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Geographic trends in mangrove crab abundance in East Africa

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Abstract

The aim of this work was to determine the abundance of crabs in mangrove communities along a latitudinal gradient along the eastern coast of Africa from 4°S to 32°S. Surveys were made at Mombasa (Kenya), Zanzibar (Tanzania), Maputo (Mozambique) and in the Transkei (South Africa). Crabs were estimated at three designated levels in the mangroves by visual census using a common protocol, and numbers were converted to biomass.

Even after standardising the selection of sites and methods of census there was still extensive variability in the data, emphasising the complex heterogeneity of mangrove ecosystems. Lunar phase (full versus new moon springs) did not have a consistent effect on results, but shore height had several effects. Total crab biomass was similar in the two lower shore strata examined, but about twice as high at the top-*Avicennia* level. The ratio of grapsid biomass:ocypodid biomass also changed with height: from near unity in the lower mangrove, to 0.14 in the middle strata, but to 15 at the top.

There was no consistent latitudinal trend in total crab numbers, but total crab biomass increased from north to south. In addition there was a consistent and marked change in the grapsid biomass:ocypodid biomass ratio: this swung from 0.65 at Mombasa to 6.8 in the Transkei. This has implications for the transfer of primary production through the food chain. Grapsids are important macrophagous feeders on the leaves and other parts of mangroves, whereas ocypodids are microphagous deposit feeders.

Introduction

Crabs are the most visible mangrove macrofauna, the majority burrowing in the sediment during high tide, but once the tide recedes emerging to become active on the surface (Macintosh, 1984; Hartnoll. 1988). Most are either fiddler crabs (Family Ocypodidae, Genus *Uca*), or sesarmid crabs (Family Grapsidae, Subfamily Sesarminae), though various other members of the Gecarcinidae, Grapsidae, Ocypodidae, Portunidae and Xanthidae occur. There are various accounts of the mangrove crab fauna in the East African area (Macnae and Kalk, 1962; Derijard, 1966; Macnae, 1968; Hartnoll, 1975; Kalk, 1995).

Few of these crabs are of direct economic importance, though several species may be caught and consumed at a subsistence level. The only species of substantial commercial importance is the 'mud crab', *Scylla serrata* (Forskål) (see Keenan and Blackshaw, 1999 for recent review). However this inhabits the creeks, rather than the mangrove thickets themselves, and is active at high tide rather than low tide. Furthermore it is a carnivore, and occupies a higher trophic level than most of the other mangrove crabs.

One basic aim of the MEAM project (EU INCO-DC) was to evaluate the role of mangrove macrofauna in the energy flux of the mangrove ecosystem, in particular the extent to which macrofauna are responsible for the trapping and conversion of mangrove primary production within the immediate environment, and its transfer to higher trophic levels (see Giddings et al., 1986; Robertson and Daniel, 1989; Micheli, 1993; Lee, 1997, 1998; Skov and Hartnoll, 2002). This transfer may be within the mangroves, or further afield via the export of larvae. Mangrove crabs play various roles. A limited number feed directly upon living leaves on mangrove trees – the only important species is *Sesarma leptosoma* Hilgendorf (Vannini and Ruwa, 1994). Others feed on fallen mangrove leaves. Some by sitting in the trees and picking them from the surface of the water at high tide, as in *Selatium elongatum* (A. Milne Edwards) (Cannicci et al., 1999), others by collecting fallen leaves from the substratum at low tide, as in *Neosarmatium meinerti* (De Man) (Micheli et al., 1991; Emmerson and McGwynne, 1992) and *N. smithi* (H. Milne Edwards) (Giddins et al., 1986). In contrast the species of *Uca* are deposit feeders, sorting the organic fraction from the sediment (Crane, 1975). However, most of this organic fraction is presumed to have resulted from the breakdown of mangrove material. Other species are opportunistic, such as *Metopograpsus thukuhar* (Owen) (Fratini et al., 2000) and *Thalamita crenata* (Latreille) (Cannicci et al., 1996), or predatory as in *Epixanthus dentatus* White (Cannicci, et al., 1998).

Initially this investigation set out to quantify the mangrove crabs, though there are no simple methods applicable to all species at all levels in the mangrove. Only recently Lee (1998) remarked in his review that 'one area of uncertainty in the overall importance of the crabs arises from the lack of a satisfactory method for the estimation of field density'. In this study it was decided to use direct visual census as the primary assessment method, and it is the result of that work which is presented here. The method involves various uncertainties, and collateral studies to validate and calibrate the visual census method are being presented elsewhere (e.g. Skov and Hartnoll, 2001). The studies were carried out along the East African coastline from Mombasa in the north at 4°S to Transkei at 32°S. This compared fully tropical mangroves with ones near to their southern limit, to determine whether the role of the macrofauna varied latitudinally.

Methods

The work was conducted in four geographic areas or 'locations'. They were determined at the outset of the project by both biological and logistic considerations: Mombasa, Kenya, 4°S; Zanzibar, Tanzania, 6°S; Maputo, Mozambique, 26°; Transkei, South Africa, 32°S. Within each location surveys were conducted at two 'sites' situated >10 km apart, selected because they included communities which matched the criteria set out in the protocol. In some, but not all locations, two sites were sufficient for the full sampling procedure.

Quadrat selection

Ideally a full vertical transect through the mangrove would have been assessed, but it became apparent at an early stage that the enormous variations in mangrove infrastructure made this unproductive. So three 'levels' within the mangroves were prescribed on biological and physical criteria, which could be identified within each location. The criteria for positioning quadrats within these evolved during field trials, but the definitive protocols were as follows. 1. *Lumnitzera/*top *Avicennia* quadrats. To measure 2 m by 2 m with an *Avicennia* tree in one corner. At the top of the *Avicennia* zone, maybe with *Lumnitzera* mixed in, and expecting evidence of *Neosarmatium meinerti* presence. 2. Mid *Avicennia* quadrats. To measure 2 m by 2 m, and to be half in and half out of shade of tree canopy. *Avicennia* zone to have muddyish substrate, to be fairly flat, and quite broad. Trees to be 4–5 m high or more, c. 20 cm trunk diameter. In middle of zone, above area where pneumatophores are densely encrusted with barnacles. 3. *Rhizophora* quadrats. To measure 2 m by 2 m, with mangrove tree in one corner. Fairly pure *Rhizophora* stand with soft mud substrate. Trees to be 4–5 m or more high with root area of c. 4 m^2. Approximately 50% of area bare mud, that is not containing mangrove roots. Quadrats should not contain drainage channels or running water.

At each level 12 quadrats were marked, and six randomly selected for the first survey. For the second survey the six used plots were discarded, and the pool made up to 12 by identifying six more. From these twelve, six were randomly selected for the second survey.

Survey timing

All surveys were carried out between July and December 1998: once at each site on full moon springs, and again on the following new moon springs. The total work period at each location was spread over six weeks (except where it was possible to work the two sites on the same tidal cycles): Full moon springs 1, Site 1; New moon springs 1, Site 1; Full moon springs 2, Site 2; New moon springs 2, Site 2.

Observation protocol

The plots were selected and the guide ropes positioned a day before observation, avoiding trampling the quadrats. The upper and mid level quadrats were divided into eight 0.5 m by 1 m strips to help visual counts. The low quadrats were subdivided into three strips of 0.67 m by 2 m, which better suited the abundance of crabs in that area.

Surface activity was evaluated twice for each quadrat – one hour after emersion, and at low water. Once the observer was stationary in position 3–4 m from the quadrat there was a wait of 15 minutes (30 minutes in the upper *Avicennia*) to allow normal activity to resume – these times were found to be adequate. For each category the maximum count in either evaluation was used in the estimates presented. This was to compensate for differences in the timing of peak activity. Binoculars (8 by 40) were used to count the specimens of a single species in each strip in turn, storing the data in a dictaphone. Male and female *Uca* were scanned separately. The process was repeated for each additional species. Where specimens could not be fully identified (e.g. juvenile *Sesarma*), they were allocated *pro rata* amongst the relevant identified categories.

Physical and chemical variables

Immersion time was determined for the centre of the set of quadrats at each level of each site, using only tides with a predicted high water at Zanzibar of 3.9 to 4.1 m above chart datum. The time of immersion and subsequent emersion were recorded. Sediment particle size and sediment organic content were determined for each quadrat by taking five cores – near each of the corners and in the centre. The cores were 5 cm deep and 2.5 cm wide, and were mixed prior to analysis. For particle size a sample of 60 g wet weight was first wet sieved to separate particles of <64 μm, which were dried and weighed. The remainder was dried and sieved following standard protocols, and median particle diameter, quartile deviation and skewness calculated (Holme and McIntyre, 1971). For organic content a sample of 30–50 g wet weight was dried and weighed, and then incinerated in a muffle furnace at 500°C for 24 hours and reweighed. A series of trials showed that this temperature produced full combustion of the organic component, but did not result in weight loss due to breakdown of carbonates (confirmed by acid decalcification trials).

Results

Immersion periods

There was considerable variation (Table 1) within what were chosen to represent comparable levels. However, at the three northernmost sites – Mombasa, Zanzibar and Maputo – there was increasing immersion from top *Avicennia* to *Rhizophora* (less clearcut in Zanzibar). However, at the southernmost location in Transkei this relationship broke down, perhaps reflecting changes in the infrastructure of the mangrove near its geographical limit.

Sediment characteristics

For each location values were averaged by site and by level (Table 1) – the median particle size for each level was substantially smaller at Umtata than at the other three locations. Both Mngazana and Mntafufu are estuarine sites: the enhanced degree of shelter and availability of fine sediment will both contribute to the fine sediment grade. When the levels were compared, the mid *Avicennia* had the coarsest sediment, the top *Avicennia* was finer, and the *Rhizophora* the finest. This is not intuitively what might be expected – a gradient of increasing coarseness with shore height might be anticipated.

Organic content was averaged by site and by level (Table 1). No location had a clearly higher organic content, and there were in some cases very wide differences between the two sites at a location. When the levels were compared there was a similar trend to that noted for particle size, with high organic content correlated with finer particle size. This relationship was highly significant ($r^2 = 0.21$, $p < 0.001$). The highest organic content was in the *Rhizophora* stratum, and the lowest in the mid *Avicennia* stratum.

Table 1. Values for each level at each site: immersion time, mean sediment particle size, mean sediment organic content.

Level	Location	Site	Immersion (hours-mins)	Median size (phi)	Median size (mm)	Organic content (%)
Upper *Avicennia*	Mombasa	Mida	1–00	1.78	0.3	13.13
		Gazi	0–40	1.99	0.25	1.07
	Zanzibar	Maruhubi	1–00	1.34	0.39	7.24
		Unguja Ukuu	2–00	1.5	0.35	3.95
	Maputo	Saco Inhaca	1–49	2.17	0.22	4.85
		Escola Noge	2–01	1.84	0.28	4.69
	Umtata	Mntafufu	5–45	4.34	0.05	11.76
		Mngazana	3–15	3.65	0.08	3.9
	Mean UA			2.33	0.24	6.32
Mid *Avicennia*	Mombasa	Mida	2–40	2.24	0.21	2.49
		Gazi	2–40	2.03	0.24	0.94
	Zanzibar	Maruhubi	4–47	0.95	0.51	0.87
		Mbweni	5–05	1.17	0.44	1.62
	Maputo	Saco Inhaca	3–48	2.2	0.22	5.3
		Escola Noge	4–20	1.72	0.3	4.75
	Umtata	Mntafufu	5–20	2.7	0.15	4.29
		Mngazana	3–00	3.6	0.08	5.7
	Mean MA			2.08	0.27	3.25
Rhizophora	Mombasa	Mida	4–00	2.53	0.17	4.33
		Gazi	5–00	1.7	0.3	5.25
	Zanzibar	Kisakasaka	5–00	2.03	0.24	13.53
		Unguja Ukuu	4–28	3.01	0.13	15.1
	Maputo	Saco Inhaca	5–00	1.68	0.31	10.2
		Escola Noge	5–10	1.91	0.26	5.3
	Umtata	Mntafufu	3–35	4.3	0.05	8.46
		Mngazana	3–45	4.47	0.04	13.12
	Mean RH			2.70	0.19	9.41

Crab numbers and biomass

Sampling covered a considerable latitudinal range, and over this range species can be expected to vary in abundance, or to disappear and be replaced by ecologically similar species. Examining such changes would have little relevance to the aims of the study, so analysis of individual species was restricted to examining their correlation with physical and chemical variables. *Uca annulipes* (H. Milne Edwards) and *Neosarmatium meinerti* were selected for this because both are common over the full geographical extent of the project, and because they have quite different trophic niches. *Uca annulipes* is a selective deposit feeder, and *Neosarmatium meinerti* feeds predominantly upon fallen mangrove leaves. Abundance within individual quadrats was regressed upon the values of each variable for that quadrat. *Uca annulipes* showed a highly significant correlation with both median particle size ($p < 0.0001$) and with sediment organic content ($p < 0.0001$), but no significant correlation with immersion period ($p = 0.094$). This is appropriate for a deposit feeder with a sorting mechanism attuned to a certain particle grade (Icely and Jones, 1978), where sediment quality is more relevant than shore level. When stepwise regression was calculated all three variables were judged relevant in the order organic content>particle size>inundation time. However, the final r^2 value was raised to only 0.29, so most of the variability in crab number was still not explained. In contrast *Neosarmatium meinerti* showed no significant correlation with either sediment characteristic ($p = 0.29$, 0.91 respectively), but a highly significant correlation with immersion period ($p < 0.0001$). This crab is little affected by sediment

Table 2. Crab counts at each site on each survey. Numbers are totals for six 4 m^2 quadrats.

Location	Level	Site	Date	Tot. grapsids	Tot. ocypod.	Tot. crabs
Mombasa	UA	Mida	NM	56	189	245
			FM	55	406	461
		Gazi	NM	49	173	222
			FM	56	157	213
	Mean UA			54	231.3	285.3
	MA	Mida	NM	126	237	365
			FM	1	223	224
		Gazi	NM	6	716	722
			FM	11	506	517
	Mean MA			36	420.5	457
	Rh	Mida	NM	85	37	132
			FM	46	45	95
		Gazi	NM	68	508	578
			FM	54	506	561
	Mean Rh			63.3	274	341.5
	Mean Mom			51.1	308.6	361.3
Zanzibar	UA	Maruhubi	NM	96	161	259
			FM	104	186	290
		Unguja	NM	164	111	280
			FM	102	193	297
	Mean UA			116.5	162.8	281.5
	MA	Maruhubi	NM	2	1160	1162
			FM	0	1140	1140
		Mbweni	NM	3	899	902
			FM	3	809	812
	Mean MA			2	1002	1004
	Rh	Kisaka	NM	78	178	257
			FM	89	270	359
		Unguja	NM	92	277	369
			FM	72	282	354
	Mean Rh			82.8	251.75	334.75
	Mean Zan			67.1	472.2	540.1
Mozambique	UA	Saco	NM	117	75	192
			FM	64	118	182
		Escola	FM	35	255	290
			NM	31	167	198
	Mean UA			61.8	153.8	215.5
	MA	Saco	NM	15	879	895
			FM	9	935	944
		Escola	NM	33	766	801
			FM	20	723	743
	Mean MA			19.3	825.8	845.8
	Rh	Saco	NM	341	269	610
			FM	365	68	434
		Escola	NM	271	57	328
			FM	331	8	339
	Mean Rh			327.0	100.5	427.8
	Mean Moz			136.0	360.0	496.3

Table 2. Continued.

Location	Level	Site	Date	Tot. grapsids	Tot. ocypod.	Tot. crabs
Umtata	UA	Mntafufu	NM	796	0	796
			FM	433	0	433
		Mngazana	FM	87	0	87
			NM	70	12	82
	Mean UA			346.5	3.0	349.5
	MA	Mntafufu	NM	5	794	799
			FM	6	741	747
		Mngazana	NM	4	175	179
			FM	3	398	401
	Mean MA			4.5	527	531.5
	Rh	Mntafufu	NM	158	0	158
			FM	207	1	208
		Mngazana	NM	247	34	281
			FM	251	22	273
	Mean Rh			215.8	14.3	230
	Mean Umt			188.9	181.4	370.3

type, but its ability to collect fallen leaves is very dependent on a prolonged exposure to air. For *N. meinerti* under stepwise regression two variables were judged relevant in the order inundation time>particle size, and the final r^2 value was only 0.15. Data are available for other species but not reported in detail here: under stepwise regression the final r^2 values were 0.17 for *Uca chlorophthalmus* (H. Milne Edwards) and 0.28 for *Sesarma guttatum* A. Milne Edwards.

For further analysis the crabs were grouped into broader categories – total grapsids, total ocypodids and total crabs. The first two of these roughly equate to trophic subdivisions. The grapsids are largely generalist vegetarians (leaves, roots, propagules) and scavengers, though they also consume quantities of sediment. The ocypodids are predominantly selective deposit feeders which sort the sediment and consume the more edible fraction. In these categories the crabs were analysed both in terms of numbers, and in terms of wet weight biomass. Numbers were converted to biomass using size frequency distributions and weight-length relationships derived in another part of the MEAM project (Hartnoll et al., unpublished data).

Data for the six quadrats at each site on each survey were totalled for numbers (Table 2) and biomass (Table 3). Both lunar phase and site affect the results obtained at a location. Each site was examined on two occasions, corresponding to new moon and full moon spring tides respectively. In the majority of instances there was reasonable agreement between the two, though on occasion very marked differences were noted. For example the number of total grapsids at the mid *Avicennia* level of Mida Creek was 126 at new moon but only 1 at full moon. An examination of the totals for ‘all crabs’ showed that these were higher on full moon at 7 sites, on new moon at 8 sites, and that the difference was trivial at 9 sites. Thus there was no consistent effect of lunar phase. In the majority of instances the agreement between the two replicate sites of a shore level at a location was quite good (at least in terms of the broad categories). However, there were sometimes substantial differences, such as in the *Rhizophora* level at Mombasa, and the upper *Avicennia* at Umtata: in fact results for the Mida site at Mombasa, for the middle and lower levels, were outside trends for all other sites. Such differences increase the noise in the system, and make geographical comparisons more difficult.

The second level of consolidation was to combine the two dates and two sites for each location by number and biomass (Table 4). This was to facilitate the comparison of overall differences between shore levels and geographic locations. Values are given as total grapsids, total ocypodids, total crabs, and as the grapsid:ocypodid ratio.

A consistent feature at each location was that the total number of crabs was generally similar at the upper and lower levels, but appreciably higher in the

Table 3. Crab biomass (g wet wt.) at each site on each survey. Numbers are totals for six 4 m^2 quadrats.

Location	Level	Site	Date	Tot. grapsids	Tot. ocypod.	Tot. crabs
Mombasa	UA	Mida	NM	341	167	508
			FM	652	388	1041
		Gazi	NM	472	157	629
			FM	435	136	572
	Mean UA			475	212.0	687.5
	MA	Mida	NM	832	256	1099
			FM	2	203	206
		Gazi	NM	13	662	674
			FM	22	465	487
	Mean MA			217.25	396.5	616.5
	Rh	Mida	NM	208	42	327
			FM	118	133	273
		Gazi	NM	167	1166	1354
			FM	166	1479	1655
	Mean Rh			164.8	705	902.25
	Mean Mom			285.7	437.8	735.4
Zanzibar	UA	Maruhubi	NM	1944	134	2078
			FM	2313	146	2458
		Unguja	NM	1457	68	1724
			FM	1547	174	1801
	Mean UA			1815.25	130.5	2015.3
	MA	Maruhubi	NM	4	978	982
			FM	0	959	959
		Mbweni	NM	6	683	689
			FM	6	634	640
	Mean MA			4	813.5	817.5
	Rh	Kisaka	NM	285	271	562
			FM	318	409	727
		Unguja	NM	344	514	858
			FM	216	609	825
	Mean Rh			290.8	450.75	743
	Mean Zan			703.3	464.9	1191.9
Mozambique	UA	Saco	NM	3599	68	3666
			FM	1984	102	2086
		Escola	NM	629	212	841
			FM	512	136	648
	Mean UA			1681.0	129.5	1810.3
	MA	Saco	NM	42	840	887
			FM	23	799	822
		Escola	NM	151	681	842
			FM	144	712	856
	Mean MA			90.0	758.0	851.8
	Rh	Saco	NM	1023	582	1605
			FM	1095	151	1251
		Escola	NM	1149	102	1251
			FM	1329	24	1353
	Mean Rh			1149.0	214.75	1365.0
	Mean Moz			973.3	367.4	1342.3

Table 3. Continued.

Location	Level	Site	Date	Tot. grapsids	Tot. ocypod.	Tot. crabs
Umtata	UA	Mntafufu	NM	4578	0	4578
			FM	3743	0	3743
		Mngazana	NM	2596	0	2596
			FM	1666	9	1675
	Mean UA			3145.75	2.3	3148.0
	MA	Mntafufu	NM	15	819	834
			FM	15	731	746
		Mngazana	NM	117	213	329
			FM	43	364	407
	Mean MA			47.5	531.75	579
	Rh	Mntafufu	NM	478	0	478
			FM	744	2	746
		Mngazana	NM	662	83	745
			FM	686	51	737
	Mean Rh			642.5	34.0	676.5
	Mean Umt			1278.6	189.3	1467.8

mid *Avicennia* stratum. The picture changed considerably, however, when biomass was considered. The upper level now had a much higher value, followed by the lower level, with the mid level having the least. This is because the mid level was dominated by small *Uca*, whereas the upper and lower levels had larger sesarmids. Ignoring for the present geographic trends, the grapsids and ocypodids were numerically similar at the upper and lower levels (G/O ratio 1.1), but in the mid *Avicennia* there were few grapsids but many ocypodids (G/O ratio 0.02). Conversion to biomass presented a different view. At the top level grapsids became very dominant (G/O ratio 15) due to the large individual size of *Neosarmatium meinerti*. Ocypodids still dominated the mid level, though to a lesser degree (G/O ratio 0.14), and grapsids became modestly dominant at the low level (G/O ratio 1.6).

Geographical trends can be examined by combining the data from all three levels. Crab numbers showed no consistent trend, but biomass values showed a consistent increase from 735 g wet weight $24m^{-2}$ at Mombasa to 1468 g wet weight $24m^{-2}$ at Umtata. The grapsid/ocypodid ratio also shifted latitudinally, most consistently in terms of biomass: Mombasa – 0.65; Zanzibar – 1.5; Maputo- 2.6; Umtata – 6.8.

Discussion

Heterogeneity in habitats and communities

The complex protocols for selecting sampling areas and conducting visual census aimed to minimise the effects of the heterogeneous mangrove environment. This heterogeneity has confounded many previous efforts to quantify mangrove crab populations (Lee, 1988). It is clear from the results that this was only partly successful. Thus the variability in immersion period for what were selected as equivalent areas by substratum and biological criteria was unexpected. Clearly the relationship between the hydrological regime in a mangrove and the distribution of biotopes is both complex and variable – thus the rhizophoran biotope can exist at quite different shore levels . The stepwise regression of species abundance on the measured environmental variables (immersion period, median sediment particle size, sediment organic content) overall explained less than 30% (and for some species much less) of the variability in abundance, indicating that other variables also affected crab density. Finally the substantial variation in some instances between the two sites at a location indicated that other factors (not considered in the strict protocol) were involved. Consequently the trends in relation to tidal height and latitude, discussed below, have to be treated with a degree of caution. Future studies will have to critic-

Table 4. Crab numbers and biomass (g wet wt.) per 24 m^2 summarised by level and location. Grapsid/ocypodid ratio averaged for locations and levels.

Level	Crab type	Mombasa	Zanzibar	Mozambique	Umtata	Mean	G/O ratio
Number							
Upper Av.	Grapsids	54	117	62	347	145	
	Ocypodids	231	163	154	3	138	
	Total	285	282	216	350	283	1.1
Mid Av.	Grapsids	36	2	19	5	16	
	Ocypodids	421	1002	826	527	694	
	Total	457	1004	846	532	710	0.02
Rhizophora	Grapsids	63	83	327	216	172	
	Ocypodids	274	252	101	14	160	
	Total	342	335	428	230	334	1.1
All levels	Grapsids	51	67	136	189	111	
	Ocypodids	309	472	360	181	331	
	Total	361	540	497	371	442	
G/O ratio		0.17	0.14	0.38	1.04		
Biomass							
Upper Av.	Grapsids	475	1815	1681	3146	1779	
	Ocypodids	212	131	130	2	119	
	Total	687	2015	1810	3148	1915	14.9
Mid Av.	Grapsids	217	4	90	48	90	
	Ocypodids	397	814	758	532	625	
	Total	617	818	852	579	717	0.14
Rhizophora	Grapsids	165	291	1149	643	562	
	Ocypodids	705	451	215	34	351	
	Total	902	743	1365	677	922	1.6
All levels	Grapsids	286	703	973	1279	810	
	Ocypodids	438	465	368	189	365	
	Total	735	1192	1342	1468	1184	
G/O ratio		0.65	1.5	2.6	6.8		

ally address the questions of site selection criteria and levels of site replication.

The effects of lunar phase

Although there were often large differences between the new moon and full moon spring tide observations at a given site, there were no consistent trends apparent.

The effects of tidal level

Patterns in relation to tidal level differ between crab numbers and biomass. Since the ultimate aim of this study is to analyse energy pathways, biomass is the more relevant. However, it must be kept in mind that a unit biomass of small crabs is likely to have a greater metabolic throughput than the same mass of large specimens. The total crab biomass was generally of a similar order in the two lower strata, but about twice as high in the top-*Avicennia* level. This trend is not typical of intertidal transects of other ecosystems such as rocky shores, where the abundance of organisms of marine origin typically declines towards the top of the shore. However, mangrove crabs are almost entirely limited to activity whilst emersed, and the increased exposure time upshore will give greater feeding opportunities. At the same time the heavily shaded mangrove environment will offer protection from the stresses which inhibit high shore populations in more open habitats such as rocky shores and sandy beaches.

There were also substantial variations in the grapsid/ocypodid (G/O) ratio with tidal level on the shore. Overall the ratio was near unity on the low shore (though with considerable geographical variation), but ocypodids dominated in the mid zone (G/O ratio = 0.14), and grapsids at the top (G/O ratio = 15). The increasing abundance of the leaf eating grapsids in the drier high shore substrate was perhaps expected, but the ocypodids could be anticipated to predominate at the low level: they did not, except at the northernmost location. However, there were geographical trends (see below), which interact with the tidal level effects.

The effects of latitude

There was no consistent latitudinal trend in total crab numbers: Mombasa was rather lower, then numbers declined somewhat from Zanzibar to Umtata. However, for total crab biomass there was a consistent southerly increase from Mombasa (31 g wet wt. m^{-2}) to the Transkei (61 g wet wt. m^{-2}). This was surprising, as it was expected that in the more stressed southern mangrove systems this stress would be reflected in reduced macrofaunal biomass. In addition there were marked latitudinal changes in the grapsid/ocypodid ratio. The G/O ratio for biomass increased consistently from 0.65 at Mombasa to 6.8 in the Transkei. This was expected, since overall grapsids show a greater incursion into temperate climates than do ocypodids. This very marked change in dominance will have implications for energy flow patterns, with an apparent shift from deposit feeders in the tropics to leaf eaters in more temperate areas. The impact of this on the retention or export of mangrove primary production will need to be studied. Robertson and Daniel (1989) raised this same point in connection with grapsid and ocypodid dominated mangroves in Australia. They, and McIvor and Smith (1995), also pointed out the contrast between new world mangroves, where crabs play a minor role in leaf breakdown, and old world mangroves, where their role is generally important. McIvor and Smith (1995) suggested that increased tidal amplitude in Australia, compared to Florida, may be a factor in this difference: the role of the even greater tidal amplitude in East Africa must be considered.

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