bivalves %	92	83		
Conus betulinus	0.01	0.04	0.2	0.4	Total gastropods %	8	17		
Conus textile	0.00	0.01	0.2	0.1	Mean number of shells/midden	3304	1178		
Cronia heptagonalis	0.02	$-$	0.2	$-$					
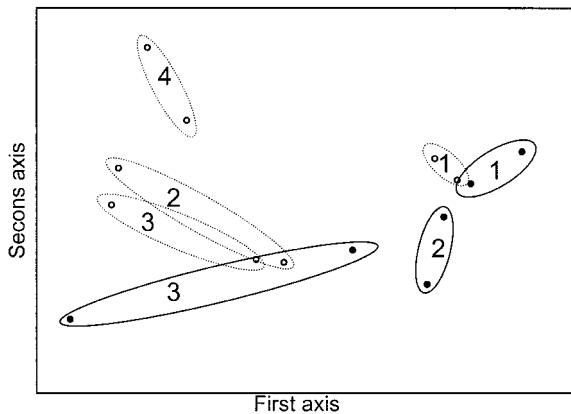
Figure 4. Sample ordination through non-metric Multi-Dimensional Scaling of Bray-Curtis similarity coefficients of square-root transformed abundance data. The four locations (1–4, compare with Figure 1), and the different ages of middens are indicated (open circle = abandoned; solid circle = recent midden). Middens of equal age and location are enclosed by ovals.

smallest sample size ($n = 354$), resulting in 16.2 ± 3.4 species for recent and 18.4 ± 1.8 for older middens.

Species similarity between recent and abandoned middens was also compared using Bray–Curtis similarity coefficients. Sample ordination through non-metric Multi-Dimensional Scaling resulted in the pattern illustrated in Figure 4. The pattern is basically a scatter in which samples from similar sites and ages are plotted next to each other. Samples from recent middens are separated from older middens in the graphs, but the ordination did not separate the samples in clear distinct groups, although the stress factor was relatively low (0.09).

A two-way nested analysis of similarity did not detect significant differences for samples of different ages or sites (R respectively 0.019 and 0.306), so the samples of different sites were lumped. The average dissimilarity between recent and abandoned middens was 37.8%. Half of the dissimilarity was explained by 18 species and none of the species attributed more than 4.4% to the total dissimilarity. The four most important species were *A. antiquata*, *T. flavum*, *T. palustris*, and *S. cuccullata*, explaining together 16.1% of the dissimilarity between the samples.

Discussion

Although crustaceans comprise a majority of the diet (de Boer et al., subm.), their remains are rare in middens, because small crabs (*Uca* spp., *Macrophthalmus* spp., *Dotilla* sp., *Thalamita* spp.) are eaten entirely with the carapace after being crushed, and their remains are not specially discarded at middens. Carapaces of larger species (*Scylla* sp., *Portunus* spp.) break into numerous small pieces and as a result, were not analysed in the present study.

The mollusc species comprising the middens have suffered a small, but significant, reduction of the mean size over time. Only *T. palustris* showed a large significant reduction of the mean shell length, whilst for other species, the reduction is not directly apparent from the size-frequency graphs (Figure 2). At present *T. palustris* is an abundant species in Inhaca's mangrove forest. As a result, the species is even available during neap tides, when the relatively low-lying, species-rich mudflats and tidal channels remain inundated. Also important is the fact that *T. palustris*, like *Polynices* spp., and *Mimachlamys senatoria*, *S. cuccullata*, and *Chicoreus ramosus* are the only mollusc species that are surface dwelling or found attached to mangroves trees (Tables 1 and 2). These species are conspicuous and can be detected easily. All these species have shown size reductions in the comparison between abandoned and recent middens, and a significant decrease in shell size of surface-dwelling species compared to burrowers was confirmed. The population structure of surface-dwelling species was changed, they had a smaller mean shell size in recent middens. This size reduction could have been caused by human exploitation, but Lasiak (1991b, 1992) showed that size difference of *P. perna* in middens were encountered regularly, even in samples taken months apart. Our samples were mixtures of different subsamples, and hence less influenced by temporal variation in shell size. However, both human exploitation, and temporal variation in the size of accessible shell species (Lasiak, 1991b) could contribute to the mean decrease in shell size.

The most abundant species, *P. nigra*, showed a similar size-frequency graph in recent and old middens. The species is normally collected on off-shore sandbanks in the Maputo Bay, accessible only by boat. Moreover, the species lives hidden in the sand. These factors are probably the reason shell size was unaffected by human exploitation. This species is bed-forming and collected in large quantities per foraging trip. Like *S. cuccullata*, some catches are field-processed and not taken directly home (own observation). These two species are therefore certainly underrepresented in the middens. The ratio of transport costs to field processing costs can influence relative abundance in household middens as has been documented

Table 4. Mean (±*s.d.*) number of shells identified per midden, number of species, and richness, eveness and dominance indices for recent and abandoned middens

	Total number of shells	Total number of species	Richness (Margalef index)	Richness (Shannon–Wiener index)	Eveness (Pielou index)	Dominance (Simpson index)
Recent	3304 ± 1817	28 ± 8	3.4 ± 0.8	1.6 ± 0.4	0.5 ± 0.1	0.29 ± 0.11
Abandoned	1178 ± 904	25 ± 5	3.4 ± 0.5	1.9 ± 0.3	0.6 ± 0.1	0.25 ± 0.09

by Metcalfe & Barlow (1992), Bettinger & Malhi (1997) and Bird & Bliege Bird (1997).

The species composition of recent and abandoned middens was different; recent middens had a lower species richness. The effect was small and not detected by all analyses. The disappearance of some species in recent middens or the appearance of new ones could be a sampling artefact. Larger samples would also have improved the interpretation of the data as the number of species increased with the number of shells in the sample, and only remained stable in the largest samples (Figure 3). However, the results are certainly not consistent with a higher species richness under increased human exploitation as predicted by the intermediate disturbance hypothesis (Connell, 1978; Hockey & Bosman, 1986). Hockey & Bosman (1986), and Lasiak & Field (1995) worked on rocky shores in Southern Africa. The shores of Inhaca are mainly composed of sandy beaches and mudflats. This difference is probably the key to understanding why the impact of human exploitation is so small. Species can hide from exploitation by burying in the substrate. The impact of predators is normally smaller in soft bottom substrates than in rocky shores (Menge et al., 1994). Moreover, the total annual human exploitation is estimated at <5% of the available biomass (de Boer & Prins, in prep.) and therefore the impact of human exploitation on the intertidal ecosystem could not be easily measurable. Another possible explanation could be that the time span between recent and abandoned middens was too small to detect the impact of exploitation. Archaeological excavations of older middens in Southern Mozambique, from 12 000 to 1000 bp (Barradas, 1967; Morais, 1988), normally identified fewer species, with *P. perna*, *Saccostrea* spp, and *Thais* spp. as the dominant species. The Inhaca middens studied here are composed of a large number of species, 78, which is partially explained by the availability of different habitats around the island. However, this could also be the effect of a high exploitation pressure leading to an impoverished situation of the intertidal area, which in turn leads to a less specialized diet, comprised of an increased number of species (de Boer et al., submitted). We therefore recommend further investigation of middens covering a longer time span.

Species with a significant size reduction were less abundant in recent middens. The oyster *S. cuccullata*, although vulnerable to exploitation because of its accessibility, large size of maturity, and possibility of recruitment failure (Swadling, 1976; Catterall & Poiner, 1987; Lasiak, 1991a), was relatively more abundant in recent middens. When the species composition of abandoned and recent middens was compared, no effect could be found in the mean size of the species, the location in the substrate (burying versus surface-dwelling species), the distribution range (tropical versus temperate species), the limit of the distribution range (species with/without Inhaca at the extreme end of their distribution range), or the preferred tidal zone (intertidal versus subtidal species).

The disappearance of *P. perna* in recent middens could be related to overexploitation. The disappearance of or decrease in this favoured mussel also has been documented by other studies (Siegfried et al., 1985; Hockey et al., 1988; van Erkom Schurink & Griffiths, 1990; Dye et al., 1997). The species lives on exposed rocks, and forms mats, which are normally exploited by cutting off large clumps of mussel. The relatively high human exploitation pressure, together with the low occurrence of suitable habitat for the mussel and the population dynamics of the species, are probably the reason for the disappearance of *P. perna* from the middens on Inhaca.

Conclusions

A total of 78 species were identified in 29252 shells collected from 6 recent and 8 abandoned middens from Inhaca island, Mozambique. The majority (83–92%) were bivalves. The most abundant species were the bivalves *Pinctada nigra*, *Anadara antiquata*, *Saccostrea cuccullata*, *Modiolus philippinarum*, *Trachycardium flavum*, *Gafrarium divaricatum*, and the gastropods *Polynices tumidus*, and *Terebralia palustris*. The mean size of the shells was significantly reduced in recent middens. *Terebralia palustris* had the largest size-reduction. Size reduction was related to life history. Surface-dwelling species suffered a significantly larger reduction than burrowers, which can be explained by their conspicuousness. In recent middens, species with a significant size reduction were relatively less abundant. Abandoned middens had a slightly, yet significantly, greater species richness. Therefore, the intermediate disturbance hypothesis was rejected. The disappearance from recent middens of the mussel *Perna perna* normally found on rocky substrate, was thought to be related to overexploitation. The species composition of recent and older middens was relatively similar, because sandy beaches and mudflats prevail around Inhaca, and they allow species to escape detection by burying. The relatively low human exploitation pressure is another possible explaination for the similarity. The differences in species composition could not be explained by a different life history of the species.

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