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PRIMARY RESEARCH PAPER

Species composition, comparative size and abundance of the genus *Littoraria* (Gastropoda: Littorinidae) from different mangrove strata along the East African coast

Paulo Torres · Avelino Alfiado · David Glassom ·
Narriman Jiddawi · Adriano Macia · David G. Reid ·
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Abstract Variation in the abundance, distribution and size of four species of mangrove littorinid gastropods (genus *Littoraria*) was investigated using a nested sampling design at different spatial scales along the East African coast, from Tanzania to South Africa. Littorinid abundance and diversity decreased abruptly south of Inhaca Island at the southern end of the study area. All species presented a large-scale spatial variation in abundance, with *L. subvittata* showing the greatest abundance while *L. intermedia* was rare. *Littoraria scabra* and *L. intermedia* were found mainly at the seaward edge of the forests. *Littoraria subvittata* increased in abundance in the middle of the forest and towards the landward side. *Littoraria pallescens* occurred mainly at the seaward edge and in the middle areas in the *Rhizophora* zone. These small-scale variations show contrasting specific distribution patterns within the mangrove, likely reflecting different tolerances to physical factors and biological interactions. All species appeared decreased in shell height from north to south. *Littoraria scabra* was always significantly larger than other species at all mangrove study sites.

Keywords Spatial distribution · Size composition · *Littoraria* · Mangrove · East Africa

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Introduction

Gastropods play a vital role at the detrital interface in a variety of wetland systems, as many consume living and decaying plant material. Littorinids are small and abundant herbivorous gastropods commonly found in intertidal habitats around the world (Reid, 1989, 1996). They are most species-rich in the tropical Indo-West Pacific, where they constitute an important component of mangrove and rocky shore communities (Reid, 1986, 2007). Mangroves of the Indo-Pacific region harbour a varied and usually abundant fauna of littorinids, most belonging to the genus *Littoraria*.

This genus includes 39 littorinid species and its taxonomy, geographical distribution, and anatomy have been described by Reid (1986, 1989, 1999, 2001) and Stuckey & Reid (2002). Its members are mainly tropical in distribution, and although some of the species occur in the intertidal zone of rocky shores, the majority can be found in association with mangroves, wood and salt-marsh vegetation (Reid, 1986).

The mangrove periwinkles spend all of their adult lives on stems, prop roots and leaves of the trees, often above the regular reach of the tide, and adaptive variation in shell morphology (Reid, 1992) and colour (Reid, 1986) allow several species to exploit different environments. This variation might be under either ecophenotypic or genetic control (Janson, 1985; Cook & Garbett, 1992; McQuaid, 1996; Merkt & Ellison, 1998). *Littoraria* species exhibit vertical and horizontal distribution patterns through the mangroves (Reid, 1985; Ohgaki, 1992), showing behavioural and reproductive specializations, including vertical migration (Reid, 1984; Yipp, 1985; Ohgaki, 1992), lunar spawning rhythms (Berry & Chew, 1973; Gallagher & Reid, 1974) and ovoviviparity (Reid, 1986, 1989). Several aspects of the biology of these species are correlated with their distribution patterns within the mangrove; these include migratory behaviour, reproduction, population dynamics, predation ecology and the form and coloration of the shell.

Numerous studies of distribution patterns of littorinids in mangrove forests (e.g. Berry, 1963; Sasekumar, 1974; Cook et al., 1985; Reid, 1985; Ohgaki, 1992; Boneka, 1994; Duncan & Szelistowski, 1998; Lee & Williams, 2002a) have demonstrated the occurrence of sympatric *Littoraria* species at partially separate tidal levels, exhibiting differential distribution patterns. Other accounts of the habitat and zonation have referred to single species (Abe, 1942; Macnae & Kalk, 1962; Nielsen, 1976; all as '*Littorina scabra*' before revision of taxonomy by Reid, 1986; *L. melanostoma* by Berry & Chew, 1973; *L. pallescens* by Boneka, 1996). Regarding the East African coast, four *Littoraria* species have been recorded in mangroves (Reid, 1986). Although the geographical distribution patterns and habitats exhibited by these *Littoraria* species are known in broad terms (Reid, 1985, 1986, 2001), there have been no local or regional comparisons of the abundance, zonation and size structure of *Littoraria* species along the East African coast.

So far, there have been few quantitative studies of the abundance of littorinids in mangroves. Reid (1985) used a semi-quantitative transect technique to assess horizontal and vertical distribution at mangrove sites throughout the Indo-West Pacific. Abundance of two *Littoraria* species at a local scale in Hong Kong was described using a nested sampling design by Lee & Williams (2002a). Nested sampling designs are a method for assessing the distribution of organisms at different scales, and quantify the relative contribution of different scales to the overall spatial variability (Morrisey et al., 1992; Underwood & Chapman, 1996). Furthermore, the study of spatial patterns is essential for assessing the status, ecology and conservation value of a natural community (Brown et al., 1995; Underwood &Chapman, 1996; Lee & Williams, 2002a). This technique has not previously been applied at a geographical scale to mangrove animal communities.

The aim of this study is to determine spatial distribution patterns of *Littoraria* species in three different mangrove strata (previously referred to as 'zones', from seaward to landward) at several locations along the East African coast, from Tanzania to South Africa, to test the hypothesis of variable littorinid abundance at regional and local scales for each species. For that purpose species composition, size structure and abundance were evaluated and compared in eight different mangroves.

This study is part of a wider research programme aiming to understand latitudinal gradient effects on coastal organisms along the East African coast within the EU-funded research project TRANSMAP. The wider objective is to gather information regarding biodiversity aspects of the eco-region, which may modulate the establishment of the regional network for marine conservation.
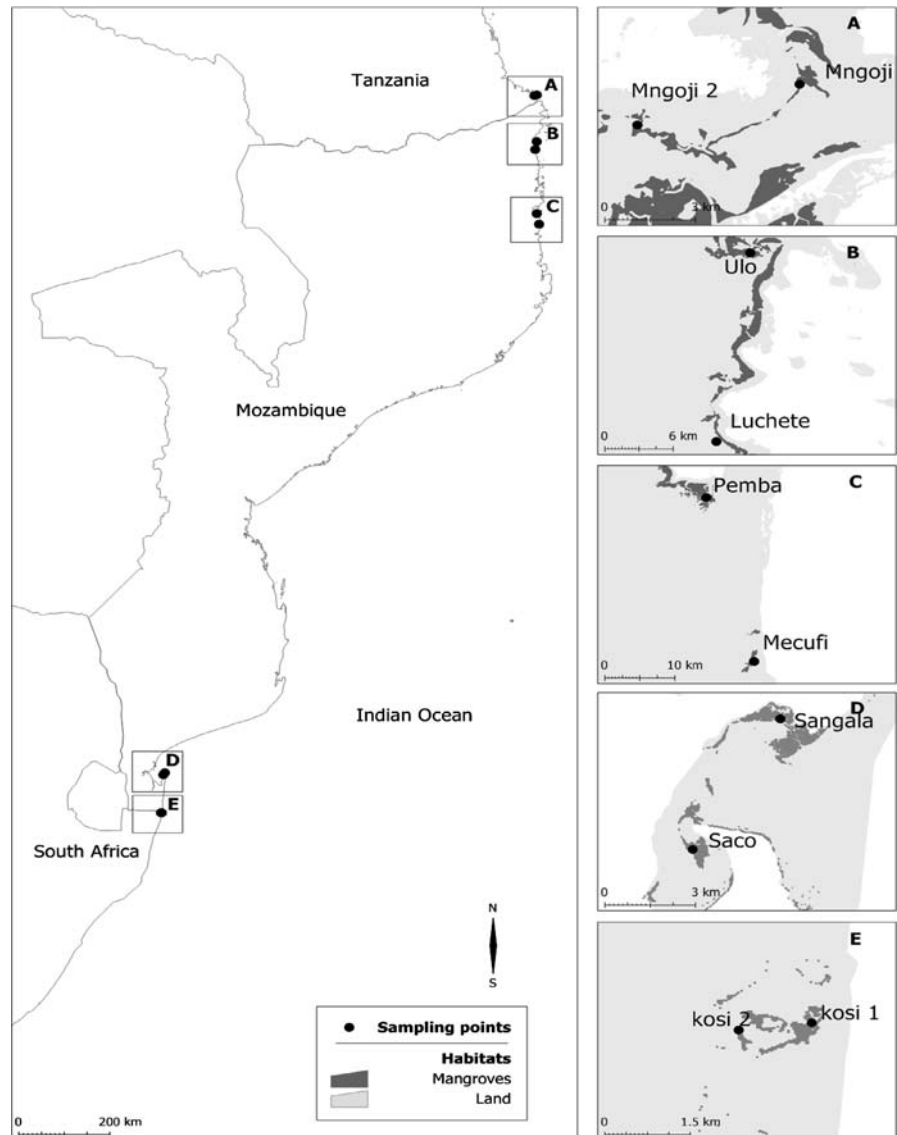
Material and methods

Study sites

The field research and assessment took place at five distinct locations (Lo) along the Eastern African coast from Tanzania to South Africa. In each location two mangrove forest sites (Si) were selected (Fig. 1):

Location 1—Mngoji 1 and Mngoji 2 in southern Tanzania,

Location 2—Ulo and Luchete in northern Mozambique,

Location 3—Pemba and Mecufi in northern Mozambique,

Location 4—Sangala and Saco Bay at Inhaca Island in southern Mozambique,

Location 5—Kosi 1 and Kosi 2 in northeastern South Africa.

In Mngoji and Kosi mangroves two areas were sampled to complete the nested sampling design. Each mangrove site was divided into three strata (Sr) corresponding to particular mangrove associations and representing successive levels of inundation across the mangrove. The Seaward level (at the seaward edge of the mangrove forest) is usually dominated by the tree species *Avicennia marina* or *Sonneratia alba*. The former species dominates in the mangroves of the southern subtropical East Africa, and the latter in those of central Eastern African tropical regions. The Middle level, occupying areas inundated by all medium high tides, is dominated by dense *Rhizophora mucronata* forest. The Landward level is situated at the landward side of the mangroves, and is dominated by *Avicennia marina*, usually of shrub-like growth and often fringing salt

pans. Although the existence of significant zonation patterns of mangrove tree species has been disputed (Ellison, 2002), the three mangrove levels correspond to commonly recognized qualitative 'zones' of the mangrove (see Macnae, 1968, for description of zonation in East African mangrove forests). The zonation pattern of the mangroves is believed to be influenced by various environmental factors, namely tidal inundation, rainfall and freshwater input (Macnae, 1968; Ellison & Farnsworth, 2001).

Sampling and laboratory procedure

Sampling was conducted during July of 2006 at spring tides in all sites. In each stratum, five squares of 10 × 10 m were randomly set at a minimum distance of 10 m, and *Littoraria* snails were collected by hand by two experienced workers searching for 15 min, during day-time low tide. All collected individuals were labelled and preserved in buffered 4% formalin diluted with seawater. Examination was carried out in the laboratory, where four species were identified according to Reid (1986, 2001): *L. scabra* (Linnaeus, 1758), *L. pallescens* (Philippi, 1846), *L. subvittata* (Reid, 1986) and *L. intermedia* (Philippi, 1846). Specimens were then counted and shell height (maximum linear dimension of the shell from the apex to the anterior edge of the lip) determined with a digital calliper (±0.05 mm accuracy), which constitutes a suitable measure since apices are usually intact (Reid, 1986). Also, in the same stratum, the DBH (Diameter at Breast Height) was measured for each mangrove tree to estimate total area covered by mangrove trees within each mangrove level.

Statistical analysis

A one-way ANOVA was used to compare the total littorinids captured at the five different locations and to compare shell height between species from each mangrove. The degree of association between littorinid abundance and the area covered by mangrove tree in each stratum was assessed using Pearson's correlation coefficient.

A three-factor, mixed-model ANOVA, with Location (Lo) and Site (Si) as random factors, and Stratum (Sr) as a fixed orthogonal factor nested within Site and Location, was used to analyze variation in abundance. To test the shell height data a similar

ANOVA was performed, a Means and Variances Analysis (MVA), which uses average and variance data since the numbers of replicates were different. All results were considered statistically significant at $P < 0.05$ level. Homogeneity of variances was tested using Cochran's C-test (Underwood, 1997) and, where data failed to meet this assumption, square-root transformation was applied. If homogeneity of variances could still not be achieved by any logical transformation and because heterogeneous variances increase the likelihood of type I errors, a more conservative significance level ($P < 0.001$) was used when testing for differences (Underwood, 1997). An SNK multiple comparison test was used if ANOVA showed a significant treatment effect. ANOVA analysis was performed using GMAV software (University of Sydney).

Results

Littoraria abundance

During the sampling period a total of 46,699 snails were collected along the East African coast. Total numbers of snails increased irregularly from Tanzania (Location 1) southward until Inhaca Island (Location 4) and then decreased abruptly (Fig. 2). Comparing the relative abundance of species at each mangrove site, *L. subvittata* is almost always the most abundant species; however where its abundance decreases (Mngoji 2 and Mecufi) other species increase their numbers (Fig. 3, Table 1). *Littoraria intermedia* was the least abundant of the four along the East African coast.
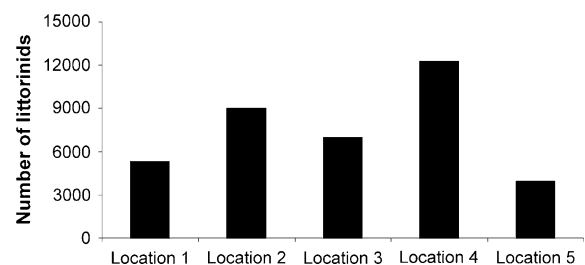

Fig. 2 Total littorinids collected at the five locations along the East African coast. Location 1—Mngoji 1 and 2, Location 2—Ulo and Luchete, Location 3—Pemba and Mecufi, Location 4—Sangala and Saco, Location 5—Kosi 1 and 2

Fig. 3 Relative abundance of each *Littoraria* species at the mangrove sites along the East African coast
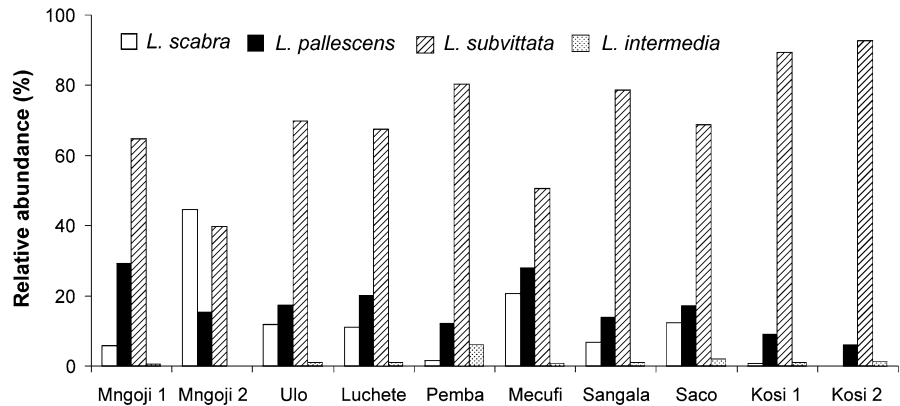
Figure 4 shows the relation between the area covered by mangrove trees at each site and littorinid abundance. According to Table 2 only in the landward level is there a significant correlation between the variables, although the middle level is strongly influenced by the results obtained for Sangala site. The South African sites, Kosi 1 and 2, were not used in this analysis because of the scarcity of the snails there.

Littoraria scabra appears to have a narrower distribution, suffering the most pronounced decrease in South Africa, although its abundance does not vary significantly between locations (Fig. 5, Table 3), and it reaches its significantly maximum density at Mngoji 2 and Mecufi (Table 3). Along the mangrove strata (St) its abundance follows a similar pattern in all sites, with a higher value in the seaward level (St1) although this was narrowly non-significant (Table 3). There is a significant Strata × Sites interaction, which indicates that the strata difference in abundance varies between mangrove sites, namely at locations 1, 2 and 4 (Table 3).

Littoraria subvittata is the dominant species in almost every mangrove except at Mngoji in Tanzania (Fig. 5). In Mozambique it is the most abundant species, reaching its maximum density at Sangala mangrove, (Fig. 5, Table 3) and decreasing to South Africa. Although there are no significant differences between strata, this species often shows higher abundance in the middle or landward level of the mangrove sites (Fig. 5, Table 3).

Littoraria pallescens shows a similar pattern of regional abundance to that of *L. subvittata*, although it is significantly less abundant. However, it prefers seaward and middle levels of mangroves, and is significantly more abundant in Mecufi, Luchete and

Sangala (Fig. 5, Table 3). This species also presents a significant Strata × Sites interaction (as does *L. scabra*), regarding two strata, the seaward and middle levels (Table 3).

Littoraria intermedia is the least abundant, showing a more variable pattern and a significant peak of abundance at Pemba (Table 3) where other species, namely *L. scabra* and *L. pallescens*, are less abundant (Fig. 5, Table 3). This species shows significantly higher abundance values in the seaward level (St1), similar to *L. scabra* (Table 3).

Littoraria size structure

There is a tendency for all species to decrease in size towards the south. *Littoraria scabra* is always significantly larger than the other species ($P < 0.05$) at each mangrove site, reaching its largest mean height of 36.80 mm at Pemba (Fig. 6, Table 1) and decreasing significantly towards the south (Table 4). Shell height also varies significantly between strata, and a Strata × Sites interaction is significant, mainly between seaward and middle strata (Table 4).

Both *L. subvittata* and *L. intermedia* follow a similar pattern, presenting a significantly smaller size in southern locations (Table 4). Only *L. pallescens* did not show differences between any locations or mangrove sites (Table 4).

Discussion

The nested sampling design has demonstrated significant variation in the abundance of *Littoraria* species at three spatial scales: between geographical regions

Table 1 Number of snails collected in each level (from five 10 × 10 m quadrats) for each species and mean (±SD), maximum and minimum shell height of total individuals from each mangrove

		Number of snails			Shell height (mm)		
		Lower	Middle	Upper	Mean (+SD)	Minimum	Maximum
Mngoji 1	L. scabra	149	1	0	14.61 ± 1.05[a]	7.23	25.94
	L. pallescens	476	195	93	10.70 ± 2.32[b]	4.05	21.61
	L. subvittata	395	598	705	10.59 ± 2.49[b]	3.20	17.80
	L. intermedia	7	5	0	11.12 ± 1.56[c]	7.68	13.74
Mngoji 2	L. scabra	1,198	10	0	15.16 ± 2.61[a]	6.68	27.83
	L. pallescens	221	180	18	11.08 ± 2.10[b]	5.29	17.02
	L. subvittata	92	579	406	11.24 ± 2.36[b]	4.78	30.97
	L. intermedia	1	2	0	12.17 ± 0.29[c]	10.32	13.53
Ulo	L. scabra	484	7	0	17.27 ± 3.61[a]	6.36	29.65
	L. pallescens	279	405	37	11.04 ± 2.17[b]	3.50	24.92
	L. subvittata	475	650	1,777	12.12 ± 3.26[c]	3.50	26.42
	L. intermedia	13	14	15	12.30 ± 2.35[c]	7.57	19.84
Luchete	L. scabra	541	1	0	17.28 ± 1.59[a]	4.96	26.80
	L. pallescens	265	630	90	9.92 ± 1.59[b]	5.02	15.79
	L. subvittata	231	1,504	1,562	10.75 ± 2.15[c]	4.08	18.79
	L. intermedia	11	33	10	11.95 ± 1.47[d]	7.67	14.52
Pemba	L. scabra	26	21	0	17.52 ± 4.18[a]	7.65	36.80
	L. pallescens	204	77	118	12.67 ± 2.59[b]	5.47	21.93
	L. subvittata	426	710	1,546	11.89 ± 2.87[c]	4.79	26.90
	L. intermedia	126	64	15	11.78 ± 2.29[c]	5.87	18.43
Mecufi	L. scabra	690	69	0	15.37 ± 3.71[a]	7.00	25.56
	L. pallescens	283	703	38	10.68 ± 2.13[b]	4.98	17.53
	L. subvittata	464	917	466	11.12 ± 2.53[b]	5.30	22.94
	L. intermedia	8	17	1	11.84 ± 1.43[c]	7.62	18.17
Sangala	L. scabra	625	25	0	13.09 ± 4.85[a]	5.30	28.75
	L. pallescens	456	757	121	9.98 ± 2.28[b]	4.61	19.76
	L. subvittata	2,676	1,850	3,087	9.69 ± 2.07[b]	3.71	19.68
	L. intermedia	51	21	24	9.85 ± 1.62[b]	6.24	15.45
Saco	L. scabra	306	9	0	12.57 ± 4.08[a]	5.13	30.34
	L. pallescens	150	269	22	9.85 ± 2.72[b]	4.30	18.88
	L. subvittata	698	441	633	8.99 ± 2.22[b]	3.46	21.77
	L. intermedia	25	16	8	10.06 ± 1.78[b]	7.23	13.92
Kosi 1	L. scabra	13	1	0	9.39 ± 2.89[a]	6.36	17.81
	L. pallescens	101	66	12	9.79 ± 1.92[a]	4.87	15.59
	L. subvittata	641	840	294	9.50 ± 1.85[a]	4.60	17.63
	L. intermedia	10	6	3	9.01 ± 0.97[a]	7.34	11.56
Kosi 2	L. scabra	1	0	0	11.58[a]	11.58	11.58
	L. pallescens	39	61	17	9.73 ± 2.52[b]	4.55	16.68
	L. subvittata	549	1,025	240	9.47 ± 1.89[b]	4.48	16.63
	L. intermedia	12	13	2	9.15 ± 1.11[b]	6.04	12.62

Within columns, different superscript letters represent significant differences between species at each site ($P < 0.05$)
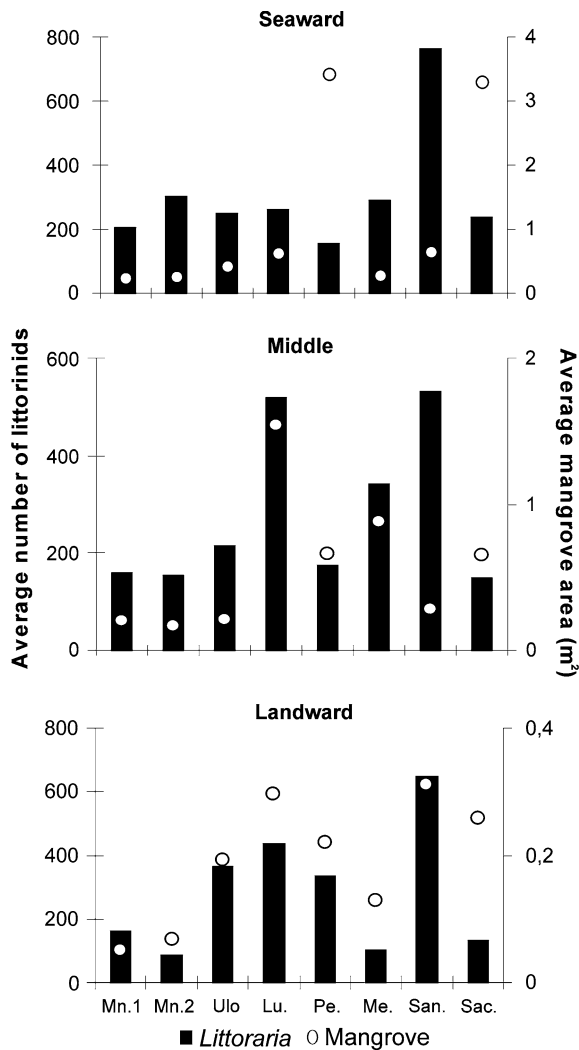
Fig. 4 Relation between littorinid abundance and mangrove tree area in each mangrove site with the exception of Kosi 1 and 2. Mn.1—Mngoji 1, Mn.2—Mngoji 2, Lu.—Luchete, Pe.—Pemba, Me.—Mecufi, San.—Sangala, Sac.—Saco

Table 2 Pearson correlation analysis between littorinid abundance and mangrove tree area within horizontal strata

Mangrove strata	Correlation coefficient (r)	Coefficient of determination (r^2)	P
Lower	−0.3012	0.09074	0.4684
Middle	0.5091	0.2592	0.1976
Upper	**0.7541**	**0.5687**	**0.0307**

Significant P-values ($P < 0.05$) are indicated in bold

within East Africa, between local mangrove sites, and among horizontal strata (zones) within mangrove forests. Although Lee & Williams (2002a) have
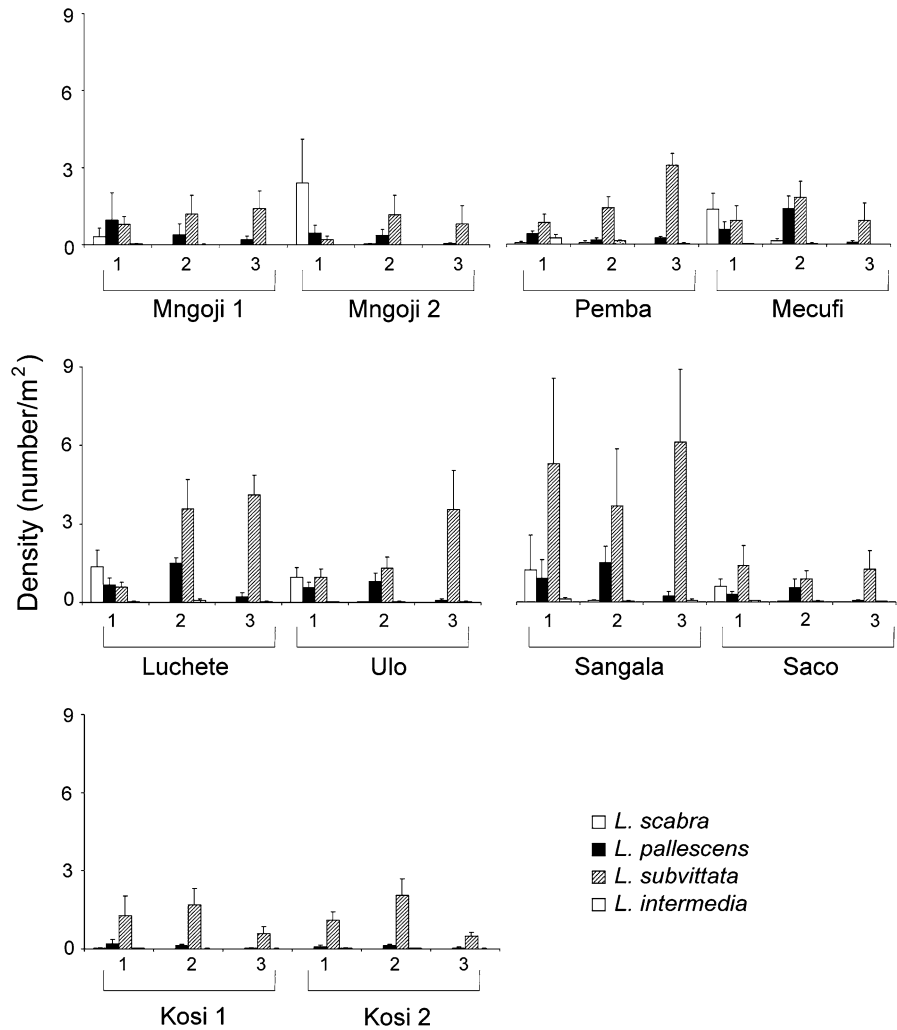
applied this methodology to the assessment of local variation in littorinid abundance in Hong Kong mangroves, the present study is the first application of nested sampling to the description of geographical and zonational variation in mangrove fauna.

Global distribution records of *Littoraria scabra*, *L. pallescens*, *L. intermedia* and *L. subvittata* have been given by Reid (1986, 2001); the first three have wide distributions throughout the tropical Indo-West Pacific, but *L. subvittata* is limited to the western Indian Ocean. Our results confirm the occurrence of these species in East Africa and demonstrate that *L. intermedia* is the least common in the region. Latitudinal limits of tropical littorinids are presumed to be set in some way by temperature (Reid, 1986; Williams & Reid, 2004), and the low abundance of *L. scabra*, *L. pallescens* and *L. intermedia* at the southernmost locality, in northeastern South Africa, may be related to the decline of the Indo-West Pacific faunistic component southward along the coast of Kwazulu-Natal (Kilburn & Rippey, 1982). Of the four mangrove littorinids, *L. subvittata* extends furthest south (to Algoa Bay, Reid, 1986), and remains common at the South African locality. Our records extend the known range of *L. pallescens* from central Mozambique to South Africa.

All *Littoraria* species showed a small reduction in shell height towards the south of the study region. The explanation is unknown, but adult shell size is likely to be determined by a complex interaction of ecophenotypic effects of factors including productivity, time available for feeding and calcification efficiency, by natural selection by predators and by extremes of temperature and desiccation (see reviews by Vermeij, 1973, 1978; Reid, 1996). Some *Littoraria* species at the extremes of their geographical range and from apparently unfavourable habitats (e.g. depauperate mangroves in arid areas) show smaller sizes (e.g. *L. pallescens*, Reid, 1986).

There were striking differences between the two mangrove sites sampled at each location. For each *Littoraria* species either the effect of site within location or the interaction between site and stratum was significant. Previous descriptive accounts have often emphasized localized distribution patterns (Reid, 1985; Ohgaki, 1998), and local differences between sites were also a feature of the distribution of *Littoraria* species sampled in Hong Kong (Lee & Williams, 2002a). These differences are not yet understood, but

Fig. 5 Average density (± SD) in *Littoraria* species at different horizontal levels within each mangrove site. 1—Seaward level, 2—Middle level, 3—Landward level

are likely the result of the topographic and floristic complexity of mangrove forests in estuarine environments, distribution of predators, and probable variations in environmental variables such as salinity, turbidity, water flow, etc., none of which was quantified in the present study. Reid (1985, 1986) emphasized local (and regional) differences between 'continental' and 'oceanic' mangrove sites, viewed as extremes of a continuum, the former being broad, productive mangrove forests fringing large land masses and sheltered estuaries, with turbid water and muddy substrates, whereas the latter are narrow mangrove belts on islands and relatively exposed continental shores, where water is clear. He grouped the associated *Littoraria* species in the same way, classifying *L. scabra*, *L. pallescens* and *L. intermedia* as relatively 'oceanic' in their local and geographical

distributions. The present results offer limited support for this generalization. While all sites are towards the continental end of the spectrum, those at Luchete, Mecufi and Sangala were each closer to the open sea than the other site at the same location (Fig. 1), and in each case the abundance of both *L. scabra* and *L. pallescens* was higher at the open sites (Fig. 5). *Littoraria intermedia* at Pemba and Mecufi did not confirm to this pattern, however. With little habitat information available, Reid (1986) speculated that *L. subvittata* was also an 'oceanic' species, but the present results show that this is more tolerant of 'continental' conditions than its three congeners.

At the scale of strata (zones) of the mangrove, the distribution of *Littoraria* is complex. The mangrove is a three-dimensional environment with both vertical (up the trees) and horizontal (seaward to landward)

Table 3 Three-factor ANOVA to investigate variation in abundance of *Littoraria* in strata (St) within mangrove sites (Si) in different locations (Lo)

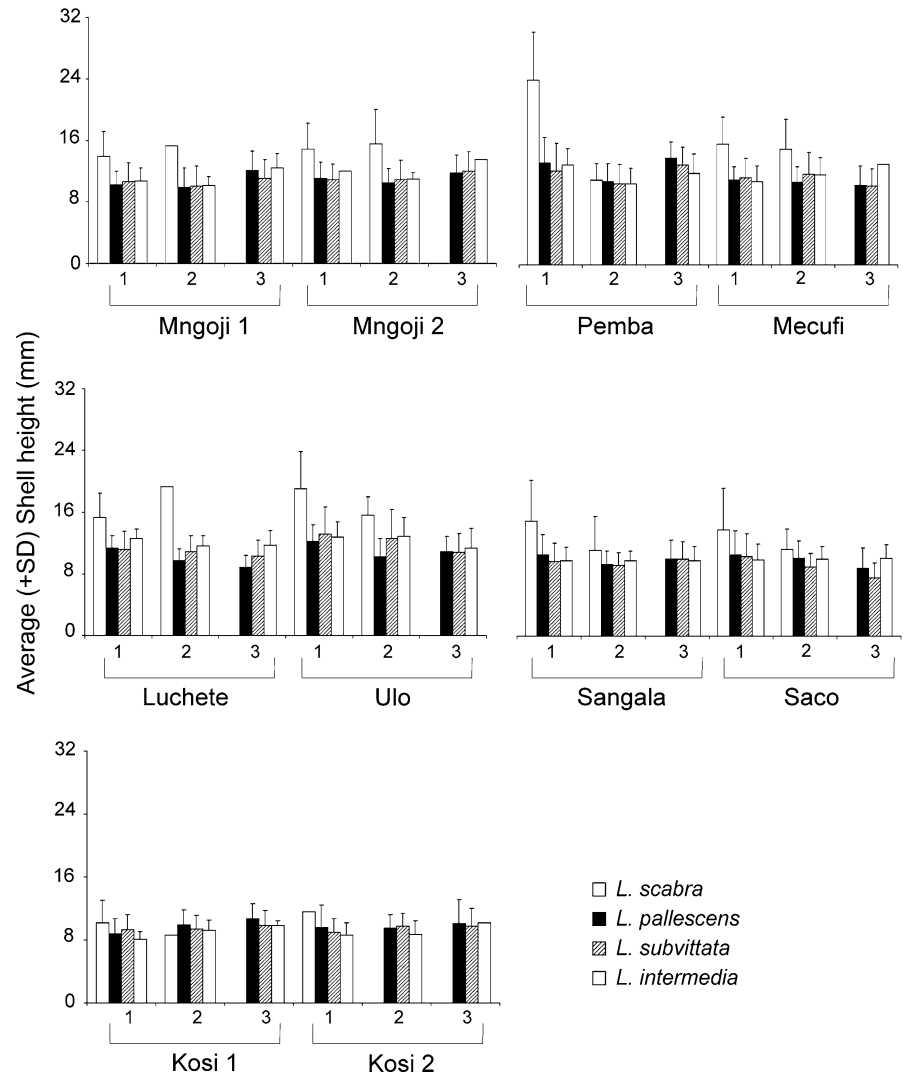|	Source of variation	df	Mean squares	*F*-ratio	*P*	SNK tests ("≠" significant differences)
L. scabra	Lo	4	89,233.767	0.75	0.5959	
	Si (Lo)	5	118,219.867	6.05	**0.0000**	Lo1,2: Si1 ≠ Si2
	St	2	1,119,517.867	12.55	0.0034	
	Lo × St	8	89,192.117	0.82	0.6050	
	St × Si (Lo)	10	109,164.467	5.58	**0.0000**	St1 Lo1,2,4: Si1 ≠ Si2
	Residual	120	19,546.100			
L. pallescens	Lo	4	136,174.233	1.34	0.3721	
	Si (Lo)	5	101,894.533	9.37	**0.0000**	Lo2,3,4: Si1 ≠ Si2
	St	2	431,688.800	8.35	0.0110	
	Lo × St	8	51,716.133	1.18	0.3966	
	St × Si (Lo)	10	43,937.733	4.04	**0.0001**	St1 Lo1,4: Si1 ≠ Si2
						St2 Lo2,3,4: Si1 ≠ Si2
	Residual	120	10,874.200			
L. subvittata	Lo	4	2,412,314.933	0.99	0.4904	
	Si (Lo)	5	2,441,367.267	12.31	**0.0000**	Lo4: Si1 ≠ Si2
	St	2	1,072,137.600	1.54	0.2715	
	Lo × St	8	695,586.433	2.76	0.0679	
	St × Si (Lo)	10	252,434.267	1.27	0.2535	
	Residual	120	198,376.300			
*L. intermedia***	Lo	4	55.192	3.72	0.0913	
	Si (Lo)	5	14.856	6.53	**0.0000**	Lo2: Si1 ≠ Si2
	St	2	44.019	9.05	**0.0088**	St1 = St2 ≠ St3
	Lo × St	8	0.4866	1.65	0.2254	
	St × Si (Lo)	10	0.2949	1.30	0.2396	
	Residual	120	0.2273			

Significant *P*-values are indicated in bold. Significance level *P* < 0.001, since homogeneity of variances was not achieved; asterisk indicates that homogeneity of variances was achieved with square-root transformation, and significance level was then *P* < 0.05

patterns of distribution, both of which are related to tidal levels. Furthermore, littorinids are highly mobile, migrating vertically downwards to feed at lower levels on the trees or to spawn, and upwards to avoid submersion by the rising tide (Reid, 1984; Yipp, 1985; Kohlmeyer & Bebout, 1986; Ohgaki, 1992; Lee & Williams, 2002b). Horizontal migration between trees is, however, very limited, because most snails are unable to crawl on the mud surface (Reid, 1985; but see Sanpanich et al., 2004), so that horizontal distribution cannot be ascribed to adult behaviour patterns. The present study quantifies differences in abundance between three horizontal strata: seaward, middle and landward, but did not examine vertical distribution. In agreement with previous accounts (Reid, 1985, 1986), *L. scabra* and

L. intermedia were found almost exclusively at the seaward side, whereas *L. pallescens* was distributed in both seaward and middle zones. Information on the zonation of *L. subvittata* is provided for the first time, and shows that this species is distributed throughout the width of the mangrove and may reach maximum abundance in the middle and landward areas.

The control of vertical and horizontal distribution of littorinids in mangroves remains poorly understood. Reid (1985) speculated that vertical distribution is determined largely by proximate behavioural responses, under the ultimate selective influence of predation at lower tidal levels and climatic extremes above. Landward limits, on the other hand, may be determined directly by physiological tolerance and perhaps by settlement patterns of the planktonic

Fig. 6 Average shell height (± SD) in *Littoraria* species at different horizontal levels within each mangrove site. 1—Seaward level, 2—Middle level, 3—Landward level

larvae. Predation by crabs and fish is undoubtedly a strong selective force in the mangrove environment, with important effects on behaviour, shell size and architecture (e.g. Reid, 1985, 1986, 1992, 2001; Duncan & Szelistowski, 1998). The distribution of aquatic predators and tree-climbing grapsid crabs in the mangrove have not been studied in detail, but they are believed to be most frequent at the seaward edge of the mangrove, and therefore cannot account for the prevalence of some *Littoraria* species at the seaward edge. Predators of terrestrial origin include birds and flies (Cook & Garbett, 1992; McKillup & McKillup, 2000), but the extent of their influence is unknown.

Since the mangrove trees themselves show horizontal zonation patterns (e.g. Macnae, 1968; but see Ellison, 2002), associations between tree and littorinid species could determine distribution of the snails. However, although differences in occurrence of *Littoraria* species on mangrove genera have been observed, these appear to be mainly the incidental consequences of tree architecture combined with a substrate preference for bark or leaves, and no obligate or dietary associations have been recorded (Reid, 1985, 1986; Ohgaki, 1992; Boneka, 1994; Lee & Williams, 2002a; Sanpanich et al., 2004). *Littoraria* species are generalist feeders on plant material, epiphytic microalgae and fungal hyphae, but (with the exception of leaf hairs of *Avicennia*) rarely ingest living leaf cells (Kohlmeyer & Bebout, 1986; Reid, 1986; Bärlocher & Newell, 1994; Lee et al., 2001). In view of the dependence of the snails on mangrove trees as a substrate (at least in sedimentary environments), it

Table 4 Three-factor ANOVA to investigate variation in sizes of *Littoraria* in strata (St) within mangrove sites (Si) in different locations (Lo)

	Source of variation	df	Mean squares	F-ratio	P	SNK tests ("$\neq$" significant differences)
L. scabra	Lo	4	1,990.806	16.42	**0.0044**	Lo1 = Lo2 = Lo3 = Lo4 $\neq$ Lo5
	Si (Lo)	5	121.223	1.48	0.1999	
	St	2	32,926.854	39.48	**0.0001**	St1 = St2 $\neq$ St3
	Lo $\times$ St	8	833.992	2.00	0.1502	
	St $\times$ Si (Lo)	10	416.327	5.10	**0.0000**	St1 Lo2,3: Si1 $\neq$ Si2
						St2 Lo2,3,5: Si1 $\neq$ Si2
	Residual	120	81.672			
L. pallescens	Lo	4	181.919	2.25	0.1986	
	Si (Lo)	5	80.826	1.55	0.1799	
	St	2	91.532	1.55	0.2691	
	Lo $\times$ St	8	58.906	2.13	0.1303	
	St $\times$ Si (Lo)	10	27.639	0.53	0.8664	
	Residual	120	52.193			
L. subvittata	Lo	4	332.047	6.57	**0.0317**	Lo3 $\neq$ Lo5
	Si (Lo)	5	50.536	0.85	0.5155	
	St	2	18.448	0.53	0.6105	
	Lo $\times$ St	8	35.127	1.00	0.4888	
	St $\times$ Si (Lo)	10	35.058	0.59	0.8185	
	Residual	120	59.292			
L. intermedia	Lo	4	531.570	27.40	**0.0013**	Lo1 = Lo2 = Lo3 $\neq$ Lo4 = Lo5
	Si (Lo)	5	19.397	0.69	0.6286	
	St	2	89.104	1.68	0.2452	
	Lo $\times$ St	8	52.906	2.13	0.1311	
	St $\times$ Si (Lo)	10	24.887	0.89	0.5438	
	Residual	120	27.933			

Significant P-values ($P < 0.05$) are indicated in bold

is at first surprising that a correlation between tree area and snail abundance was found only in the landward stratum. Here, the trees were usually small bushes, so that the number of trees and their diameter at breast height (DBH) provided a good estimate of surface area available for the snails. However, in the middle and seaward strata tree architecture was more variable. In particular, the surface area of branches and leaves provided by the few, very large *Sonneratia* trees sometimes found in the seaward stratum was not adequately estimated by DBH.

Few previous studies have counted numbers of *Littoraria* per unit ground area in tropical mangrove habitats. Ohgaki (1992) recorded 4.2 *L. pallescens* per 100 m^2 in Okinawa; Boneka (1994) recorded 273 *L. pallescens* per 100 m^2 in Sulawesi; Lee & Williams

(2002a) recorded up to 21 *L. melanostoma* per 100 m^2 in Hong Kong. Other studies have reported numbers per tree, or per unit collecting effort, and cannot easily be compared. The numbers recorded here range up to 240 *L. scabra*, 151 *L. pallescens*, 617 *L. subvittata* and 25 *L. intermedia*, all per 100 m^2 (totals for five 10 $\times$ 10 m squares in Table 1). This abundance of littorinids is typical in tropical mangrove habitats (D.G. Reid, personal observation), but has seldom been quantified in this way.

Conclusion

The results obtained in this work demonstrated significant variation in the abundance of the

Littoraria species at three spatial scales: between geographical regions within East Africa, between local mangrove sites, and among horizontal strata (zones) within mangrove forests. Of the four mangrove littorinids identified, *L. subvittata* extends furthest south and *L. intermedia* is the least common throughout the African coast. All *Littoraria* species showed a small reduction in abundance and shell height towards the south of the study region. Among horizontal strata (zones), *L. scabra* and *L. intermedia* were found almost exclusively at the seaward side, *L. pallescens* was distributed in both seaward and middle zones and *L. subvittata* is distributed throughout the width of the mangrove. The distribution and abundance of *Littoraria* species in mangroves is complex and dynamic, and improved understanding will require detailed local studies of population dynamics, vertical migratory behaviour, horizontal distribution in mangroves of different topography and hydrology, and replication throughout the year.

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