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Kenyan coral reef-associated gastropod assemblages: distribution and diversity patterns

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Abstract. A survey of Kenya's shallow water (<2 m) coral reef-associated prosobranch fauna was undertaken to determine patterns of distribution, density, diversity and species richness, and the possible role of other reef fauna and human utilization on these patterns. The sample assemblage of 135 species from 25 families is similar to other Indian Ocean regions with no apparent endemism or subregional faunal affinities. Species richness, determined by species-individual relationships, has been reduced by approximately 45% since the Pleistocene. Northern Kenya, typified by small coral islands experiencing river and estuarine discharges had low densities and species richness and high species variability. This is attributable to the interrelated factors of river discharge, small reefs and reduced predator refuge. Southern Kenya's more expansive fringing reef has a denser and richer fauna but appears less species rich than Tanzania. Variation within reefs suggests similarities in diversity between reef lagoons, flats and edges, but lagoons had lower densities than reef flat or edge sites. This is attributable to greater predation rates within lagoons. Species composition between reef locations was variable but differed for comparisons between reef lagoons and reef flats. The population densities of thirty commercially collected species were compared between shelled and unshelled reefs. Only two commercial strombids, *Lambis truncata* and *L. chiragra,* had lower densities within shelled compared to unshelled reefs. Within six southern Kenyan reef lagoons, total gastropod densities were negatively correlated with the Balistidae (triggerfish) and total fish densities and positively with sea urchin densities. The removal of balistids through fishing appears to lead to co-occurring population increases in gastropod and sea urchin populations which, in most instances, appears to negate the effect of shell collecting.

Introduction

Shell collection and the extent of the international shell trade has generated conservation and environmental concerns (Knowles 1970; Evans et al. 1977; Wells 1981; Wells et al. 1983; Villanoy et al. 1988). Kenya was reported to export between 84 and 107 tons/year of coral and shells in 1977 and 1978 (Wells 1981). Although less than the Philippine trade, this is representative of other developing countries with coral reefs (Wells 1981). The effect of shell collection is poorly documented, but within the central Pacific the over-collection of the Triton shell (*Charonia tritonis*) has been suggested to cause *Acanthaster* population breakouts (Endean 1973). Within Kenya, shell collecting has been suggested to lead to reef degradation by reducing predators of sea urchins and starfish which feed on living coral and increase reef bioerosion rates (NEHSS 1984). But, McClanahan's (1989) data suggests that only a few species may be affected by shell collection and that reef predators may be more important than shell collectors in regulating gastropod populations. Consequently, basic population and ecological data must be collected in order to understand the role of shell collection on the gastropod fauna. This study attempts to place shell collecting and the Kenyan gastropod fauna within a larger historical and coral-reef community context and reports specifically on (1) the large scale distribution patterns of Kenyan gastropods, (2) within and between reef patterns of species composition, distribution and diversity, (3) the densities of commercially collected species and (4) the interrelationship between gastropods and other members of the reef community (i.e. fish and sea urchins).

Material and methods

Kenya's coast and coral reefs have recently been described by Khamala (1971), Hamilton and Brakel (1984), Crame (1986), McClanahan (1988a) and McClanahan and Muthiga (1988). The southern section of Kenya's coastline south of Malindi (Fig. 1) is characterized by a nearly continuous fringing reef with the Malindi Marine National Park (MNP) as the northern and Msambweni as

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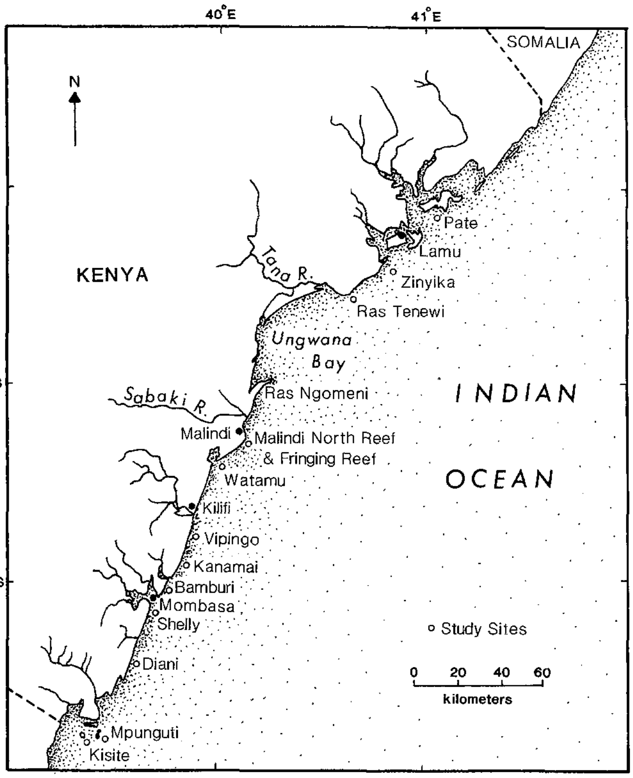

Fig. 1. Kenyan coastline and study site locations

the southern terminus of this reef. South of Diani coral rock islands, including the Kisite-Mpunguti MNP, typify the reef geomorphology also typical of northern Tanzania's coastline. North of Malindi, the Sabaki and Tana rivers discharge into the Indian Ocean and coral reefs are patchily distributed up to the Somali border around coral rock islands.

Thirteen sites along the Kenyan coast were chosen for surveying (Fig. 1) including four protected parks (Malindi, Watamu, Bamburi and Kisite) and the Mpunguti Reserve. The Bamburi MNP was surveyed before it was established as a Park and therefore not considered protected in the data analysis. All other Parks and Reserves have existed for over 15 years. Parks exclude fishing and shell collecting and reserves exclude shell collection and some fishing methods.

Sampling was undertaken by a random walk or swim procedure (Kohn 1968; McClanahan 1989) which allows greater time efficiency within the intertidal zone; Kenya has a 4 m tidal range (Brakel 1982). McClanahan (1989) details the sampling procedure. Briefly, all sampling was undertaken within shallow (<2 m) reef locations (reef edges, reef flat and reef lagoons) during daylight spring low tides using a one hour sample. When a species was first encountered the time was recorded and subsequently encountered individuals of the species tallied. Sites were visited at different times and sampling included broad surveys to include the largest area possible. During samples small coral boulders were overturned but only as frequently as they were encountered. Continuous movement during sampling may have caused some smaller and cryptic species to be missed or under-sampled, but McClanahan (1989) found no significant difference between 2 independent observers using this method. Most reef locations were sampled a minimum of three times (i.e. 3 h) but this depended on the reef's size. Sample sizes are given in Table 1. Sampling was undertaken at various times between November 1986 and July 1988. A 1 h sample is estimated to cover approximately 1000 m^2 (McClanahan 1989).

Spry (1968) is the most complete reference for East African gastropods but some nomenclature has changed since this publication. Therefore, the works of Dance (1974), Oliver (1975), Richards (1984) and Abbott and Dance (1986) were also consulted. Only live prosobranch gastropods were identified and included within this study.

Kenya's fringing reef consists of three locations; reef edges, flats and lagoons. Reef edges exist between MLWN and MLWS and are directly exposed to waves. Reef flats are shallow reef tops and exposed to air during most low tides. Reef lagoons are the shallow protected areas landward of the reef flat. Kenya's reef lagoons are often composed of extensive seagrass beds but during sampling these areas were generally avoided in favor of hard substrate and coral outcrop areas. No back-reef rock platforms or rocky shores were sampled. Some reefs lacked one or more of the three reef locations and some sites such as the rock islands of Kisite, Mpunguti wa Juu, Ras Tenewi, Zinyika and Pate lacked true reef lagoons but the deeper leeward sides of these sites were included as lagoons in the data analysis. The Pate site included samples from three adjacent

Table 1. Reef flat heights in relation to datum (m) and total densities (#/h, $x \pm$SEM) (n = number of samples) of the gastropod fauna at the studied locations. Portions of this data are from McClanahan (1989). Correlation between reef height and density not significant

Location	Heigth m	Reef edge	Reef flat	Reef lagoon
Kisite	1.37	122.0±17.8 (6)	108.8±10.3 (4)	12.3± 1.5 (8)
Mpunguti	1.20	64.0± 8.9 (4)	174.5± 5.3 (4)	17.6± 7.6 (8)
Diani	0.80	27.9± 3.7 (3)	84.3±14.3 (4)	68.3± 3.0 (7)
Shelly	1.40	102.3±36.0 (3)	113.0±33.6 (3)	93.3±12.8 (3)
Bamburi	1.05	45.7± 6.7 (3)	68.0±13.9 (4)	21.0± 7.4 (6)
Kanamai	1.40	93.0± 7.6 (3)	127.0±22.9 (3)	47.8± 6.7 (8)
Vipingo	1.45	114.0±10.6 (3)	59.0± 6.4 (3)	81.3±52.4 (3)
Watamu	–	–	–	14.0± 4.4 (5)
Malinidi North Reef	0.80	33.7± 5.5 (3)	62.4±13.6 (3)	15.2± 2.3 (6)
Malindi Fringing Reef	1.50	52.3±13.3 (4)	91.7±28.3 (3)	–
Ras Tenewi	–	–	24 (1)	10.2± 4.1 (6)
Zinyika	–	–	–	29.5±23.5 (2)
Pate	–	–	24.3± 5.6 (6)	14.7± 3. (3)
Total		72.8±11.9 (32)	91.3±13. (38)	35.4± 8.6 (65)

reefs known locally as Pezali, Mwendo wa Pate and Kitwayu Upuu. Reef flat heights were estimated by observing the time that water crossed the reef and calculating the height in relation to datum (Kenya Tide Table 1987).

Data allowed the calculation of diversity, relative density, and species richness. Diversity (D) was calculated using a modification of Simpson's (1949) equation where:

$$D=1-\sum_{i=1}^{n} p_i^2 . \qquad (1)$$

p_i is the number of individuals of species i divided by the total number of individuals in the sample. D varies between 0 and 1, 0 the lowest and 1 the highest possible diversity. Species richness was principally estimated by species-time relationships fitted to the equation:

$$S=Ct^z, \qquad (2)$$

where S is the number of species found at time t; C and the exponent z are constants determining the shape of the curve. Species-individual curves were also generated for comparisons of reef locations.

Comparisons of species composition were made between sites using similarity indices and cluster analysis. Sorensen's (1948) index was principally used to calculate similarity (S) by the equation:

$$S=2C/A+B, \qquad (3)$$

where A and B are the number of species in each of the two sampling location and C is the number of species in common. The ten most common species within each site were used for this comparison. The Sorensen index considers only the presence or absence of a species and therefore the Bray-Curtis measure of similarity (Bray and Curtis 1957) was also used to compare selected southern Kenyan reefs. All cluster analysis used average between-group linkages.

Comparisons between protected and unprotected reefs were made between community structure variables and population densities of commonly collected shells. Gastropod population density variables were regressed against sea urchin and fish population density data within six southern Kenyan reef lagoons (Diani, Bamburi, Kanamai, Vipingo, Watamu and Malindi's North Reef) collected by McClanahan and Shafir (in press), McClanahan and Muthiga (1989) and this study. Fish surveys consisted of transects ($n=$ 3 to 6 per site; 5 m × 100 m) in which total observable fish and species from potential invertebrate predator families (Labridae, Diodontidae, Lagocephalidae and Balistidae) were counted. Movements were slow (20 to 30 min per transect) and visibility was never less than 8 m during surveys. Sea urchins were counted in 10 or 25 m^2 areas ($n=$ 9 to 27 per site) at random locations within reef lagoons.

Results

The gastropod assemblage is characterized by low population density, high diversity and high variability in species composition. Densities were highest on reef flats and edges and lowest in reef lagoons (Table 1). Southern Kenyan reefs appeared to have similar between site densities, but the northern rock islands of Ras Tenewi and Pate were characterized by low densities within both reef flats and lagoons. Regressing gastropod density and reef height produces a positive ($r=0.38$) but insignificant relationship. Overall diversity was high and there were no clear distinctions in diversity among reef locations (Table 2). There was notably lower diversity in some of the southern unprotected reef lagoons such as Diani, Shelly and Vipingo. This is attributable to the relatively high densities of a few species within these locations (Table 3). For instance, Diani had high densities of the corallivore *Coralliophila violacea*, Shelly the herbivore *Cypraea annulus* and Vipingo the detritivore/herbivore *Strombus gibberulus*. High densities of *Cerithium alveolus* were also observed within Kanamai's reef lagoon, although not during sampling.

Table 2. Diversity of the gastropod fauna at the studied locations, sites and totals ($x \pm$SEM). Kruskal-Wallis test of totals not significant. Portions of these data are from McClanahan (1989)

Location	Reef edge	Reef flat	Reef lagoon
Kisite	0.87	0.79	0.88
Mpunguti	0.78	0.88	0.89
Diani	0.90	0.84	0.44
Shelly	0.86	0.86	0.59
Bamburi	0.77	0.89	0.92
Kanamai	0.66	0.75	0.85
Vipingo	0.79	0.89	0.51
Watamu	–	–	0.85
Malindi North Reef	0.90	0.92	0.91
Malindi Fringing Reef	0.83	0.90	–
Ras Tenewi	–	0.76	0.81
Zinyika	–	–	0.84
Pate	–	0.88	0.81
Total	0.82±0.03	0.86±0.02	0.78±0.05

Species composition comparisons between reef locations indicates high variability (Table 3; Figs. 2, 3). Cluster analysis of the southern reefs (Fig. 2) indicates species composition differences based on reef locations. Reef lagoons clustered into one group with the exception of the shallow (ca. 0.3 m deep) Kanamai reef lagoon. There was greater species composition similarity between reef flats and edges. These patterns were consistent regardless of the similarity index. Average species similarity (Sorensen's index) for the common (top ten) species was 0.34±0.18 ($x \pm$SD) for reef lagoons, 0.43±0.13 for reef flats and 0.32±0.11 for reef edges. Reef flats appeared to have slightly higher similarities due to the ubiquity of some species such *Morula granulata, M. marginatra, Cypraea annulus* and *Vasum turbinellus* (Table 3). Cluster analysis of within site comparisons for the entire Kenyan coastline failed to show distinct regional associations or distinctions based on management practices with the exception of reef lagoons (Fig. 3). Protected reef lagoons clustered into a group which included Bamburi, Diani and Ras Tenewi. Kenya's northern reefs, Zinyika and Pate, appeared to share few species with other reefs.

Species richness data (Table 4) and the species list (Appendix) indicate a high faunal diversity. A total of 135 species from 25 families were recorded. Data fit well to species-time curves. r values were above 0.95 but averaged 0.989±0.012 (±SD). Overall, z values were high for an assemblage; being higher within sites (Table 4) than for combined sites (Fig. 4). Species-time and species-individual curves (Fig. 4) indicate that species richness within reef locations did not reach an asymptote. Randomly combining sites and locations for a Kenyan total (Fig. 5) indicates that species richness approached an asymptote.

Table 3. The ten most common species and their densities (#/h, $x \pm$SEM) within studied locations

Location	Reef edges		Reef flats		Reef lagoons	
Kisite	*Cypraea annulus*	31.3± 5.3	*Cypraea annulus*	45.3±10.4	*Coralliophila violacea*	3.8± 1.7
	Vasum turbinellus	14.5± 4.6	*Thais savignyi*	11.8± 1.2	*Vasum ceramicum*	2.5± 1.3
	Thais tuberosa	12.8± 3.4	*Vasum turbinellus*	8.5± 0.6	*Vasum rhinoceros*	1.2± 0.4
	Cypraea lynx	10.3± 2.2	*Cypraea tigris*	7.8± 2.2	*Pleuroploca trapezium*	1.0± 0.3
	Conus fulgetrum	5.8± 1.5	*Cerithium caeruleum*	6.5± 4.3	*Cypraea annulus*	0.7± 0.3
	Conus rattus	4.7± 1.4	*Nerita albicilla*	5.8± 2.8	*Lambis lambis*	0.7± 0.5
	Vasum rhinoceros	2.5± 1.1	*Vasum rhinoceros*	3.5± 1.3	*Lambis truncata*	0.7± 0.3
	Strombus gibberulus	2.5± 0.9	*Engina mendicaria*	3.3± 1.0	*Strombus gibberulus*	0.7± 0.3
	Drupa morum	2.3± 2.0	*Conus rattus*	2.8± 1.4	*Vasum turbinellus*	0.7± 0.3
	Conus miles	2.2± 0.5	*Morula marginatra*	2.5± 1.9	*Strombus lentiginosus*	0.5± 0.2
Mpunguti	*Vasum turbinellus*	28.0± 3.2	*Cerithium caeruleum*	31.0±18.5	*Lambis chiragra*	4.6± 1.9
	Vasum rhinoceros	5.3± 0.5	*Thais savignyi*	27.8± 6.0	*Vasum ceramicum*	2.3± 0.8
	Morula granulata	4.0± 1.3	*Conus ebraeus*	25.8± 5.3	*Vasum turbinellus*	2.1± 2.6
	Conus ebraeus	3.5± 1.9	*Vasum turbinellus*	21.8± 2.6	*Lambis truncata*	1.8± 0.7
	Thais tuberosa	3.3± 0.8	*Cypraea annulus*	19.3± 7.5	*Cerithium nodulosum*	1.4± 0.3
	Drupa morum	2.8± 1.8	*Engina mendicaria*	12.5± 1.9	*Lambis scorpius*	1.3± 0.8
	Conus flavidus	2.3± 1.0	*Morula granulata*	9.5± 5.5	*Lambis lambis*	0.5± 0.2
	Thais savignyi	2.3± 1.4	*Morula marginatra*	9.0± 3.7	*Strombus gibberulus*	0.5± 0.3
	Conus fulgetrum	1.5± 0.3	*Conus flavidus*	7.5± 2.1	*Conus virgo*	0.5± 0.2
	Mitra chrysalis	1.5± 0.6	*Conus musicus*	2.0± 0.9	*Cypraea tigris*	0.4± 0.3
Diani	*Latirolagena smaragdula*	5.3± 2.6	*Morula granulata*	21.8± 5.9	*Coralliophila violacea*	59.2±32.0
	Conus lividus	4.8± 0.8	*Cypraea annulus*	19.8± 7.0	*Cerithium pipertum*	3.2± 3.2
	Conus fulgetrum	3.5± 1.0	*Morula marginatra*	11.5± 4.0	*Vasum turbinellus*	2.5± 0.9
	Thais tuberosa	3.3± 0.8	*Vasum rhinoceros*	10.8± 2.1	*Vasum rhinoceros*	1.4± 0.7
	Conus rattus	2.3± 0.8	*Conus ebraeus*	5.0± 1.0	*Strombus lentiginosus*	1.2± 0.5
	Cypraea moneta	1.1± 1.1	*Conus coronatus*	2.5± 1.0	*Cerithium nodulosum*	1.1± 0.6
	Cypraea annulus	0.8± 0.8	*Conus lividus*	2.0± 1.1	*Pleuroploca trapezium*	1.1± 0.3
	Conus miles	0.8± 0.5	*Conus fulgetrum*	1.8± 0.5	*Conus fulgetrum*	1.0± 0.6
	Turbo brunneus	0.8± 0.5	*Conus musicus*	1.5± 1.7	*Conus leopardus*	0.8± 0.6
	Morula spinosa	0.6± 0.3	*Engina mendicaria*	1.5± 1.0	*Conus lividus*	0.8± 0.4
Shelly	*Morula granulata*	27.0±19.0	*Morula granulata*	33.0±10.4	*Cypraea annulus*	58.7±16.1
	Drupa morum	23.7± 7.9	*Cypraea annulus*	16.7± 8.7	*Strombus gibberulus*	9.3± 2.0
	Cypraea annulus	9.0± 5.9	*Vasum rhinoceros*	12.3± 3.5	*Pleuroploca trapezium*	3.3± 1.8
	Vasum turbinellus	5.7± 4.3	*Conus ebraeus*	9.0± 6.1	*Strombus mutabilis*	3.3± 2.9
	Thais savignyi	5.7± 4.3	*Nerita albicilla*	8.3± 8.3	*Vasum rhinoceros*	3.0± 1.0
	Morula marginatra	5.0± 3.6	*Morula marginatra*	7.0± 4.0	*Cypraea tigris*	3.0± 1.7
	Thais tuberosa	3.3± 0.9	*Cypraea tigris*	3.7± 1.8	*Conus lividus*	1.3± 0.3
	Morula spinosa	2.3± 1.2	*Strombus gibberulus*	3.3± 2.4	*Conus virgo*	1.3± 0.9
	Trochus erythraeus	2.0± 0.6	*Conus rattus*	2.7± 2.2	*Vasum turbinellus*	1.3± 0.7
			Conus miles	2.3± 2.3	*Cerithium nodulosum*	1.3± 0.7
Bamburi	*Drupa morum*	19.7± 6.5	*Morula granulata*	18.3± 5.3	*Strombus gibberulus*	2.9± 1.9
	Conus flavidus	4.7± 2.3	*Thais tuberosa*	6.8± 1.1	*Cerithium nodulosum*	2.8± 2.8
	Thais tuberosa	4.7± 0.7	*Peristernia forskali*	6.0± 2.9	*Pleuroploca trapezium*	2.4± 0.2
	Latirolagena smaragdula	3.7± 2.7	*Vasum rhinoceros*	4.5± 1.2	*Lambis lambis*	2.1± 0.7
	Conus rattus	3.0± 0.0	*Cypraea lynx*	4.0± 1.5	*Coralliophila violacea*	2.0± 2.0
	Bursa bufonia	2.3± 2.1	*Morula marginatra*	2.3± 1.0	*Vasum rhinoceros*	1.7± 0.7
	Conus lividus	2.3± 1.5	*Turbo brunneus*	2.0± 0.9	*Conus leopardus*	1.5± 1.0
	Trochus tentorium	1.0± 0.6	*Conus flavidus*	1.5± 1.0	*Vasum turbinellus*	1.5± 0.9
	Bursa rosa	0.7± 0.6	*Pyrene scripta*	1.5± 1.0	*Conus litteratus*	1.2± 0.6
	Conus miles	0.7± 0.6	*Vasum turbinellus*	1.5± 0.7	*Conus lividus*	0.8± 0.4
Kanamai	*Drupa morum*	50.7± 6.2	*Cypraea annulus*	26.3±13.2	*Cypraea annulus*	13.1± 2.2
	Thais tuberosa	14.0± 1.2	*Morula granulata*	23.8± 5.3	*Cerithium pipertum*	5.6± 3.6
	Morula granulata	12.0± 2.5	*Vasum rhinoceros*	16.5± 5.2	*Strombus gibberulus*	5.2± 1.4
	Morula marginatra	4.3± 1.5	*Nerita albicilla*	11.5± 5.4	*Strombus mutabilis*	3.7± 2.4
	Drupa albolabris	3.3± 0.3	*Morula marginatra*	11.0± 5.5	*Nassarius margaritiferus*	2.5± 1.5
	Drupa ricinus	2.0± 1.0	*Peristernia forskali*	6.7± 2.8	*Cypraea tigris*	1.9± 0.8
	Conus rattus	1.3± 0.3	*Engina mendicaria*	6.3± 1.5	*Vasum rhinoceros*	1.6± 0.5
	Latirolagena smaragdula	1.0± 1.0	*Mitra chrysalis*	6.0± 3.0	*Conus lividus*	1.7± 0.2
	Conus fulgetrum	0.7± 0.7	*Cypraea lynx*	5.7± 5.7	*Cerithium nodulosum*	0.8± 0.4
	Thais echinulata	0.7± 0.7	*Conus rattus*	4.3± 4.3	*Conus musicus*	0.8± 1.7
Vipingo	*Morula granulata*	34.3± 9.2	*Morula granulata*	13.7± 1.9	*Strombus gibberulus*	53.0±51.0
	Drupa morum	28.7±11.6	*Vasum rhinoceros*	10.0± 3.0	*Vasum rhinoceros*	8.7± 5.6
	Drupa albolabris	17.3± 2.6	*Conus rattus*	5.3± 0.7	*Conus lividus*	2.3± 0.9
	Morula marginatra	14.3± 5.4	*Morula marginatra*	4.7± 0.7	*Cypraea annulus*	2.3± 1.5
	Thais echinulata	8.3± 5.9	*Conus musicus*	3.3± 2.0	*Cerithium nodulosum*	1.3± 1.3
	Thais tuberosa	2.3± 1.5	*Cypraea annulus*	2.7± 1.2	*Lambis lambis*	1.3± 1.3

Table 3 (continued)

Location	Reef edges		Reef flats		Reef lagoons	
	Conus flavidus	2.3 ± 1.2	*Mitra chrysalis*	2.7 ± 1.5	*Conus musicus*	0.7 ± 0.7
	Drupa ricinus	1.7 ± 0.7	*Mitra stictica*	2.7 ± 1.5	*Conus litteratus*	0.7 ± 0.3
	Conus rattus	0.7 ± 0.7	*Conus fulgetrum*	2.0 ± 2.0	*Harpa amouretta*	0.7 ± 0.7
	Purpura panama	0.7 ± 0.7	*Drupa morum*	1.7 ± 0.9	*Conus ebraeus*	0.7 ± 0.3
			Cypraea moneta	1.7 ± 1.2	*Strombus mutabilis*	0.7 ± 0.3
					Engina mendicaria	0.7 ± 0.3
Watamu					*Coralliophila violacea*	5.4 ± 4.5
					Pleuroploca trapezium	1.4 ± 0.5
					Lambis lambis	1.2 ± 0.7
					Conus fulgetrum	0.7 ± 0.4
					Cerithium nodulosum	0.6 ± 0.3
					Conus litoglyphus	0.6 ± 0.6
					Drupella ochrostoma	0.6 ± 0.6
					Vasum turbinellus	0.4 ± 0.3
					Conus litteratus	0.4 ± 0.3
					Strombus gibberulus	0.4 ± 0.4
Malindi North Reef	*Vasum ceramicum*	6.7 ± 3.2	*Morula granulata*	12.6 ± 9.2	*Ovula ovum*	3.5 ± 1.8
	Latirolagena smaragdula	5.7 ± 1.2	*Cypraea annulus*	6.5 ± 3.1	*Vasum turbinellus*	2.3 ± 1.0
	Conus rattus	3.0 ± 1.5	*Thais tuberosa*	6.3 ± 2.0	*Coralliophila violacea*	2.2 ± 1.4
	Vasum turbinellus	3.0 ± 1.0	*Conus lividus*	6.3 ± 2.9	*Lambis chiragra*	2.2 ± 0.7
	Thais tuberosa	1.3 ± 0.3	*Vasum turbinellus*	4.4 ± 2.2	*Lambis truncata*	2.2 ± 1.8
	Cypraea lynx	1.3 ± 0.7	*Conus fulgetrum*	2.6 ± 0.3	*Lambis lambis*	1.8 ± 0.9
	Conus flavidus	1.0 ± 0.6	*Morula marginatra*	2.3 ± 0.9	*Vasum ceramicum*	1.5 ± 0.8
	Conus musicus	1.0 ± 1.0	*Conus ebraeus*	2.0 ± 0.6	*Conus rattus*	0.8 ± 0.5
	Turbo marmoratus	1.0 ± 1.0	*Conus musicus*	1.9 ± 0.5	*Trochus mauritianus*	0.8 ± 0.3
	Bursa bufonia	0.7 ± 0.7	*Conus rattus*	1.7 ± 1.7	*Cerithium nodulosum*	0.5 ± 0.5
					Cypraea tigris	0.5 ± 0.2
Malindi Fringing Reef	*Cypraea annulus*	19.3 ± 4.7	*Cerithium caeruleum*	19.3 ± 16.0		
	Strombus mutabilis	5.0 ± 3.3	*Pyrene scripta*	11.7 ± 8.0		
	Pyrene scripta	4.0 ± 4.0	*Cypraea annulus*	10.0 ± 5.0		
	Morula marginatra	3.5 ± 3.5	*Nerita albicilla*	9.0 ± 7.3		
	Conus lividus	3.3 ± 0.8	*Conus ebraeus*	6.0 ± 2.5		
	Thais savignyi	2.3 ± 1.1	*Morula marginatra*	6.0 ± 5.5		
	Morula ochrostoma	1.8 ± 1.0	*Strombus gibberulus*	5.0 ± 4.5		
	Thais tuberosa	1.5 ± 0.7	*Strombus mutabilis*	5.0 ± 3.2		
	Conus arenatus	1.0 ± 0.7	*Cypraea tigris*	3.0 ± 3.0		
	Conus coronatus	1.0 ± 0.6	*Conus lividus*	2.3 ± 1.3		
Ras Tenewi			*Vasum turbinellus*	10.0	*Vasum turbinellus*	3.8 ± 2.6
			Morula marginatra	5.0	*Peristernia forskali*	1.5 ± 1.0
			Morula granulata	3.0	*Vasum ceramicum*	0.8 ± 0.5
			Turbo brunneus	2.0	*Lambis lambis*	0.5 ± 0.2
			Nerita albicilla	1.0	*Conus lividus*	0.5 ± 0.2
			Conus tessulatus	1.0	*Pleuroploca filamentosa*	0.5 ± 0.2
			Cypraea helvola	1.0	*Ovula ovum*	0.3 ± 0.2
			Drupa lobata	1.0	*Pleuroploca trapezium*	0.3 ± 0.3
Zinyika					*Morula granulata*	7.5 ± 7.5
					Latirolagena smaragdula	6.0 ± 5.0
					Vasum turbinellus	5.0 ± 5.0
					Drupa morum	3.5 ± 3.5
					Vasum ceramicum	1.5 ± 0.5
					Turbo marmoratus	1.0 ± 1.0
					Conus musicus	1.0 ± 1.0
					Lambis crocata	1.0 ± 1.0
					Cypraea tigris	0.5 ± 0.5
					Conus rattus	0.5 ± 0.5
Pate			*Cypraea tigris*	5.8 ± 2.0	*Drupella ochrostoma*	5.3 ± 2.6
			Strombus gibberulus	3.5 ± 2.3	*Coraliophila violacea*	2.3 ± 1.5
			Nerita albicilla	2.8 ± 2.8	*Vasum turbinellus*	1.7 ± 0.7
			Conus ebraeus	2.0 ± 1.8	*Conus vexillum*	1.3 ± 0.9
			Morula marginatra	1.7 ± 1.5	*Cypraea tigris*	0.7 ± 0.7
			Vasum turbinellus	1.5 ± 0.8	*Drupa ricinus*	0.7 ± 0.3
			Engina mendicaria	1.3 ± 1.3	*Drupa rubusidaeus*	0.3 ± 0.3
			Conus flavidus	1.3 ± 1.0	*Conus rattus*	0.3 ± 0.3
			Morula granulata	0.8 ± 0.8	*Morula uva*	0.3 ± 0.3
			Lambis lambis	0.5 ± 0.3	*Bursa lampas*	0.3 ± 0.3
			Cypraea annulus	0.5 ± 0.3		

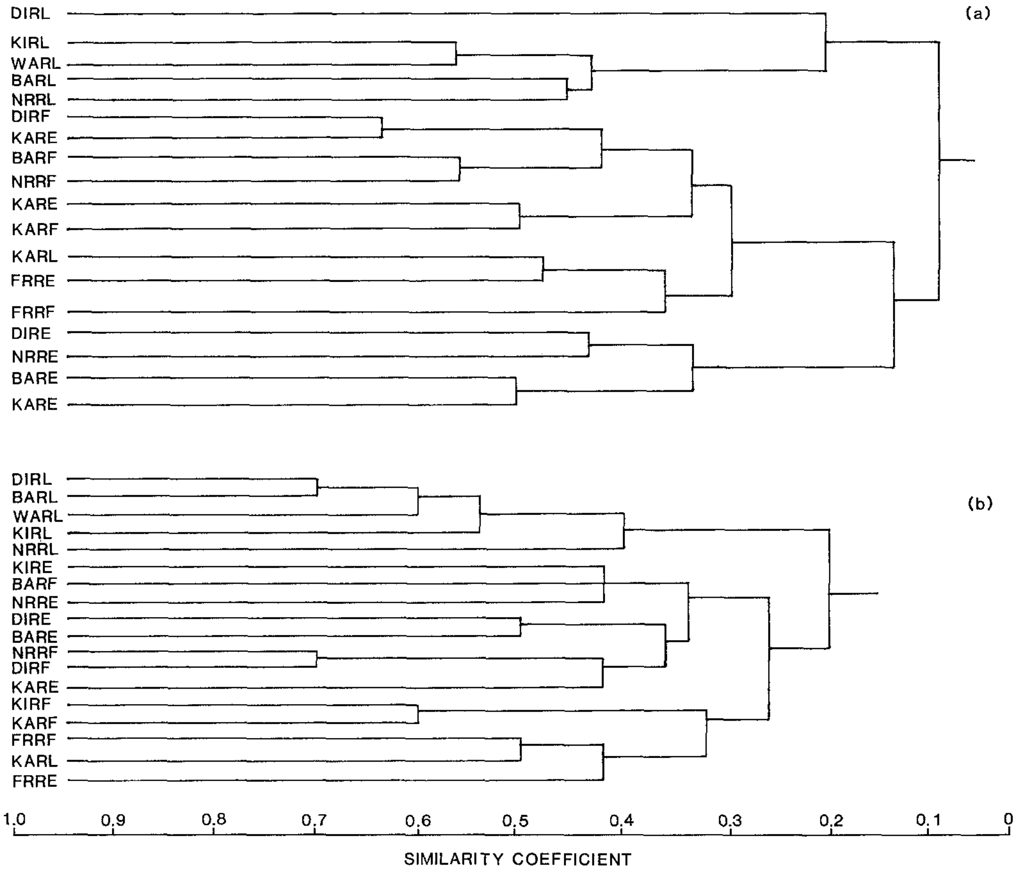

Fig. 2. Cluster analysis of selected southern Kenyan reefs combining reef locations and using **a** the Bray and Curtis (1957) measure of similarity and **b** Sorensen's Index based on the ten most common gastropod species. First two letters of the abbreviation indicate the location (see Table 1) and the last two indicate the division (site) within the reef, where RE = reef edge, RF = reef flat and RL = reef lagoon

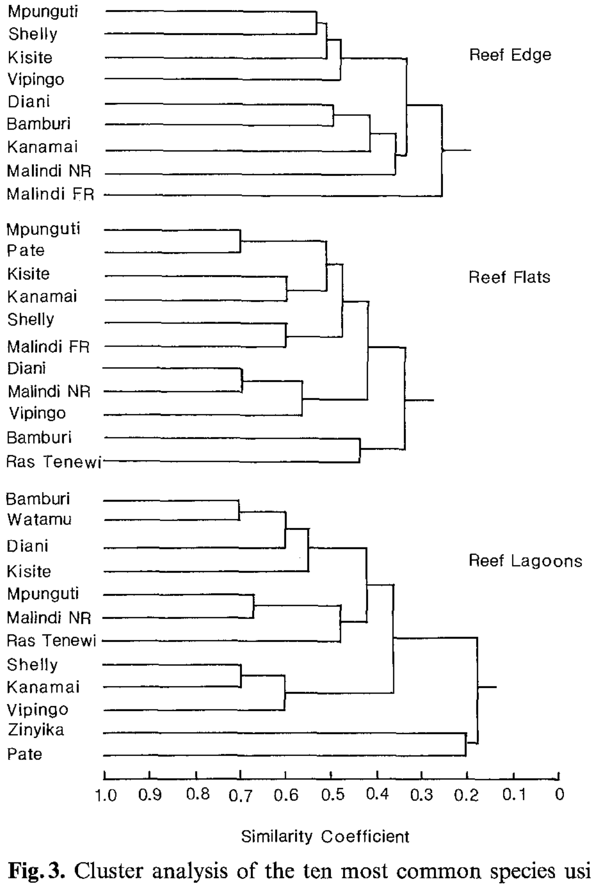

Fig. 3. Cluster analysis of the ten most common species using the Sorensen Index for comparisons of sites within reef locations

This suggests that most of the shallow-water noncryptic reef fauna was sampled. Additional sampling techniques (i.e. dredging) will probably produce additional species. Increased sampling within each reef location is likely to produce additional species but new species will probably be members of the total species pool rather than new Kenyan coral reef species.

Species richness is a function of the scale of observation and gastropod density. High z values within lagoons indicate that species richness can be highest within lagoons but this is clearly dependent on the total lagoonal area as lagoonal prosobranch population densities are low. Overall, density was inversely related with z ($y = 0.70 - 0.002x$, $r = 0.65$, $P < 0.01$) and positively with C values ($y = 2.65x^{0.37}$, $r = 0.83$, $P < 0.001$). With the exception of reef edges, these relationships were consistent for reef locations. Combining sites and comparing reef locations on a species-time basis indicates lower species richness for reef lagoons (t = test, $P < 0.01$) than reef flats and edges at the large scale (Fig. 4). Species-individual relationships (Fig. 4) suggest close similarities between locations despite differences in the equation's constants. Constants indicate that reef lagoons are more species rich when fewer individuals are sampled (t-test on C, $P < 0.01$), but reef flats are most diverse for large samples (t-test on z, $P < 0.01$). Zinyika, Ras Tenewi and Pate have the highest within site z values, but their small size and low densities suggests that they are the least species rich sites. Conversely, the southern fringing reef is broad, large and continuous and consequently should have a high species rich-

Table 4. Species richness parameters determined by regressing data to the equation $S = Ct^z$ where S is the number of species after time t, C the number of species found after 1 h and z a unitless constant which indicates the slope of the curve. The r value for each regression is included, and total site averages ($x \pm$ SEM) and a Kruskal-Wallis test of significance

Location	Reef edge	Reef flat	Reef lagoon
Kisite	C=19.43	15.31	6.82
	z = 0.61	0.42	0.67
	r = 0.99	0.99	0.99
Mpunguti	C=15.39	17.17	8.33
	z = 0.46	0.34	0.58
	r = 0.99	0.99	0.99
Diani	C=11.45	12.55	9.58
	z = 0.56	0.61	0.52
	r = 1.00	0.99	0.98
Shelly	C=18.88	16.54	10.84
	z = 0.62	0.47	0.58
	r = 1.00	0.99	0.99
Bamburi	C= 8.85	17.81	6.94
	z = 0.78	0.65	0.64
	r = 0.96	0.99	1.00
Kanamai	C=10.80	14.69	11.25
	z = 0.51	0.55	0.59
	r = 1.00	0.99	1.00
Vipingo	C=10.03	14.36	13.35
	z = 0.24	0.52	0.45
	r = 0.99	1.00	0.99
Watamu	C= –	–	6.99
	z = –	–	0.68
	r = –	–	0.99
Malindi North Reef	C=13.87	16.54	7.92
	z = 0.59	0.48	0.65
	r = 1.00	0.96	1.00
Malindi Fringing Reef	C=14.38	16.04	–
	z = 0.59	0.62	–
	r = 1.00	1.00	–
Ras Tenewi	C= –	–	5.33
	z = –	–	0.82
	r = –	–	0.95
Zinyika	C= –	–	8.33
	z = –	–	0.80
	r = –	–	0.99
Pate	C= –	7.65	6.44
	z = –	0.99	0.98
Total	C=13.68±1.26	14.87±0.94	8.51±0.67*
	z = 0.55±0.05	0.53±0.03	0.64±0.03**

* $P < 0.0005$

** $P < 0.07$, Mann-Whitney U-test between reef flat and lagoon $P < 0.02$

ness when considering the whole reef. The Park areas of Kisite, Mpunguti wa Juu and Malindi's North Reef, although larger than rock islands of northern Kenya, are small and species richness may be limited by the area of these reefs.

Reef lagoons were the only location with significant community structure differences between protected and unprotected reefs (Table 6). Unprotected reef flats had higher, although short of statistically different, z values than protected reefs. Unprotected reef flats are larger and, therefore, have greater species richness than protected reef flats. Unprotected reef lagoons had higher prosobranch population densities and lower diversity than protected lagoons. There was no statistical difference between protected and unprotected reef lagoons for z values comparisons. Removing the unprotected northern Kenya sites from the data analysis, in order to compare only the southern reefs, results in an average unprotected reef lagoon z value of 0.56±0.07 (±SD). This is significantly lower than protected southern reef lagoons (t-test, $P < 0.05$). Nonetheless, the toal area and C values (species/h) of protected reefs are smaller than unprotected reefs and therefore total species richness is greater outside protected reefs.

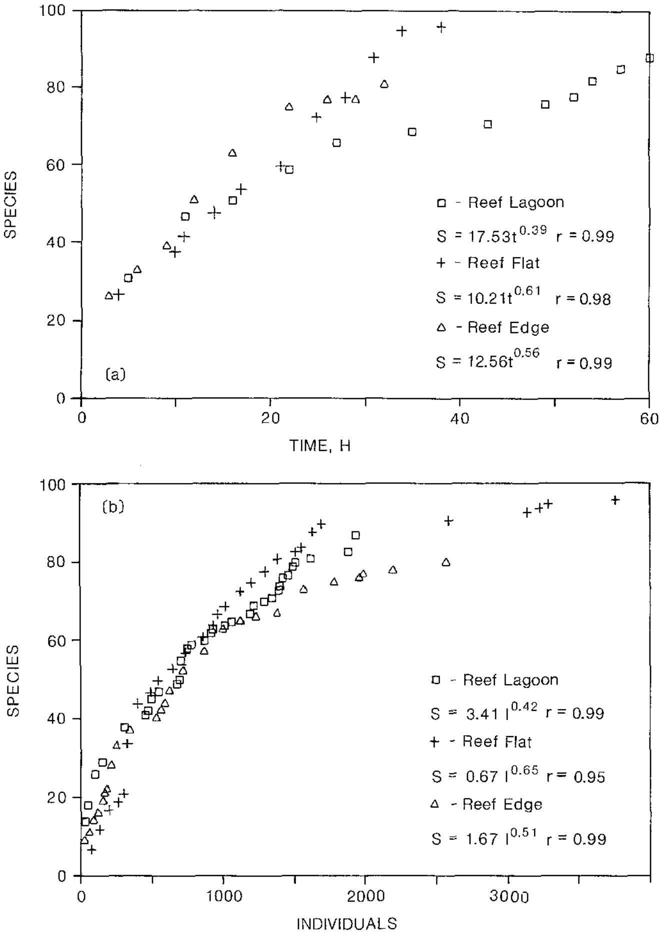

Fig. 4. Species richness determined by **a** species-time and **b** species-individual relationships for the gastropod fauna within the three reef locations (i.e. reef edges, flats and lagoons). Best-fit equations included

Population density comparisons of 30 commercially important species indicate significantly denser populations ($P < 0.05$) for 2 species of strombids, *Lambis chiragra* and *L. truncata*, in protected compared to unprotected reefs (Table 7). Two species, *Ovula ovum* and *Cypraea moneta*, were denser in Parks at the $P < 0.10$ level. Densities of these commercial species were, in general, very low regardless of the reef category.

Prosobranch density was negatively correlated with Balistidae and total fish densities (Fig. 6) in southern

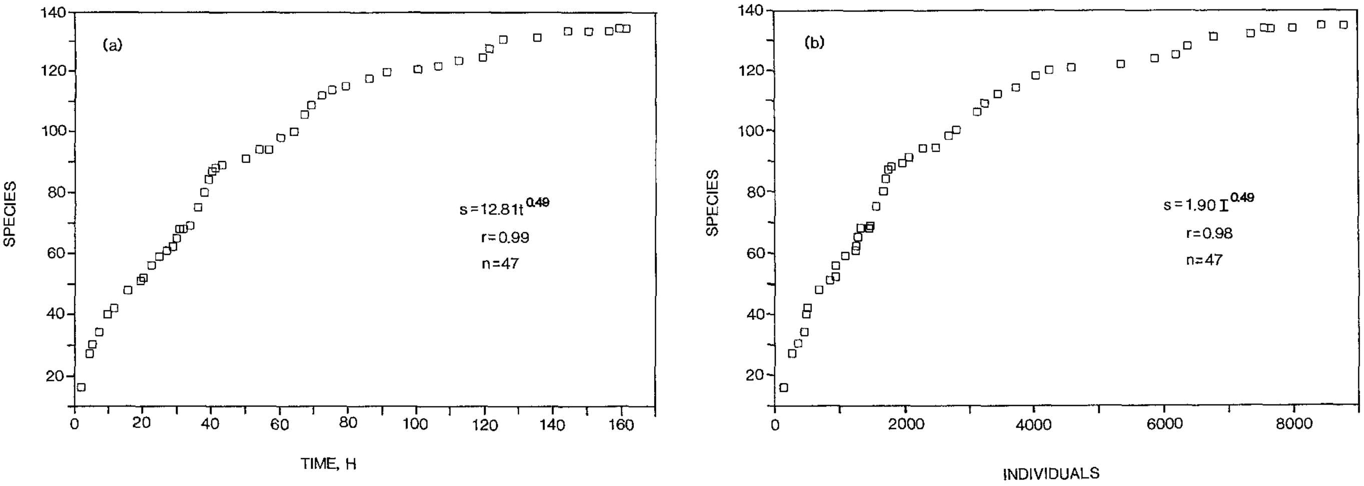

Fig. 5. Species richness expressed as **a** species-time and **b** species-individual relationships for the total Kenyan gastropod fauna combining all reef locations. Best-fit equation included

Table 5. Correlation matrix presenting the correlation coefficient, level of significance and model for correlations between the variables of the species-time relationship (C and z of the equation $S = Ct^z$), diversity (D) and density #/h) within the 3 reef locations. The best-fit of four models (1: $y = a + bx$ 2: $y = ae^{bx}$ 3: $y = a + b\log x$ 4: $y = ax^b$) and r presented. r given for the straight-line correlation if all models insignificant or the best-fit model if significant

	Reef edge			Reef flat			Reef lagoon		
	C	*z*	*D*	*C*	*z*	*D*	*C*	*z*	*D*
z	$r=0.25$			−0.34			−0.82		
	$P=$NS			NS			***		
	Model=						2		
D	$r=0.48$	0.20		0.11	0.11		−0.63	0.67	
	$P=$NS	NS		NS	NS		*	*	
	Model=						1	4	
#/h	$r=0.39$	−0.43	−0.38	0.75	−0.68	−0.40	0.90	−0.73	−0.85
	$P=$NS	NS	NS	*	*	NS	***	**	***
	Model=			4	4		4	4	1

* $P<0.05$; 0** $P<0.01$; *** $P<0.001$

Table 6. Comparisons of density ($x \pm$SEM), diversity and z (from the species-time equations $S = Ct^z$) between protected and unprotected reef locations and totals. t-test comparison between means included. NS = not significant. Protected sites include Kisite, Mpunguti, Watamu and Malindi. All other sites are unprotected

Site	Parameters	Protected	Unprotected	*t*-test
Reef edge	Density, #/h	68.0 ±19.1	76.6 ±16.8	NS
	Diversity, *D*	0.85± 0.03	0.80± 0.04	NS
	z	0.56± 0.03	0.54± 0.09	NS
	Sites, *n*	4	5	
Reef flat	Density, #/h	109.4 ±23.7	79.3 ±15.3	NS
	Diversity, *D*	0.87± 0.03	0.85± 0.02	NS
	z	0.47± 0.06	0.57± 0.03	$P<0.06$
	Sites, *n*	4	6	
Reef lagoon	Density, #/h	14.8 ± 1.1	45.8 ±11.3	$P<0.02$
	Diversity, *D*	0.88± 0.03	0.72± 0.06	$P<0.05$
	z	0.65± 0.05	0.64± 0.05	NS
	Sites, *n*	4	8	
Reef total	Density, #/h	64.0 ±14.8	64.5 ± 8.5	NS
	Diversity, *D*	0.87± 0.01	0.78± 0.03	$P<0.02$
	z	0.56± 0.03	0.59± 0.03	NS
	Sites, *n*	12	19	

Kenya's reef lagoons but not with other invertebrate-eating finfish predator families. There was no significant relationship between the mollusc-eating gastropod *Pleuroploca trapezium* and prosobranch population density. The commonly observed Balistidae were *Balistaphus undulatus* (Mungo Park) and *Rhinecanthus aculeatus* (L.). Gastropod and sea urchin population densities were strongly and positively associated (Fig. 7). The population of *Strombus gibberulus* in Vipingo was not included in the correlation. During two of the three Vipingo samples no *S. gibberulus* were found, but in one hour in one section of the reef >150 individuals were encountered. Consequently, their exclusion from this data analysis seems justified.

Discussion

Kenya's coral reef-associated gastropod fauna is similar to assemblages reported from other areas within the western Indian Ocean (Taylor 1971). Many Kenyan species are typical of the larger Indo-Pacific fauna with some species typical of the Indian Ocean Region. With the ex-

Table 7. Densities (#/h, $x \pm$SEM) of commonly collected ornamental gastropods within protected and unprotected reefs within each reef location and for all (total) reef locations. Site totals included only if individuals were commonly found in more than one reef location and sums only those locations where species were commonly (i.e. >2 individuals/location) encountered. Mann-Whitney *U*-test comparison included for individual sites or site totals dependent on the distribution of the species. NS = not significant

Species	Protected				Unprotected				
	Reef edge	Reef flat	Reef lagoon	Total	Reef edge	Reef flat	Reef lagoon	Total	
	17 h	14 h	25 h		15 h	24 h	33 h		
Turbo marmoratus	0.18 ± 0.18	0	0	0.07 ± 0.07	0.20 ±0.14	0	0.09 ±0.05	0.13 ±0.06	NS
Lambis chiragra	0	0.04 ± 0.04	2.08 ±0.71	2.08 ± 0.71	0	0	0	0	***
L. crocata	0	0	0.06 ±0.06		0	0.04 ±0.04	0.12 ±0.08		NS
L. digitata	0.12 ± 0.08	0	0.08 ±0.05	0.10 ± 0.05	0	0	0		NS
L. lambis	0.06 ± 0.06	0.14 ± 0.14	1.0 ±0.29	0.69 ± 0.29	0.06 ±0.06	0.79 ±0.23	0.40 ±0.16	0.57 ±0.14	NS
L. scorpius	0	0	0.48 ±0.28	0.48 ± 0.28	0	0	0	0	NS
L. truncata	0	0	1.28 ±0.48	1.28 ± 0.48	0	0.04 ±0.04	0.03 ±0.03		**
Strombus lentiginosus	0	0	0.20 ±0.08		0	0.08 ±0.08	0.28 ±0.11		NS
Cypraea annulus	15.7 ± 3.98	21.97 ± 5.51	0.16 0.09	10.33 ± 2.19	1.96 ±1.38	9.63 ±2.83	7.94 ±3.23	7.25 ±1.79	NS
C. caput-serpentis	0.47 ± 0.24	0	0		0.13 ±0.09	0.05 ±0.05	0		NS
C carneola	0.47 ± 0.21	0.07 ± 0.07	0		0	0.21 ±0.08	0.06 ±0.04		NS
C. isabella	0.29 ± 0.14	0	0		0	0.21 ±0.10	0		NS
C. lynx	4.05 ± 1.38	0.42 ± 0.43	0	1.48 ± 0.52	0.20 ±0.11	1.50 ±0.78	0.06 ±0.04	0.57 ±0.27	NS
C. moneta	0.71 ± 0.35	0.71 ± 0.27	0	0.71 ± 0.23	0.61 ±0.33	0.04 ±0.04	0	0.26 ±0.13	*
C. tigris	0.47 ± 0.26	3.07 ± 1.18	0.36 ±0.11	1.07 ± 0.34	0.25 ±0.15	2.09 ±0.71	0.68 ±1.25	1.14 ±0.28	NS
Ovula ovum	0	0.04 ± 0.04	0.88 ±0.49	0.88 ± 0.49	0	0.04 ±0.04	0.06 ±0.04	0.04 ±0.02	*
Cypraecassis rufa	0	0	0.05 ±0.05		0.13 ±0.09	0.08 0.06	0.01 ±0.01	0.06 ±0.03	NS
Charonia tritonis	0	0	0.04 ±0.04		0	0	0		NS
Bursa bufo	0.12 ± 0.12	0	0		0.46 ±0.32	0.04 ±0.04	0.03 ±0.03	0.13 ±0.07	NS
B. lampas	0	0	0.24 ±0.10		0	0	0.11 ±0.06		NS
Chicoreus ramosus	0	0	0.04 ±0.04		0	0.04 ±0.04	0.13 ±0.07		NS
Pleuroploca filamentosa	0.41 ± 0.21	0	0		0.06 ±0.06	0	0.09 ±0.05		NS
P. trapezium	0	0	0.60 ±0.16		0	0	0.95 ±0.25		NS
Mitra mitra	0	0	0.02 ±0.02		0	0.04 ±0.04	0.03 ±0.03		NS
Harpa amouretta	0	0.11 ± 0.08	0.02 ±0.02		0.07 ±0.07	0	0.13 ±0.07		NS
Conus leopardus	0	0.07 ± 0.07	0.04 ±0.04		0	0	0.35 ±0.19		NS
C. litteratus	0	0	0.13 ±0.08	0.08 ± 0.05	0	0.13 ±0.09	0.36 ±0.12		NS
C. miles	0.88 ± 0.31	0.14 ± 0.10	0.08 ±0.06	0.34 ± 0.11	0.36 ±0.14	0.42 ±0.30	0.05 ±0.03	0.24 ±0.11	NS
C. textile	0.06	0	0		0	0	0		NS
C. virgo	0	0.07 ± 0.07	0.16 ±0.07		0	0	0.15 ±0.10		NS

* $P < 0.10$; ** $P < 0.01$; *** $P < 0.0001$

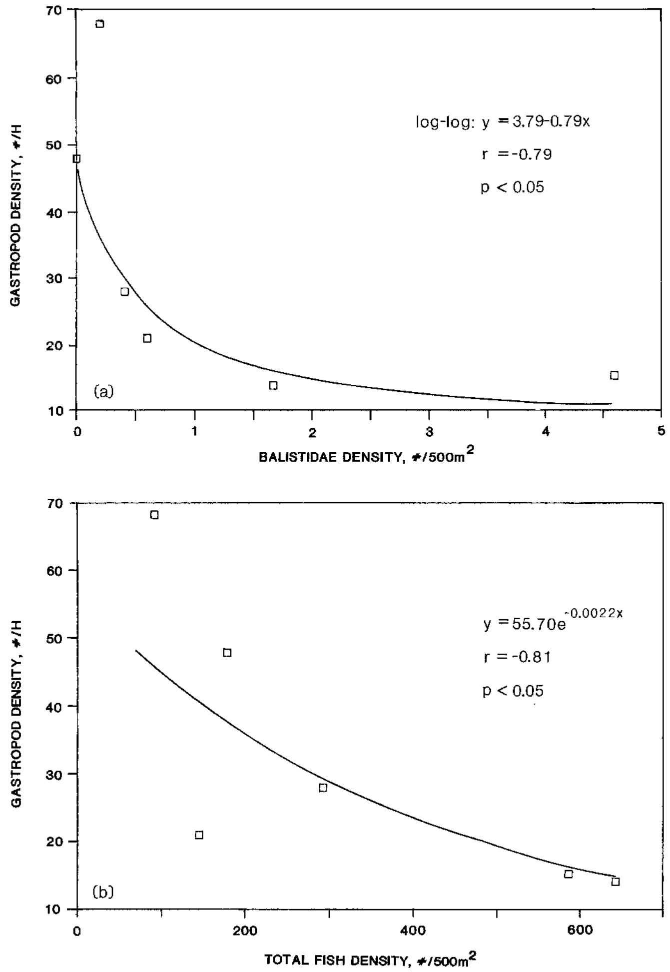

Fig. 6. Relationship between the total gastropod density and **a** Balistidae (triggerfish) density and **b** total fish density within six southern Kenyan reef lagoons. Regression excludes the population of *Strombus gibberulus* within Vipingo (see text)

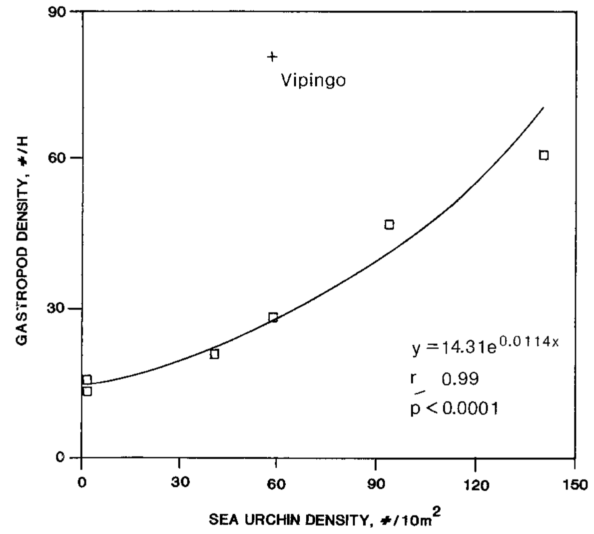

Fig. 7. Relationship between the total sea urchin density and gastropod density within six southern Kenyan reef lagoons. Sea urchin density data from McClanahan and Shafir (in press). Regression excludes the population of *Strombus gibberulus* within Vipingo

ception of *Vasum rhinoceros*, found only in Kenya and Zanzibar, there is no evidence of endemism within Kenya. Crame (1986) suggests that the East African region's gastropod species richness has declined since the Pleistocene. He lists 170 species from 32 families for Pleistocene assemblages compared to 135 species from 25 families for this study. Using Crame's (1986) species per individual data for three biotypes (Acropora-dominated, Porites-dominated and the sand patch biotype) and comparing them to presentday species-individual relationships (Fig. 5 b) indicates a 45% species richness reduction since the Pleistocene. Species composition comparisons between modern and Pleistocene assemblages suggest that the genera have remained fairly constant but changes have occurred at the species level.

There is no evidence for subregional species associations in Kenya although areas of northern Kenya appear unique, simply by their low densities and lack of species composition similarity with other sites. This may result from the small size of reefs in this region. Small island size makes species more vulnerable to local extinctions (MacArthur and Wilson 1967) and offers less predator-free refuge. River discharge and associated seasonally high water column productivity (McClanahan 1988 a) are likely causes for the small reefs. Southern Kenya's reefs are exposed to smaller freshwater inputs and are part of the northern terminus of the low nutrient equatorial current which encounters land in central Tanzania.

Tanzanian gastropod studies (Spry 1968; Yaninek 1978) suggest greater species diversity in Tanzania than Kenya. Yaninek (1978) found 38 species among 240 individuals during a daytime survey of Maziwi Island. The Kenyan total species-individual curve (Fig. 5 b) predicts 27.8 individuals for 240 individuals. Spry (1968) lists over 350 Tanzanian gastropods but includes species from non-reef locations. Nonetheless, his list includes coral reef-associated species not yet found in Kenya. Both Tanzania and Kenya are more species rich than the temperate South African fauna (Richards 1984).

Within reefs, reef edges and flats did not differ greatly in species composition and failed to cluster into distinct associations. My a priori reason for distinguishing reef flat and edges was that reef edges are, in most instances, exposed to greater wave energy. Although cluster analysis did not produce distinct species associations, species lists indicate that some species such as *Latirolagena smaragdula, Turbo argyrostoma* and *Drupa morum* are restricted to edge sites whereas other species such as *Engina mendicaria, Peristernia forskali* and *Mitra chrysalis* are most frequently restricted to reef flats. There is a great deal of overlap and many species such as *Vasum rhinoceros, V. turbinellus* and *Conus fulgetrum* are ubiquitous and can be found in all reef locations. Species composition differences between reef locations may, in some instances, have been caused by unaccounted for differences in reef height or aspect which may have overridden the reef zone distinction. There appears to be a great deal of inherent variability in this assemblage, the causes of which are not entirely clear. This variability makes predictions about species and gastropod community structure based on reef locations tenuous.

Reef lagoons clustered into a distinct but variable association. Despite species composition differences, species richness and diversity were less pronounced between reef locations. For the whole Kenyan sample, species richness based on time indicated fewer species in lagoons but comparisons on a species per individual basis resulted in greater similarities between reef locations. Additionally, many common lagoon-inhabiting species have large adult body sizes compared to reef flat and edge species. Reef lagoon environments expose gastropods (McClanahan 1989) and other invertebrates (McClanahan and Muthiga 1989) to greater predation pressure than reef flats. Larger adult body sizes of some lagoon-inhabting gastropods, may be a form of predatory escape (Connell 1972, McClanahan 1988b; McClanahan and Muthiga 1989). Lower reef lagoon population densities are also attributable to predation intensity. Yet, even on reef flats, which have higher densities and greater possibilities for predator refuge, population densities are low and intra and interspecific competition rarely occurs (Leviten and Kohn 1980; Reichelt 1982).

Data presented here on the relationship between fish and prosobranch population densities combined with McClanahan's (1989) predation experiment suggest that, although predation on prosobranchs may be relatively low (i.e. in comparison to exposed sea urchins), fish predators, particularly triggerfish, appear to be important controllers of prosobranch density and distribution patterns. McClanahan and Muthiga (1989) also emphasize the importance of balistids in regulating sea urchin populations. These two studies combined, strongly suggest that some balistids, particularly *B. undulatus* and *R. aculeatus*, are important invertebrate-eating predators. The strong relationship between sea urchins and prosobranchs is probably due to a co-occuring ecological release from predators rather than a direct causal relationship between sea urchins and gastropods (McClanahan 1989).

It is clear that fishing activities can indirectly affect gastropod densities by reducing their predators. Predator reduction affects density, but it may also affect species composition as fished and unfished reef lagoons generally clustered differently and species diversity was reduced within some heavily fished reefs. Species diversity reductions are due to increased densities of one or a few species rather than species losses. Species with elevated densities were not consistent between reefs. Presumably population increases are due to ecological release from predators but it is not clear why different species respond on different reefs. I have emphasized the importance of predation but this may be only one dominant control on prosobranch populations. Until species life histories and population dynamics are understood within an ecosystem context many of these anomalies will not be understood.

Shell collection appears to be affecting only a few shallow-water gastropods, particularly some of the large strombids. Catterall and Poiner (1987) suggest that species which remain exposed during their development and require long periods before sexual maturity will be most susceptible to population reductions through shell collection. Large adult sizes of *Lambis truncata* and *L. chiragra* suggest slow sexual development and would, therefore, fit within this category. Still, many species which fit these 2 criteria appear unaffected by shell collection pressure. Why are there so few population density differences between protected and unprotected reefs when shell collecting remains a potential limitation on prosobranch populations? Some reasons are given by McClanahan (1989), but here I present a more general model (Fig. 8). I suggest that the survival of recruiting gastropod cohorts are different on heavily fished and unfished reefs. Early differences in post-settlement mortality may have a greater inertial effect on populations than shell collecting which acts later in the individual's development. To experimentally test this hypothesis remains difficult as age-dependent mortality rates need to be measured for four replicated treatments. This is unlikely to occur within the real world of coral reef management but might lend itself to population modelling if life-history variables such as age and size-dependent recruitment rates, growth and mortality are known. Additionally, the effect of fishing on the invertebrate predator guild may rely on fish preferences of fishermen. Regions where fishermen avoid balistids may not experience invertebrate community composition changes that have occurred on Kenyan reefs.

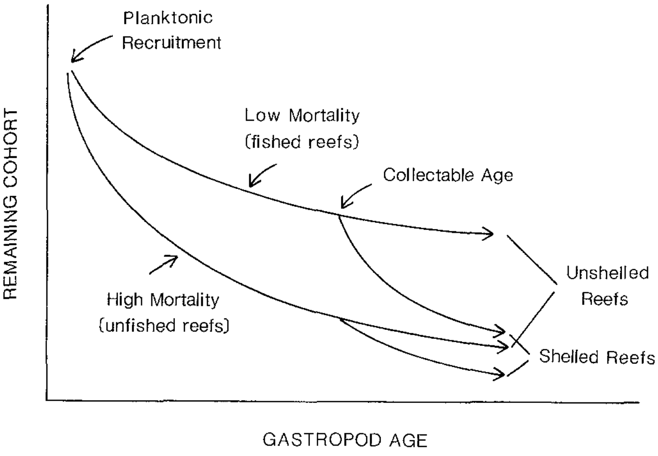

Fig. 8. Hypothetical model of the effect of shell collecting on the number of surviving gastropods within a recruiting cohort. Model shows the number of gastropods remaining as a function of age within unfished reefs with an abundance of gastropod predators and fished reefs where predators have been reduced. The effect of shell collection on survival is added when individuals reach a collectable size

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References

Abbott RT, Dance SP (1986) Compendium of seashells. American Malacologist, Melbourne, Fla

Brakel WH (1982) Tidal patterns on the East African coast and their implications for the littoral biota. Proc Symp Coastal Mar Envir Red Sea, Gulf Aden Trop West Indian Ocean 2:403–418

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Catterall CP, Poiner IR (1987) The potential impact of human gathering on shellfish populations, with reference to some NE Australian intertidal flats. Oikos 50:114–122

Connell JH (1972) Community interactions on marine rocky intertidal shores. Ann Rev Ecol Syst 31:169–192

Crame AJ (1986) Late Pleistocene molluscan assemblages from the coral reefs of the Kenyan coast. Coral Reefs 4:183–196

Dance SP (1974) The encyclopedia of shells. Blanford Press, London

Endean R (1973) Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. Biol Geol Coral Reefs 3:389–438

Evans SM, Knowles G, Pye-Smith C, Scott R (1977) Conserving shells in Kenya. Oryx 13:480–485

Hamilton HGH, Brakel WH (1984) Structure and coral fauna of East African reefs. Bull Mar Sci 34:248–266

Khamala CPM (1971) Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diani Beach, Kenya. Mar Biol 2:167–172

Kenya Tide Table (1987) Tide tables for East African ports. Rodwell, Mombasa, Kenya

Kohn AJ (1968) Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology 49:1046–1062

Knowles G (1970) Shell-collecting in Kenya. Report of the University of Newcastle-upon-Tyne Exploration Society's Expedition to Kenya. University of Newcastle-upon-Tyne, New Castle-upon-Tyne

Leviten PJ, Kohn AJ (1980) Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. Ecol Monogr 50:55–75

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

McClanahan TR (1988a) Seasonality in East Africa's coastal waters. Mar Ecol Prog Ser 44:191–199

McClanahan TR (1988b) Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. Oecologia Berlin 77:210–218

McClanahan TR (1989) Kenyan coral reef-associated gastropod fauna: a comparison between protected and unprotected reefs. Mar Ecol Prog Ser 53:11–20

McClanahan TR, Muthiga NA (1988) Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia 166:269–276

McClanahan TR, Shafir SH (in press) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia Berlin

McClanahan TR, Muthiga NA (1989) Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. J Exp Mar Biol Ecol 126:77–94

NEHSS (1984) Kwale district assessment report. Ministry of Environment and Natural Resources, Nairobi, Kenya

Oliver APH (1975) The shells of the world. Country Life Books, Middlesex, England

Reichelt RE (1982) Space: A non-limiting resource in the niches of some abundant coral reef gastropods. Coral Reefs 1:3–11

Richards D (1984) South African shells: a collectors guide. Struik, Cape Town, South Africa

Simpson EH (1949) Measurements of diversity. Nature 163:688

Sorensen T (1948) A method of establishing groups of equal amplitude in plant society based on similarity of species content. K Danske Vidensk Selsk 5:1–34

Spry JF (1968) The seashells of Dar es Salaam: 1 gastropods. Tanzania Society, Dar es Salaam, Tanzania

Taylor JD (1971) Reef associated molluscan assemblages in the western Indian Ocean. Symp Zool Soc London 28:501–534

Villanoy CL, Juinio AR, Meñez LA (1988) Fishing mortality rates of giant clams (Family Tridacnidae) from the Sulu Archipelago and Southern Palawan, Philippines. Coral Reefs 7:1–5

Wells SM (1981) International trade in ornamental corals and shells. Proc 4th Int Coral Reef Symp 1:323–330

Wells SM, Pyle RM, Collins NM (1983) The IUCN red data book. IUCN, Gland, Switzerland

Yaninek JS (1978) A comparitive survey of reef-associated gastropods at Maziwi Island, Tanzania. J E A Nat Hist Soc Nat Mus 31:1–16

Appendix

List of families and species encountered during the survey

Haliotidae: *Haliotis* sp.

Trochidae: *Clanculus puniceus* (Philippi), *Tectus dentatus* Forskal, *Trochus erythraeus*, *T. maculatus* L., *T. mauritianus* Gmelin, *T. tentorium* Gmelin

Turbinidae: *Turbo argyrostomus* L., *T. brunneus* (Roding), *T. marmoratus* L.

Neritidae: *Nerita albicilla* L., *N. undata* L.

Littorinidae: *Littorina kraussi* Rosewater

Cerithiidae: *Cerithium alveolus* Hombron and Jaquinot, *C. caeruleum* Sowerby, *C. columna* Sowerby, *C. echinatum* Lamarck, *C. nodulosum* (Bruguiere), *Rhinoclavis sinensis* (Gmelin)

Strombidae: *Lambis chiragra* Roding, *L. crocata (Link)*, *L. digitata* (Perry), *L. truncata* (Humphrey), *L. lambis* L., *L. scorpius* L., *Strombus aurisdianae* L., *S. decorus* (Roding), *S. gibberulus* L., *S. lentiginosus* L., *S. mutabilis* Swainson

Cypraeidae: *Cypraea annulus* L., *C. asellus* L., *C. caputserpentis* L., *C. carneola* L., *C. caurica* L., *C. chinensis* Gmelin, *C. erosa* L., *C. felina* Gmelin, *C. helvola* L., *C. histrio* Gmelin, *C. isabella* L., *C. lynx L.*, *C. moneta* L., *C. tigris* L., *C. vitellus* L.

Ovulidae: *Ovula ovum* (L.)

Naticidae: *Natica marochiensis* L.

Cassidae: *Cypraecassis rufa* (L.)

Cymatiidae: *Charonia tritonis* (L.), *Cymatium aquatile* (Reeve), *C. gemmatum* (Reeve), *C. muricinum* (Roding), *C. parthenopeum* (von Salis), *Cymatium* sp., *Distorsio anus* (L.), *Gyrineum gyrinum* (L.), *Gyrineum pusillum* (Broderip)

Bursidae: *Bursa bufonia* (Gmelin), *B. granularis* (Roding), *B. lampas*, L., *B. livida*, *B. rhodostoma* (Sowerby), *B. rosa* (Perry), *B. rugosa*

Muricidae: *Chicoreus ramosus* (L.)

Thaididae: *Drupa albolabris* Blainville, *D. lobata* (Blainville), *D. morum* Roding, *D. ricinus* (L.), *D. rubusidaeus* Roding, *Drupella cornus* (Roding), *D. ochrostoma* Blainville, *Morula cavernosa* Reeve, *M. granulata* (Duclos), *M. iostoma* (Reeve), *M. marginatra* (Blainville), *M. spinosa* (H&A Adams), *M. uva* (Roding), *Nassa francolina* (Bruguiere), *Purpura panama* Roding, *Thais alouina* (Roding), *T. blanfordi* (Melvill), *T. echinulata* Lamarck, *T. savignyi* (Deshayes), *T. tuberosa* (Roding), *Thais* sp.

Coralliophilidae: *Coralliophila costularis* Lamarck, *C. violacea* (Kiener)

Columbellidae: *Pyrene flava* (Bruguiere), *P. scripta* Lamarck, *P. testudinaria* (Link)

Buccinidae: *Cantharus* sp., *Engina mendicaria* L.

Fasciolariidae: *Fusinus colus* L., *L. polygonus* (Gmelin), *Latirolagena smaragdula* (L.), *Peristernia forskali* (Tapparone-Canefri), *Pleuroploca filamentosa* (Roding), *P. trapezium* (L.)

Nassariidae: *Nassarius arcularis* (L.), *N. margaritiferus* Dunker

Vasidae: *Vasum ceramicum* L., *V. rhinoceros* (Gmelin), *V. turbinellus* (L.)

Mitridae: *Mitra chrysalis*, *M. mitra* (L.), *M. stictica* (Link)

Harpidae: *Harpa amouretta* Roding

Conidae: *Conus arenatus* Hwass, *C. betulinus* L., *C. chaldeus* (Roding), *C. coronatus* Gmelin, *C. ebraeus* L., *C. flavidus* Lamarck, *C. fulgetrum* Sowerby, *C. generalis* L., *C. imperialis* L., *C. leopardus* (Roding), *C. litoglyphus* Hwass, *C. litteratus* L., *C. lividus* Hwass, *C. marmoreus* Lamarck, *C. miles* L., *C. miliaris* Hwass, *C. musicus* Hwass, *C. planorbis* Born, *C. rattus* Hwass, *C. striatellus* Link, *C. tessulatus* Born, *C. textile* L., *C. vexillum*, *C. virgo* L., *Conus* sp.

Terebridae: *T. areolata* (Link), *T. crenulata* L.