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Influence of Seasonality and Bathymetry on Decapod Crustacean Community Structure in Malindi - Ungwana Bay, Kenya

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Abstract — Decapod crustaceans support both artisanal and semi-industrial fisheries in the Western Indian Ocean (WIO) region. Despite their commercial value, data on their community structure is lacking in most of the region but are important for stock management. This study provides information on seasonal and bathymetric variation in decapod crustacean community structure in Malindi-Ungwana Bay, a biodiversity rich ecosystem in coastal Kenya. Samples were collected in the northeast (NEM) and southeast (SEM) monsoon seasons during an experimental bottom trawling survey in 2011. A total of 43 transects covering an estimated area of 1 873 km^2 were trawled in four depth zones (0-10, 10-20, 20-40 and 40-100 m) in both seasons. Twenty species of decapod crustaceans belonging to the Penaeidae, Portunidae, Calappidae, Majidae, Matutidae, Palinuridae and Scyllaridae were harvested. Overall crustacean biomass was higher in the SEM than the NEM. Penaeid prawns were numerically the most abundant in both the NEM (89.3%) and SEM (85.3%) seasons, *Fenneropenaeus indicus* being the most abundant in the NEM (58%) and SEM (42%). nMDS plots revealed separation of crustacean assemblages between depth zones but not the seasons. Two-way crossed ANOSIM indicated significant difference in species composition between the depth zones but not the seasons, with higher species diversity in the shallower depth strata. Canonical Correspondence Analysis revealed that temperature, salinity, Secchi depth and dissolved oxygen influence the bathymetric distribution of species in the bay. Recommendations are made that these factors be taken into consideration in the management of the crustacean fishery in the bay.

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INTRODUCTION

Marine decapod crustaceans account for nearly 6.9% of worldwide fin and shellfish landings by weight (FAO, 2011) and these landings have been on the upward trend in recent decades (FAO, 2008, 2012). The rise in decapod crustacean catches is mostly attributable to increased effort as a result of dwindling fish stocks worldwide (Jackson *et al*., 2001; Worm *et al*., 2006; FAO, 2010). Crustacean stocks are, however, increasingly being threatened with overfishing (FAO, 2012), mostly because of the global shift in targeting these resources.

Fishing pressure can cause shifts in species community structure and ecosystem function (Jennings and Kaiser, 1998) with trophodynamic consequences (Leibold, 1996). Several abiotic and biotic factors may further influence the distribution patterns and community structure of marine benthic communities like crustaceans. Such abiotic factors include depth profile (Fanneli *et al*., 2007; Munoz, *et al*., 2008), salinity gradient (Gillett, 2008), substratum type (Lavrado *et al*., 2000) and rainfall patterns (Teikwa and Mgaya, 2003). Important biotic factors comprise environmental productivity (Follesa *et al*., 2009) and biological interactions (Jackson, *et al*., 2001).

A limited number of studies have been conducted on decapod crustaceans in the Western Indian Ocean (WIO) compared to the temperate latitudes. Most of the WIO studies have concentrated on species distribution (Mutagyera, 1984; Munga *et al*., 2012), the functional biology of single species (Wakwabi and Jaccarini, 1993; Wakwabi, 1996; Teikwa and Mgaya, 2003), and stock assessments and fisheries (Groeneveld and Melville-Smith, 1995; Groeneveld, 2000; Mwatha, 2005). Decapod crustaceans form an important link between lower and higher trophic levels and studies on factors that affect their community structure may offer useful information on ecosystem function at the local scale (Papiol *et al*., 2012). In ecosystems that are heavily fished and influenced by environmental variability, such as the expansive Malindi-Ungwana Bay in Kenya, information on variability in a resource's community structure is useful in assessing spatio-temporal drivers of assemblages. This study therefore aimed to provide information on the environmental correlates of crustacean community structure in the Malindi-Ungwana Bay.

The bay is the most productive nearshore ecosystem in coastal Kenya (Nzioka, 1981; Mutagyera, 1984) and has thus been the focus of various trawling expeditions. Recent resource-use conflict and a fishing ban in the bay (Munga *et al*., 2012) requires that scientific information be available to support management.

METHODS

Study site and survey design

The study was carried out within Malindi-Ungwana Bay on the northern coast of Kenya (Fig. 1). The bay lies between 2º 30'S - 3º 30'S and 40º 000'E - 41º 000'E. It is the only known trawlable ground on the Kenyan coast, extends along ~200 km of coastline and has a continental shelf ranging from 15-60 km in width, with an estimated fishing ground of 35 300 km^2 (Iversen, 1984; Mueni, 2006). The Athi and Tana Rivers (Fig. 1) discharge an estimated 6 000 million m3 of freshwater and 3 million tonnes of sediment annually into the bay (Tychsen, 2006), which is affected by the monsoons that prevail on the Kenyan coast (McClanahan, 1988). Briefly, the northeast monsoon season (NEM, November–March) is a period of calm seas, elevated sea surface temperatures and higher salinities, while the southeast monsoon (SEM, April–October) is characterised by rough seas, cool weather, lower salinities and higher plankton productivity. The influence of this seasonality on community structure of crustaceans in coastal East Africa is not well documented.

The data were collected during two trawl surveys in the bay using the FV Vega, a medium-sized Kenyan prawn trawler. The first survey was conducted during 22 January - 4 February 2011 (NEM), the second between

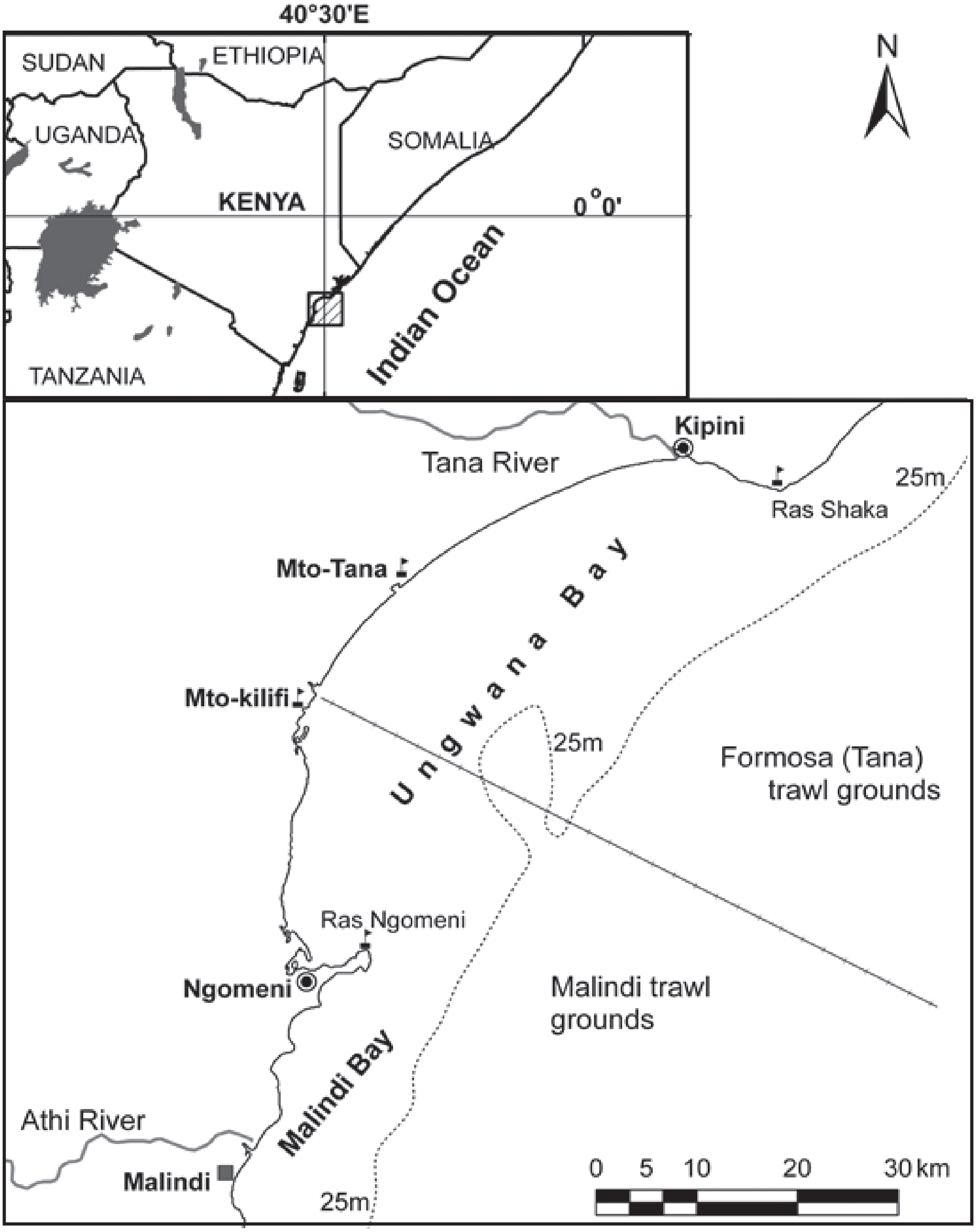

Figure 1. Map of the Malindi–Ungwana Bay area showing the discharge point of the Athi and Tana Rivers into the bay and the demarcation of the Formosa and Malindi commercial fishing (Source: Munga *et al.*, 2012).

22 May - 4 June 2011 (SEM). The trawler was fitted with two outrigger trawl nets made of nylon, comprising wings, a net body and cod-end with a total length of 44.3 m. The wings were 19.1 m long with a mesh size of 45 mm; the net body was also 19.1 m long but with a mesh size of 70.4 mm, and the cod-end was 6.1 m long with a mesh size of 45 mm. The nets each had a 22.5 m head rope length, a 25.4 m foot rope and a 28 m restraining chain

between the two trawl doors. They were lowered simultaneously by hydraulic winch and the trawl start time recorded when the nets reached the sea floor, while the trawl end time was recorded when the vessel started retracting the nets.

A total of 43 trawl transects were surveyed within the bay during a 13-day period in each season. The surveys were stratified by depth into four zones: 0-10 m (zone 1); 10-20 m (zone 2); 20-40 m (zone 3) and 40-100 m (zone 4). The depth zone intervals were not uniform because the shelf steepens rapidly a few miles from the shore.

The percentage area of each depth zone within the trawlable area was used to determine the proportion of sampling time apportioned to each zone in each season, given that a maximum of four trawls could be conducted per day. The four depth zones were 471, 803, 468 and 133 km^2 in area and were allocated 8 (zone 1), 17 (zone 2), 13 (zone 3) and 5 (zone 4) trawls, respectively, totalling 43 trawls in each seasonal survey. The trawl transects ran parallel to the shoreline to remain within the respective depth zone as much as possible; shallow areas, coral and rocky areas were avoided. The geographical coordinates of the start and end point of each trawl transect were determined using a GPS. Trawling was done at a speed of 2.5-3.0 knots during the day between 06:00-18:00 h and each trawl lasted an hour. The same transects were trawled during the NEM and SEM.

Sampling methods

Data on environmental variables were recorded at the start of each trawl during the NEM. A bottom water sample was collected using a Niskin bottle and dissolved oxygen, temperature and salinity measured using a digital meter. Water transparency was measured from the side of the boat using a Secchi disc. The depths of each transect position were measured using an echo sounder. The net was hauled onto the deck at the end of each trawl and the decapod crustaceans sampled using a protocol that depended on the catch size. When the catch was small and manageable (e.g. the total catch could be worked within an hour), the total haul was processed and sorted into the various crustacean groups. These were identified to species following identification keys by the FAO (1984) and De Grave and Fransen (2011) for prawns, and Stephenson (1948), Branch *et al*. (2007), Ng *et al*. (2008) and Richmond (2011) for crabs. Species were weighed to the nearest 0.1 g, and carapace lengths and widths measured to the nearest 1 mm using a Vernier caliper. Catches that were too large (requiring over an hour to work) were sub-sampled. All large specimens in the haul were first removed, identified and weighed individually to the nearest gram. The remaining catch was turned to achieve uniform mixing and then sub-divided into portions (sub-samples) of approximately equal size, one of which (b, kg) was randomly selected for analysis. The total weight (a, kg) of the other portions was also recorded. These weights were later added to that of the large specimens to determine the weight of the total haul. The weight of each species in the haul was estimated by multiplying their weight in the sub-sample (b, kg) by a raising factor (RF): RF= (a + b) / b.

Data analysis

Biomass estimates of penaeid prawns were calculated using the Swept Area Method (Sparre & Venema, 1998). The distance trawled (D) per transect was estimated in units of nautical miles (nm) as:

$$D=60*Sqrt((Lat1-Lat2)^2+(Lon1-Lon2)^2*\cos^2(0.5*(Lat1+Lat2))) \quad ......(1)$$

Where:

Lat1= Latitude at start of haul (degrees)
Lat2 = Latitude at end of haul (degrees)
Lon1 = Longitude at start of haul (degrees)
Lon2 = Longitude at end of haul (degrees)

The estimated trawl distance was then multiplied by the length of the head rope (22.5 m) to get the trawled area (A, nm^2), with a correction factor of 0.5 for the net configuration (Pauly, 1980):

$$\text{Swept Area (A)} = D * 22.5 * 0.5 \quad ......(2)$$

The catch densities (converted to $kg.km^{-2}$) of species were then derived for each haul, while species biomass (B, Kg) in each haul was derived as:

B = density x A / X1 ....(3)

Where X1 is sampling proportion of crustaceans present in the swept area (X1 = 1, assuming all the crustaceans were fully accessible to the trawl).

Multivariate non-metric multi-dimensional scaling (MDS) was used to describe the community structure by depth zones and season (NEM and SEM) based on the Bray-Curtis similarity index (Clarke and Warwick, 2001). Two-way ANOSIM was used to test for differences in community structure with depth zones and seasons as factors, while two-way SIMPER analysis identified which crustacean species contributed most to the dissimilarity. The resulting R-values provided a measure of variation between samples, ranging from -1 to 1. Values tending to zero indicated little difference in species composition between depths/seasons, while values tending to +1 inferred differing composition (Clarke & Warwick, 2001). Canonical Correspondence Analysis (CCA) was used to analyse the influence of environmental factors (depth, temperature, dissolved oxygen, Secchi depth and salinity) on species distribution only during the NEM. The statistical analyses were performed using PRIMER version 6.

Two-way ANOVA (on log (x+1) transformed data) was used to test for the effect of seasons and depth on overall crustacean biomass, species richness and diversity in the bay. Taxonomic richness (S) and the Shannon-Wiener diversity index (H') were used to describe the community structure. As S reflected the total number of species of crustaceans in a stratum, the mean richness was calculated according to the depth zones and season. H' was calculated following Magurran (1988):

$$H' = - \Sigma i \; pi \log (pi)$$

Where pi is the proportion of the total count arising from the ith species in the stratum or season.

RESULTS

Species composition, abundance and catch rates

Totals of 767 and 1 808 crustaceans were sampled during the NEM and SEM, respectively, including 20 decapod crustacean species belonging to seven families. During the NEM, 11 species were harvested, mostly penaeid prawns (5 species), but relatively more portunids (9 species) made up the 19 species were caught during SEM (Table 1). Among the penaeid species, *Fenneropenaeus indicus* had the highest mean abundance (individuals. km^{-2} ± SE) of 8 318 ± 4 132, followed by *Metapeneus monoceros* (1 489 ± 689), *Penaeus semisulcatus* (1 069 ± 415) and Penaeus monodon (1 008 ± 439) (Table 1). The other crustaceans were recorded in low numbers of <400 individuals.km^{-2} (Table 1). Penaeid prawns were numerically the most abundant both in the NEM and SEM (89.7% and 85.3 %, respectively), with *F. indicus* making up the greatest proportion of the catch (NEM, 57.6%; SEM, 41.5%). The other penaeids occurred in variable proportions (Table 1). The Portunidae made up 9.4% and 12.3% of the numbers caught in the NEM and SEM, respectively, while the Palinuridae were very low in abundance in both seasons (Table 1).

Higher mean catch rates ($kg.km^{-2}$ ± SE) were recorded in depth zone 1 (64.2 ± 18.7 $kg.km^{-2}$) during the NEM, with catch rates of 15.7 ± 5.5 and 17.9 ± 9.5 $kg.km^{-2}$ being obtained in zones 2 and 3, respectively, during this season. During the SEM, catch rates of 67.14 ± 18.6 and 56.6 ± 18.1 $kg.km^{-2}$ were obtained from depth zones 1 and 2, respectively, while zones 3 and 4 yielded lower rates of 14.25 ± 5.8 and 1.31 ±1.1 $kg.km^{-2}$, respectively. Two-way ANOVA revealed that depth had a significant effect on the crustacean harvest ($F = 3.89$; df = 2, 130; $P = 0.022$). This was not the case with season ($F=0.014$; df= 1, 130; $P=0.95$), or the interaction of season and depth ($F = 0.57$; df = 2,130; $P = 0.54$).

Table 1. Mean abundance (individuals.Km^2 ± SE) and percentage composition of decapod crustaceans caught in trawls during the northeast (NEM) and southeast monsoons (SEM) in Malindi-Ungwana Bay. Values without standard errors indicate that species appeared in only one transect; (-) indicates absence of catch.

Species	%	NEM	%	SEM
Penaeidae				
Fenneropenaeus indicus	57.6	8318 ± 4132	41.5	12151 ± 3329
Marsupenaeus japonicus	0.9	149 ± 35	0.6	418 ± 135
Metapenaeus monoceros	12.5	1489 ± 688.8	27.0	6790 ± 1580
Penaeus monodon	8.9	1008 ± 439.3	5.9	1233 ± 294
Penaeus semisulcatus	9.8	1069 ± 414.6	10.3	3777 ± 1784
Portunidae				
Portunus sanguinolentus	9.3	347± 156.1	9.7	331 ±106
Thalamita crenata	0.1	19	0.05	20
Charybdis feriata	-	-	0.6	38 ±7
Charybdis hellerii	-	-	0.8	144 ± 124
Charybdis natator	-	-	0.2	81
Charybdis smithii	-	-	0.5	172
Podophthalmus vigil	-	-	0.05	21
Portunus pelegicus	-	-	0.05	21
Scylla serrata	-	-	0.3	33 ± 13
Calappidae				
Calappa calappa	0.3	40	-	-
Calappa sp.	0.1	21	0.4	168
Matutidae				
Ashtoret lunaris	0.7	97	1.0	91 ± 17
Majidae				
Majid sp.	-	-	0.2	31 ± 11
Scyllidae				
Thenus orientalis	0.4	20 ± 0.4	0.7	58 ± 24
Palinuridae				
Panulirus ornatus	0.3	-	0.1	21± 0.3

A greater harvest of prawns (the most abundant crustaceans in the bay) was obtained from depth zone 1 (78.7 ± 22.6 kg.km^{-2}) during the NEM. Depth zones 2 and 3 yielded near equal catches of 20.4±7.0 and 20.9±11 kg.km^{-2}, respectively. During the SEM, depth zones 1 and 2 yielded near equal catches of prawns of 112.4 ± 30.3 and 103 ± 31.01 kg.km^{-2}, respectively, higher than those recorded during the NEM. One-way ANOVA showed no significant difference in prawn catch rates during the NEM ($F = 2.14$; $df = 2, 36$; $P = 0.13$) or SEM ($F=0.93$; $df = 2, 43$; $P = 0.40$) in the three shallower depth zones. No prawns were harvested in depth zone 4 (40-100 m) in either season.

Bathymetric and seasonal distribution of species

Among the penaeid prawns, *F. indicus* and *M. japonicus* were restricted to depth zones 1 and 2 during both the NEM and SEM (Table 2). *M. monoceros* occurred in depth zones 1-3 during both seasons, but higher numbers were harvested in depth zones 1 and 2 during SEM. *P. monodon* and *P. semisulcatus* occurred in depth zones 1-3 during the SEM, with *P. semisulcatus* harvested in higher numbers in zones 1 and 2 during SEM (Table 2). Amongst the portunid crabs, only *Portunus sanguinolentus* was harvested in considerable numbers in both

Table 2. Seasonal distribution and abundance (individuals.Km^2 ± SE) of decapod crustaceans within depth zones during a) the northeast monsoon (NEM) and b) southeast monsoon (SEM) in Malindi-Ungwana Bay. Values without standard errors indicate that species appeared in only one transect; (-) indicates absence of catch.

Species	Depth Strata			
	Zone 1 (0-10 m)	Zone 2 (10-20 m)	Zone 3 (20-40 m)	Zone 4 (40-100 m)
a) NEM				
Fenneropenaeus indicus	11265 ± 5383	458 ±386	-	-
Marsupenaeus japonicus	248	116 ± 16	-	-
Metapenaeus monoceros	1918 ± 953	735	367 ±320	-
Penaeus monodon	1239 ±539	199 ± 74	-	-
Penaeus semisulcatus	-	564 ±544	1405 ± 577	-
Portunus sanguinolentus	576± 201	117 ± 12	-	-
Thalamita crenata	19	-	-	-
Charybdis feriata	-	-	-	-
Charybdis hellerii	-	-	-	-
Charybdis natator	-	-	-	-
Charybdis smithii	-	-	-	-
Podophthalmus vigil	-	-	-	-
Portunus pelagicus	-	-	-	-
Scylla serrata	-	-	-	-
Calappa calappa	40	-	-	-
Calappa sp.	-	21	-	-
Ashtoret lunaris	97	-	-	-
Majidae sp.	-	-	-	-
Thenus orientalis	20	21	20	-
Panulirus ornatus	-	-	-	-
b) SEM				
Fenneropenaeus indicus	15437± 4217	8208± 5210	-	-
Marsupenaeus japonicus	520 ± 294	350± 161	-	-
Metapenaeus monoceros	7003± 2046	7024±3141	4342	-
Penaeus monodon	1127 ± 428.2	1799 ± 250	632	-
Penaeus semisulcatus	1799 ± 250	6680 ± 3144	461± 234.0	-
Portunus sanguinolentus	486 ±168	176 ±59	21	-
Thalamita crenata	20	-	-	-
Charybdis feriata	41±1.0	41±12	21	-
Charybdis hellerii	-	20	-	268
Charybdis natator	-	81	-	-
Charybdis smithii	-	-	-	172
Podophthalmus vigil	-	-	21	-
Portunus pelagicus	-	21	-	-
Scylla serrata	20	39±19	-	-
Calappa calappa	-	-	-	-
Calappa sp.	-	-	167	-
Ashtoret lunaris	90 ± 24	98	-	-
Majidae sp.	20	42	-	-
Thenus orientalis	20 ± 0.2	54±34	145	-
Panulirus ornatus	20	21	-	-

seasons, and mainly at shallower depths (Table 2). Amongst the Palinuridae (lobsters), *Thenus orientalis* was harvested in depth zones 1-3 in both seasons, while *Panulirus ornatus* was caught in depth zones 1 and 2 during the SEM.

MDS plots revealed that different crustacean assemblages were found in the depth zones but not the seasons (Fig. 2). Two-way crossed ANOSIM indicated that the difference in these assemblages between

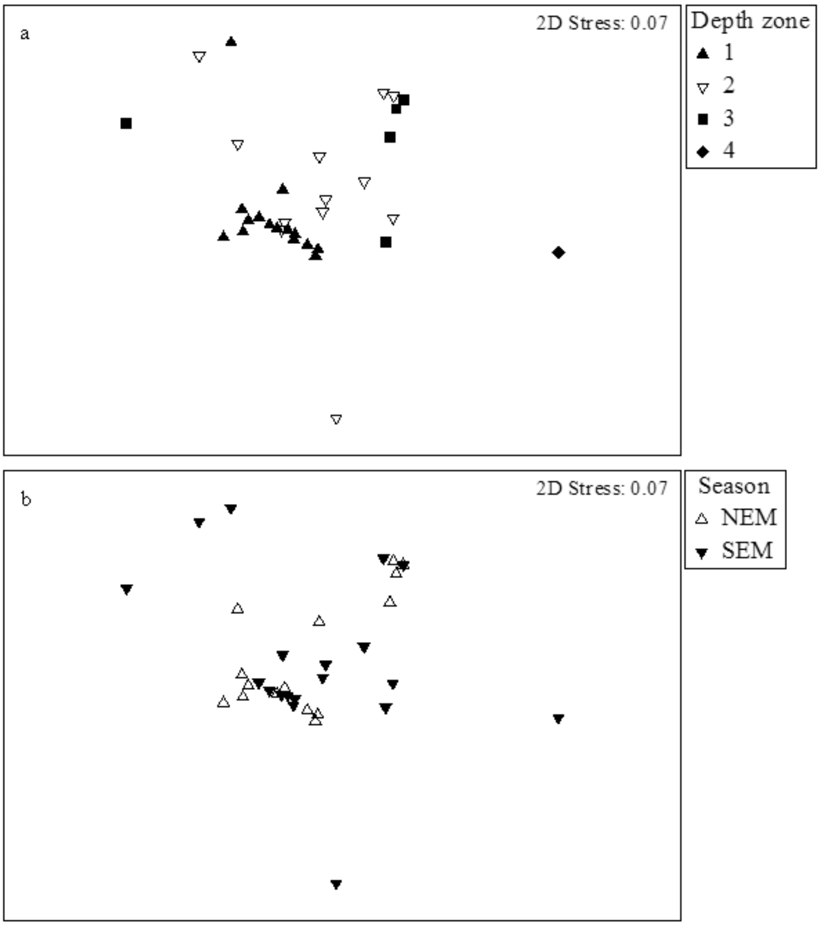

Fig. 2. Non-metric MDS plots showing decapod crustacean abundance according to a) depth zones and b) season in Malindi-Ungwana Bay, Kenya, based on combined northeast (NEM) and southeast monsoon (SEM) data.

the depth zones were significant but again not the seasons (R = 0.410; p = 0.002 and R = -0.029; p = 0.598 respectively). A pair-wise ANOSIM comparison test further confirmed the significance of the differences in the assemblages between depth zones 1 and 2, and between 1 and 3 (P < 0.05 in all cases; Table 3). A greater abundance of *F. indicus* in depth zone 1, and *P. semisulcatus* and *Charybdis natator* in depth zone 2, was responsible for the difference between these depth zones (two-way SIMPER: Table 4). Similarly, a greater abundance of *F. indicus* in zone 1 and *P. semisulcatus* and *Calappa pelii* in depth zone 3 (two-way SIMPER: Table 5) was responsible for the difference between these depth zones.

Species richness and diversity

Depth zones 1 and 2 were more diverse than zones 3 and 4, evidenced by the results on species richness (S) and the Shannon-Wiener diversity index (H') (Fig. 3a). Also, species diversity was higher in the SEM than NEM (Fig. 3b). Results of two-way ANOVA yielded significant differences in crustacean species richness (nos.transect^{-1}) between depth zones (df = 2; F = 3.651; P = 0.039). However, the test revealed no significant difference between seasons or the interaction of depth zone and season (df = 1; F = 1.872; P = 0.182 and df = 2; F = 0.196; P = 0.823, respectively). A post hoc Fisher LSD

Table 3. Pair-wise ANOSIM comparison of differences in crustacean composition between depth zones in Malindi-Ungwana Bay based on abundance (%). Significance at P ≤0.05 in bold.

Depth zones	R statistic	p-value	Possible permutations	Actual permutations	Number ≥observed
1, 2	0.232	**0.013**	3185325	999	12
1, 3	0.806	**0.001**	54450	999	0
1, 4	0.952	0.125	8	8	1
2, 3	0.083	0.271	17325	999	270
2, 4	0.638	0.111	9	9	1
3, 4	0.5	0.400	5	5	2

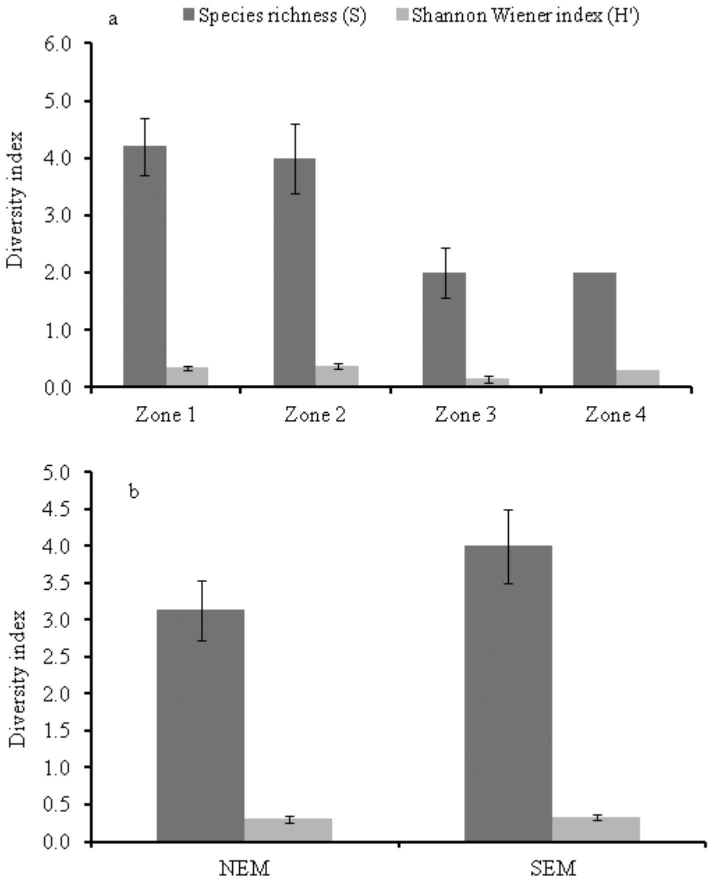

Fig. 3. Bathymetric variation of diversity measures (S ± SE and H' ± SE) of decapod crustacean species according to a) depth and b) season in Malindi-Ungwana Bay, Kenya.

test confirmed that depth zone 2 differed significantly from depth zone 3 in both the NEM and SEM, and depth zone 3 differed significantly from depth zone 1 in the SEM (P <0.05 in all cases).

Environmental measurements and species associations

No significant differences were encountered in temperature, salinity, dissolved inorganic nutrients (phosphates and nitrates), chlorophyll-*a* or biological oxygen demand

Table 4. Two-Way SIMPER Analysis of decapod crustacean species contribution to dissimilarity in terms of abundance (%) between depth zones 1 and 2 in Malindi-Ungwana Bay. The average dissimilarity was 65.3%, notable contributors to this being highlighted in bold.

Species	Depth zone 1 Average abundance (%)	Depth zone 2 Average abundance (%)	Average dissimilarity	Contribution (%)
Fenneropeneaus indicus	**58.11**	22.89	19.35	29.63
Penaeus semisulcatus	1.32	**29.05**	14.47	22.15
Metapenaeus monoceros	22.26	18.65	10.89	16.67
Portunus sanguinolentus	7.13	6.95	7.07	10.81
Penaeus monodon	9.43	5.45	4.43	6.78
Charybdis natator	0.00	**6.67**	3.18	4.87

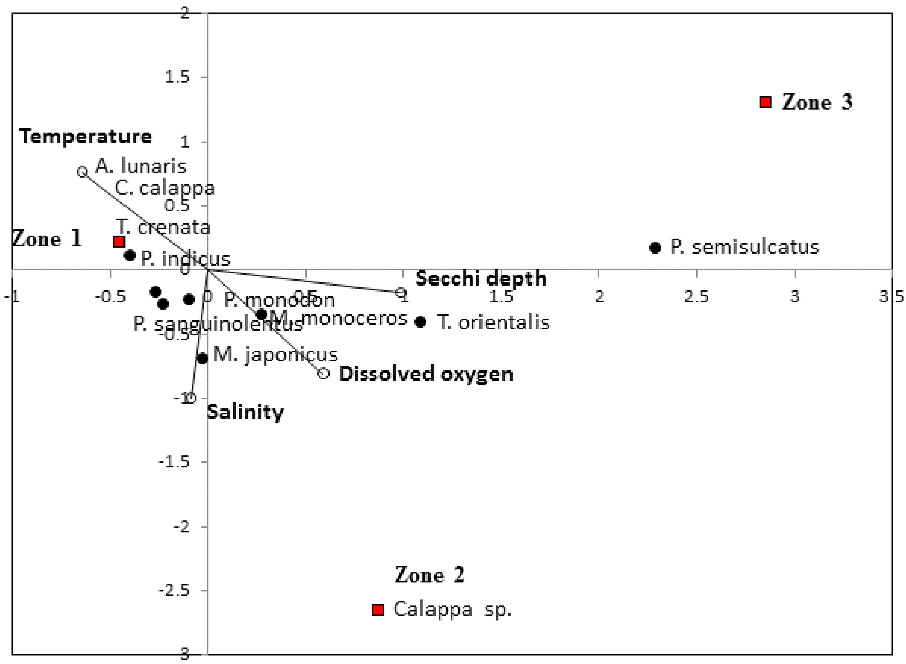

Fig. 4. Canonical Correspondence Analysis (CCA) showing the influence of physico-chemical factors on crustacean species abundance in the three shallower depth zones within Malindi-Ungwana Bay during the NEM. Species names are as shown on Table 1.

in bottom water samples collected from the different depth strata in the NEM (Table 6). Turbidity (Secchi depth) decreased with depth (0-10 m to 40-100 m); i.e. with increasing distance from the shore. Canonical Correspondence Analysis (CCA) of the influence of these environmental variables on crustacean abundance during the NEM are presented in Figure 4. Depth zones 2 and 3 are dissimilar from zone 1 on the x-axis, the differences being attributable to water temperature in zone 1, and water clarity, dissolved oxygen and salinity in zones 2 and 3. Respective indicators of this are *Ashtoret lunaris* and *Calappa calappa* in zone 1, and *M. japonicus*, *P. monodon*, *M. monoceros*, *P. sanguinolentus* and *T. orientalis* in zone 2. The *Calappa* sp. was associated with depth zone 2 but apparently was not influenced in abundance by the selected environmental variables.

Table 5. Two-Way SIMPER Analysis of decapod crustacean species contribution to dissimilarity in terms of abundance (%) between depth zones 1 and 3 in Malindi-Ungwana Bay. The average dissimilarity was 91.7%, notable contributors to this being highlighted in bold.

	Depth zone 1	Depth zone 3		
Species	Average abundance (%)	Average abundance (%)	Average dissimilarity (%)	Contribution (%)
Penaeus semisulcatus	1.32	**69.90**	35.15	38.32
Fenneropeneaus indicus	**58.11**	0.00	28.59	31.16
Metapenaeus monoceros	22.26	14.28	12.25	13.35
Calappa sp.	0.00	**10.39**	4.90	5.34
Penaeus monodon	9.43	1.54	4.58	4.99

DISCUSSION

Higher abundances of crustaceans were harvested during this study in the oceanographically rougher SEM than the calmer NEM season using the same vessel. Although previous studies have yielded similar results (e.g. Mwatha, 2005; Munga *et al*., 2012), the causes of this difference are unclear. Contributory factors may be higher recruitment to the fishery by the Penaeidae (the most abundant group), higher vulnerability to gear or higher environmental productivity during the SEM. Nonetheless, more studies are needed to determine the causal factors for seasonal variability in crustacean abundance in the Malindi-Ungwana Bay.

Significant differences in the relative abundance of penaeid prawns have been found between dry and wet seasons elsewhere (Teikwa & Mgaya, 2003; de Freitas, 2011), suggesting the influence of rainfall and hence salinity on prawn catches. Rainfall is thought to initiate the migration of prawns offshore from estuaries, either by lowering salinities or simply the mechanical disturbance of run-off and of the bottom sediments (Meager *et al*., 2003; de freitas 2011). Juvenile prawns are known to move to offshore fisheries as a result of a reduction in inshore salinities during the rainy season (Staples and Vance, 1986). The SEM in coastal Kenya is typically a wet season and there is an increase in river discharge into the Malindi-Ungwana Bay during this season which introduces organic matter to the bay (Tychsen, 2006). This probably increases primary productivity in the bay, as it does in the Mediterranean

Table 6. Environmental variables (mean ± SE) in the different depth zones measured during the northeast monsoon (NEM) in Malindi-Ungwana Bay, Kenya. Df = 3; p-values in bold are significant at P <0.05.

Environmental variables	0-10 m	10-20 m	20-40 m	40-100 m	ANOVA F	P
Temperature (°C)	27.7 ± 0.2	27.2 ± 0.3	27.7 ± 0.2	27.3 ± 0.2	1.000	0.408
Salinity	36.3 ± 0.2	36.4 ± 0.2	36.2 ± 0.1	37.0 ± 0.6	1.900	0.151
Secchi depth (m)	1.5 ± 0.2	8.6 ± 0.7	12.7 ± 1.2	14.0 ± 1.2	19.22	**0.000**
Dissolved Oxygen (mg/l)	5.5 ± 0.1	5.7 ± 0.0	5.4 ± 0.1	5.7 ± 0.2	3.050	**0.043**
Chlorophyll-*a* (µg/l)	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.557	0.647
(Nitrate + Nitrite) - N (µM)	1.8 ± 0.4	1.3 ± 0.1	1.2 ± 0.2	0.8 ± 0.2	1.084	0.370
Phosphates - P (µM)	1.1± 0.2	0.9 ± 0.1	1.1 ± 0.1	1.2 ± 0.6	0.839	0.482
BOD_{5days} (mg/l)	4.7 ± 0.2	4.6 ± 0.1	4.1 ± 0.2	3.5 ± 0.1	5.885	**0.003**

(de Juan & Cartes, 2011). Such increased nutrient input into Malindi-Ungwana Bay would suggest that productivity-induced seasonal differences cause changes in crustacean abundance in the bay. This would suggest the need for seasonally structured management regulations for exploitation of its penaeid prawns.

The penaeid prawns were mostly restricted to the shallow zones 1 and 2 (0-10 and 10-20 m) during both seasons. However, *Penaeus semisulcatus*, *Metapenaeus monoceros* and *P. monodon* had a wider bathymetric distribution that was more distinct during the SEM. This may be attributable to a higher tolerance of environmental variability by these species than the other penaeids. A similarly wide bathymetric distribution associated with temperature tolerance has been reported for *P. semisulcatus* in Kuwait (Ye *et al*., 1999), for *M. monoceros* in the Iskenderum Bay (Can *et al*., 2004) and in the Gulf of Antalya in Turkey (Yilmaz *et al*., 2009), and for both species in Mozambique (de Freitas, 2011).

Changes in salinity and temperature probably contributed to high species richness in Malindi-Ungwana Bay during the SEM, with a peak in diversity in depth zones 1 and 2. Increased runoff during the SEM results in temperature and salinity stratification (Papiol *et al*., 2012) and this may contribute to higher larval survival (due to differential thermal warming of strata) and, hence, high species diversity in the bay during this season. Other studies have found that crustacean diversity is affected by temperature, salinity and prey availability within estuaries and bays (Vance *et al*., 1985; Meager *et al*. 2003; Papiol *et al*., 2012).

The distribution of species is affected by a number of environmental variables such as temperature and productivity, which can affect both their maximum densities and the extreme limits in their distribution (Fanelli *et al*., 2007). Wienner and Read (1982) observed that decapod crustacean communities show definite changes in structure (species abundance and composition) with season and depth. However, Munoz *et al*. (2008) found no seasonality in decapod communities in the West Mediterranean Sea due to spatial interactions between assemblages. The presence of most of the species in depth zones 1 and 2 in this study may have been due to high primary productivity and other favourable environmental factors such as salinity, dissolved oxygen and substratum type. However, the study did not cover some of these parameters.

Although some studies (e.g. Fanelli *et al*., 2007; Wienner & Read, 1982) have reported the influence of both seasonality and depth on crustacean distributions, this study, like others (e.g. Munoz *et al*., 2008) found that seasonality had less influence on the crustacean assemblages than depth. Environmental variables directly related to depth, such as temperature and dissolved oxygen, may play an important role in structuring the assemblages. Canonical Correspondence Analysis indicated that temperature influenced the composition of species in depth zone 1 during the NEM, while dissolved oxygen, water clarity and salinity had a greater effect on species composition in depth zones 2 and 3. A lack of environmental parameters during the SEM precluded determination of the effects of these environmental variables during this season.

In conclusion, the study found that penaeid prawns were the most abundant group in all the depth zones and seasons in Malindi-Ungwana Bay. All crustacean groups occurred in higher abundance in the SEM than in the NEM. This variation was attributed to seasonal changes in oceanographic conditions and crustacean behaviour. Decapod crustacean assemblage structure in the bay appeared to be more influenced by depth than seasonality, and most of the biomass was found at shallower depths. The study also revealed higher crustacean species diversity in the bay during the SEM than the NEM in all depth zones. Taking these results into consideration, it is recommended that the spatial and temporal variation in crustacean community structure should be considered when developing a fisheries management plan for the bay, and that future studies should determine the parameters that influence the seasonal abundance in populations.

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