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## Species composition, distribution patterns and population structure of penaeid shrimps in Malindi-Ungwana Bay, Kenya, based on experimental bottom trawl surveys



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### ABSTRACT

The species composition, distribution patterns and abundance of penaeid shrimps in Malindi-Ungwana Bay, Kenya, were investigated after six years of no bottom trawling in the area. Two surveys undertaken during the dry Northeast Monsoon (NEM) and wet Southeast Monsoon (SEM) seasons in 2011 identified areas with abundant shrimps near the outflows of the Sabaki and Tana rivers. Distinct species composition and abundance patterns were found at the two areas, attributed mainly to depth, turbidity and season. *Penaeus semisulcatus* was more abundant at the Sabaki area, where it was deeper with a muddy bottom and less turbid waters. *Fenneropenaeus indicus* was more abundant in the Tana area, a shallower, more turbid area with sandy-mud sediments. *Penaeus monodon*, *Penaeus japonicus* and *Metapenaeus monoceros* were found in both areas, suggesting wider tolerance to environmental conditions. Shrimp total biomass and catch rates were significantly greater during the SEM survey, and decreased as depth increased beyond 10 m. Small-sized *M. monoceros* and *P. monodon* individuals were abundant during the SEM survey, whereas large ones with ripe and spent gonads were more common during the NEM survey, suggesting that spawning took place between the two surveys. Seasonal patterns in gonad maturity were less clear for *F. indicus* and *P. semisulcatus*. The length at first maturity ( $L_{50}$ ) varied among species, suggesting that different species in the bay start spawning at different sizes, an important biological reference for sustainable resource exploitation. This study confirms the importance of the Sabaki and Tana areas as important habitats for penaeid shrimps in Malindi-Ungwana Bay.

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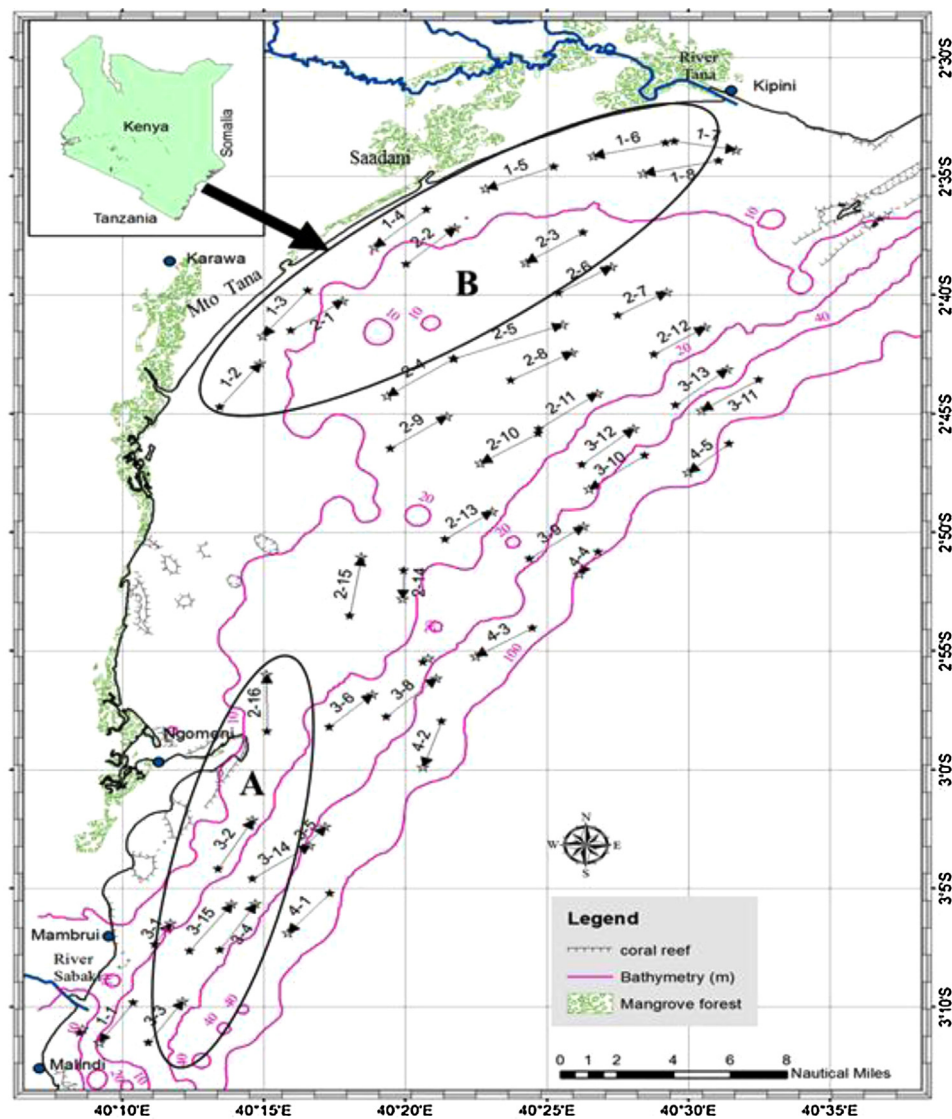
### 1. Introduction

The penaeid shrimps (or prawns) have a worldwide distribution in the tropical and subtropical seas, where they constitute an important exploitable resource in estuarine and coastal habitats (Garcia and le Reste, 1981). At least 19 species from 7 genera have been reported from the Western Indian Ocean (WIO) region (Holthuis, 1980; de Freitas, 2011), where they support artisanal and industrial shrimp trawl fisheries along the eastern coast of Africa and in Madagascar (Teikwa and Mgaya, 2003; Gillet, 2008; Le Monach et al., 2011).

Most shrimp fishing in Kenya takes place in Malindi-Ungwana Bay (Fig. 1), where two fishing sectors are active: an artisanal fishery comprising about 3500 fishers and a fleet of roughly 600 traditional fishing crafts used to catch finfish and shellfish (Fulanda et al., 2011); and a commercial bottom trawl fishery. Annual fish and shrimp landings from the artisanal fishery in this area ranged between 1013 and 1653 t between 2001 and 2008, with shrimps representing between 71.5 and 187.1 t of the landings (Munga et al., 2012). The commercial bottom trawl fishery in the bay was initiated after a series of successful surveys undertaken by the Kenya Government, UNDP and FAO since early 1960 (Iversen, 1984; Venema, 1984; Saetersdal et al., 1993). Bottom trawling with a fleet of three or more trawlers continued for several decades, landing an average of 400 t of shrimps per year in the 1970s, 80s and 90s (Mwatha, 2005). The trawl fishery was, however, banned by the Kenyan Government in 2006, as a result of user conflicts between trawl and artisanal fishers, and declining catches (Fulanda et al., 2009, 2011; Munga et al., 2012).

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**Fig. 1.** A map of Malindi-Ungwana Bay, Kenya, showing the groupings of trawl transects at the Sabaki (area A) and Tana (area B) areas. Figures on the map indicate transect number and depth stratum respectively. Transect 1–2 means transect No. 1 in depth stratum 2. Transect 1–1 was incomplete and hence excluded from the survey data.

Shrimp catches in the bay comprise mainly five species: *Fenneropenaeus indicus* (formerly known as *Penaeus indicus*), *Penaeus monodon*, *P. semisulcatus*, *P. japonicus* and *Metapenaeus monoceros* (Iversen, 1984; Mwatha, 2005; Munga et al., 2012). The post-larvae of these species prefer estuaries or estuarine-like environments, and juveniles migrate from the estuaries to shallow offshore mud banks where they grow to maturity and spawn (Garcia and le Reste, 1981; Dall et al., 1990). Post-larvae move back into the estuarine nursery grounds from the adult breeding grounds to complete their life cycle. The life span of most penaeids is between 1 and 2 years and their abundance and mean size on offshore banks may vary greatly by depth and between seasons, reflecting spawning, recruitment, population age structure and catchability (Garcia and le Reste, 1981; Dall et al., 1990; Bishop and Khan, 1991).

A major difference between closely related shrimp species is that they prefer different habitats along gradients of substrate type, depth, turbidity, temperature and salinity (Garcia and le Reste, 1981; Dall et al., 1990). Substrate preference by juveniles tends to be maintained in the adult phase. Furthermore, movement and dispersal of post-larvae in estuarine environments involve specific sets of behavioural cues and responses, which are associated with a particular developmental period, and can be species-specific (Forbes

and Benfield, 1986a, 1986b; Benfield et al., 1989; Dall et al., 1990). These differences in environmental variables may lead to differences in species composition of penaeid shrimps (Demetriades and Forbes, 1993).

Two major rivers, Tana (850 km long) and Sabaki or Athi/Galana (650 km) drain into Malindi-Ungwana Bay from the Kenyan highlands. The estuaries and nearshore mud banks with terrigenous sediments support the bulk of the shrimp fishery in the bay (Abuodha, 2003; Kitheka et al., 2005). The productivity of the bay is influenced by the river and nutrient discharge, as well as patterns of monsoon winds, tides and the offshore Somali and East African Coastal currents (McClanahan, 1988; Kitheka et al., 2005; Bouillon and Dehairs, 2007). The river discharge is highest during the wet Southeast Monsoon (SEM) season between April and October. The Northeast Monsoon (NEM) season, between November and March, receives less rain, and hence river discharge is reduced during these months. However, the influence of the sediments and the freshwater discharge by the Tana and Sabaki river systems on the bay remain poorly understood (Kitheka et al., 2005; Bouillon and Dehairs, 2007; Bouillon et al., 2009).

The aims of this study were to investigate the spatial and temporal patterns in the composition of the shrimp communities

and the population structure of the dominant shrimp species in Malindi-Ungwana Bay, and to identify the importance of a suite of environmental variables on the observed patterns. Shrimp population structure (size composition, size at first maturity, and gonad maturity stages) was used to assess differences in recruitment and breeding periods between species. Spatio-temporal information on shrimp populations in Malindi-Ungwana Bay is important for the development of fisheries management strategies to ensure sustainability, while avoiding resource user conflicts between trawl and artisanal fishing sectors.

## 2. Materials and methods

### 2.1. Survey design

Malindi-Ungwana Bay lies along the northern coast of Kenya (2°–3° S; 40°–41° E) and has an estimated trawlable area of 5824 nm<sup>2</sup> (Iversen, 1984; Fulanda, 2003) (Fig. 1). Two surveys of 13 days duration were conducted during January–February 2011 (NEM season) and May–June 2011 (SEM season). The bay was sub-divided into 4 depth strata and the area of each was estimated from the British Admiralty Chart No. 3362 (1957) using regular polygons: 0–10 m depth (137.3 nm<sup>2</sup>), 10–20 m (234.1 nm<sup>2</sup>), 20–40 m (136.3 nm<sup>2</sup>) and 40–100 m (38.7 nm<sup>2</sup>). A commercial bottom trawler (FV Vega, 25 m length, 146 t gross register tonnes) was used to conduct the surveys by towing a net with a total length of 44.3 m, mesh sizes of 70 mm in the body and 45 mm in the cod-end, and a head rope length of 22.5 m over the stern (deeper or rocky strata) or on port or starboard booms (shallow strata). Tows were conducted roughly parallel to the shoreline, for 1 h at a speed of 2.5 knots. The geographical coordinates and depth at the start and end of each tow were recorded. Tows were conducted near the outflows of the Sabaki (area A) and Tana (area B) rivers and further offshore areas A and B in depths up to 100 m (Fig. 1). Only catches along transects from area A and B contained shrimps in one or both seasons. These transects are therefore further considered in the data analysis. All other transects had no shrimps, but only bycatch.

### 2.2. Sampling methods

A neuston bottle was used to collect bottom water samples for salinity and temperature measurements. From these water samples, sub-samples of at least 3 replicates of 50 ml each were processed for determination of Chlorophyll-a (Chl-a), dissolved inorganic nutrients (phosphates and nitrates), and biological oxygen demand (BOD) in a laboratory following standard procedures (Parsons et al., 1984). A secchi disc was used to measure water transparency at the start and end of each tow, as an indication of turbidity.

All unwanted debris, plants and large organisms were first removed from catches, whereafter the remainder were sorted into fish and shrimp categories. Total catches of shrimps were weighed, a 2 kg sub-sample for large catches, and the entire catch for small catches, were frozen for species identification and further analysis in a laboratory. The FAO species identification sheets for the WIO (Fischer and Bianchi, 1984) were used to identify shrimps. The total catch of each species from each tow was calculated by multiplying the sub-sample by a raising factor derived from the sub-sample to total shrimp catch weight (see Stobutzki et al., 2001; Tonks et al., 2008). Shrimp carapace length (CL) was measured to the nearest 0.1 mm using a vernier calliper, and sex and gonad maturity stages were determined visually following King (1995).

### 2.3. Data analyses

Shrimp biomass was calculated using the swept area method (Sparre et al., 1989). The swept area ( $a$ , nm<sup>2</sup>) or 'effective path swept' for each tow was calculated as:

$$a = D \times h \times X$$

where  $D$  is the distance covered in nm ( $D = 60 \times \sqrt{(Lat_1 - Lat_2)^2 + (Lon_1 + Lon_2)^2 \cos 0.5^2 (Lat_1 + Lat_2)}$ ),  $h$  is the length of the head-rope (m), and  $X$  is the fraction of the head-rope length equal to the width of the path swept by the trawl. The value of  $X$  was set at 0.5 in this study (Pauly, 1980).

Catch rates were calculated as catch ( $C$ , kg) divided by the time spent trawling ( $t$ , h) and converted to catch per unit area (CPUA, kg/nm<sup>2</sup> = biomass  $b$  per unit area) by dividing by the swept area ( $(C/t)/(a/t) = C/a$ ).

Total biomass ( $B$ , kg) was calculated from:

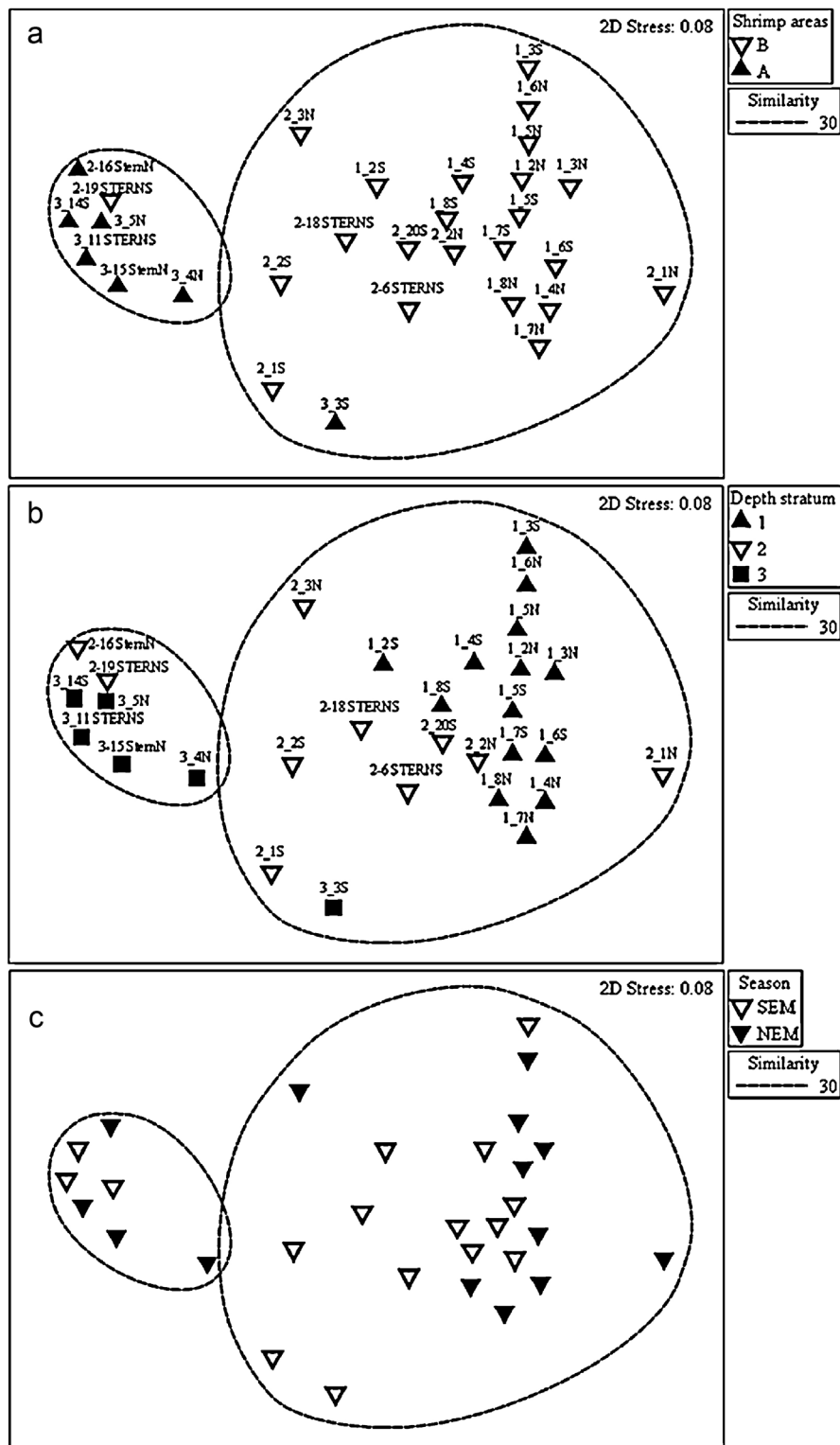
$$B = \frac{(\overline{C/a}) \times A}{X_1}$$

where  $C/a$  is the CPUA of all tows (kg/nm<sup>2</sup>),  $A$  is the overall area under investigation (nm<sup>2</sup>), and  $X_1$  is the estimated proportion of shrimps present in the area swept. We assumed that all shrimps in the path of the tow would be captured (i.e.  $X_1 = 1$ ). The total shrimp biomass for the surveyed area was calculated from 41 tows made in the NEM season (representing an area of 546.4 nm<sup>2</sup>) and from 36 tows in the SEM season (507.7 nm<sup>2</sup>).

The multivariate non-metric multi-dimensional scaling (MDS) technique was used to identify if geographical areas (Tana and Sabaki), depth strata (per 10 m depth interval) and seasons (NEM and SEM) differed in shrimp community composition based on Bray–Curtis similarity using PRIMER v6 software (Clark and Warwick, 2001). The spatio-temporal differences were further analysed by 2-way crossed ANOSIM with area or depth and season as factors. Two-way SIMPER analysis identified which shrimp species were most influential to the dissimilarity. Canonical Correspondence Analysis (CCA) using CANOCO v4.5 software was used to relate shrimp abundance to the environmental variables for the NEM survey only, because environmental data were not available for the SEM survey. Differences in environmental variables between areas and between depth strata for the NEM survey were tested using 1-way ANOVA, and differences in shrimp catch rates and biomass (catch-per-unit-area, CPUA) between depth strata and between seasons were tested using 2-way ANOVA from STATISTICA v7 software. Chi-square ( $\chi^2$ ) goodness of fit test (Zar, 1999) was used to compare sex ratios by season and area. A paired t-test was used to determine difference in sizes of shrimps between seasons. The length at first maturity ( $L_{50}$ ) was determined using unsexed shrimp individuals in gonad maturity stages I and II (immature) and III–V (mature) (King, 1995) by calculating the proportion of the mature individuals for each length class. The percentage mature by length class was fitted to a logistic function using least-squares and the solver routine on Microsoft excel. The equation used was:

$$P(l) = \frac{1}{1 + e^{-(a+bl)}}$$

where  $P(l)$  is the proportion of mature individuals at length  $l$ , and  $a$  and  $b$  the parameters of the logistic equation. The size at which 50% of individuals became mature was determined by back-calculation (King, 1995).



**Fig. 2.** Non-metric MDS plots (with indication of similarity levels of 30) showing the composition of shrimps by (a) area, (b) depth stratum and (c) season in Malindi-Ungwana Bay, Kenya, based on shrimp species abundance for the combined Northeast Monsoon (NEM) and Southeast Monsoon (SEM) surveys.

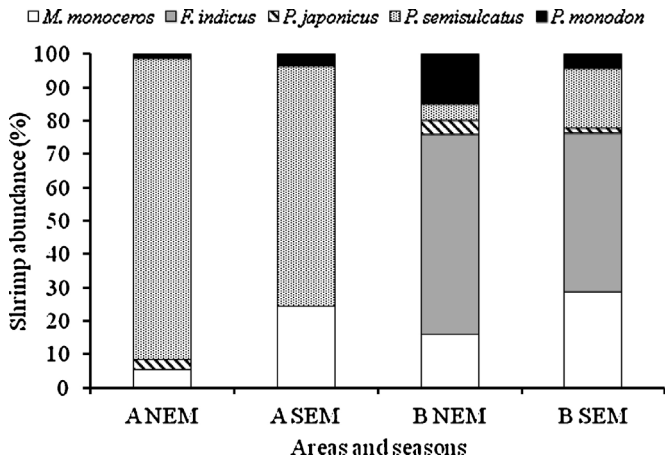
### 3. Results

#### 3.1. Shrimp distribution patterns, composition and abundance

From a total of 41 tows in the NEM survey, only 14 contained shrimps, and from 36 tows in the SEM survey, 15 contained shrimps.

The MDS plots for the two surveys combined showed a distinct separation of species composition by geographical area (2-way ANOSIM:  $R=0.708$ ;  $p=0.001$ ; Fig. 2a) and by depth (2-way ANOSIM:  $R=0.539$ ;  $p=0.001$ ; Fig. 2b), but not by season (2-way ANOSIM:  $R=0.040$ ;  $p=0.193$ ; Fig. 2c). Pair-wise comparison tests indicated that species composition at 0–10 m depth differed significantly





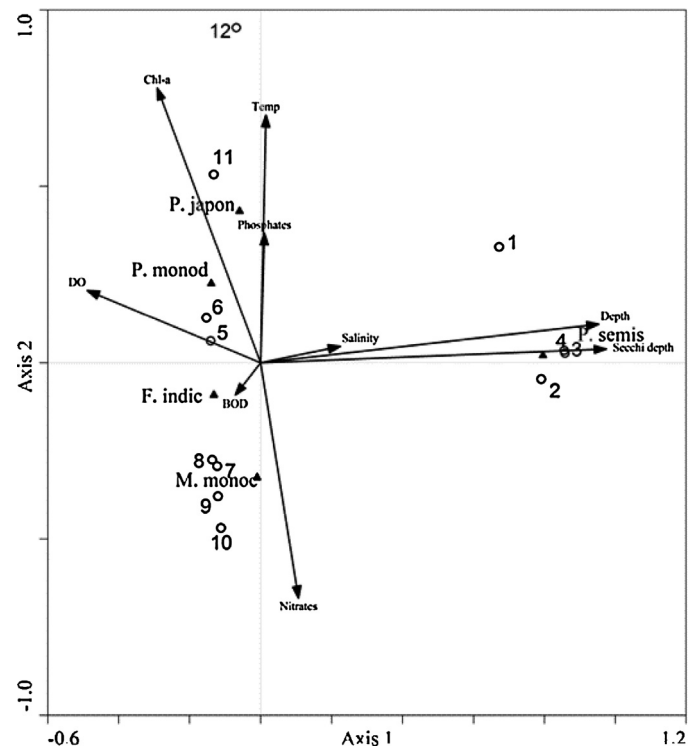
**Fig. 3.** Relative abundance (%) of shrimp species by area (A=Sabaki; B=Tana) and season (NEM=Northeast Monsoon season; SEM=Southeast Monsoon season) in Malindi-Ungwana Bay, Kenya.

from those at 10–20 m and 20–40 m ( $R=0.337$ ;  $p=0.002$  and  $R=0.970$ ;  $p=0.001$  respectively), and that composition at 10–20 m differed from 20–40 m ( $R=0.248$ ;  $p=0.047$ ).

The difference in shrimp composition between areas was due to more abundant *P. semisulcatus* in area A (Sabaki; on average 82.2%), and more abundant *F. indicus* in area B (Tana; 52.8%; Table 1). By area, *P. semisulcatus* contributed the highest dissimilarity (36.6%) and *F. indicus* followed with 26.9%. The least contributing species to the dissimilarity were *M. monoceros*, *P. monodon* and *P. japonicus* (12.5%, 5.1% and 1.8% respectively). Two-way SIMPER analysis based on depth and season indicated that *F. indicus* was most abundant in 0–10 m (66.2%) and *P. semisulcatus* in 20–40 m depth (81.1%). Neither *F. indicus* nor *P. japonicus* were recorded at 20–40 m depth.

Seasonal differences in shrimp species composition were less pronounced for *P. semisulcatus*, *F. indicus* and *P. japonicus* (Table 1). *M. monoceros* was more abundant during the SEM and *P. monodon* during the NEM season (Table 1). The seasonal dissimilarity depended mostly on *F. indicus* (14.6%), followed by *M. monoceros* (11.8%) and *P. semisulcatus* (10.4%). *P. semisulcatus* contributed on average 90% (NEM) and 72% (SEM) by numbers to catches in area A, followed by *M. monoceros* (6% in NEM and 25% in SEM) (Fig. 3). All five penaeid shrimp species were recorded in area B in both seasons; *F. indicus* contributed 60% (NEM) and 48% (SEM), followed by *M. monoceros* (16% and 29%). *P. japonicus* was the least abundant, irrespective of area, depth or season (Fig. 3).

The combined data for all shrimp species, including both seasons and all depths shallower than 40 m, indicated that shrimps were more abundant in the Tana area (3.76 kg/h) than in the Sabaki area (0.82 kg/h). The overall shrimp catch rate and biomass during the SEM (6.17 kg/h and 251 203 kg) were higher than during the NEM survey (1.45 kg/h and 74 570 kg; Table 2). In both surveys,



**Fig. 4.** Results of CCA showing relative importance of individual environmental variables to shrimp distribution based on the Northeast Monsoon (NEM) survey data in the Malindi-Ungwana Bay, Kenya. Numbers are trawl transects 1–4 in area A (Sabaki) and 5–12 in area B (Tana). Axis 1 explains up to 68.5% of the species–environment associations. Environmental data for the Southeast Monsoon (SEM) survey were not available.

biomass was greatest at the shallowest depth (0–10 m), and no shrimps were caught deeper than 40 m (Table 2). Results of 2-way ANOVA indicated that shrimp catch rates and biomass differed significantly between depths and seasons, and that the effect of the depth–season interaction was insignificant (Table 3).

### 3.2. Environmental measurements and species associations

Water depth of the trawled area was significantly greater at the Sabaki (area A) than the Tana (area B), but turbidity was greater at the Tana area (Table 4). No significant difference was observed in salinity, dissolved oxygen, dissolved inorganic nutrients (phosphates and nitrates), chlorophyll-a, or biological oxygen demand of bottom water samples collected from the two areas (Table 4). Turbidity decreased with increasing depth stratum from 0–10 m to 40–100 m, and this can be interpreted as a decrease in turbidity with increasing distance from the shore and the river outflows.

Results of CCA (Fig. 4) showed that axis 1 explains up to 68.5% of the species–environment associations. The distribution of *P.*

**Table 1**

Two-way SIMPER Analysis: shrimp species contributing to the dissimilarity in terms of abundance (%) at areal (Area A = Sabaki; Area B = Tana) and seasonal (NEM = Northeast Monsoon survey; SEM = Southeast Monsoon survey) levels. The average dissimilarity was 82.9% and 45.7%, respectively.

Species	Areal analysis				Seasonal analysis			
	Area A abundance (avg. %)	Area B abundance (avg. %)	Dissim. (avg. %)	Contrib. (%)	NEM abundance (avg. %)	SEM Abundance (avg. %)	Dissim. (avg. %)	Contrib. (%)
<i>Penaeus semisulcatus</i>	82.2	12.2	36.6	44.2	29.3	27.8	10.4	22.8
<i>Fenneropenaeus indicus</i>	0.0	52.8	26.9	32.4	42.6	38.7	14.6	31.9
<i>Metapenaeus monoceros</i>	13.9	23.4	12.5	15.0	13.3	28.1	11.8	25.8
<i>Penaeus monodon</i>	2.3	9.1	5.1	6.2	11.1	4.4	6.6	14.5
<i>Penaeus japonicus</i>	1.6	2.5	1.8	2.2	3.7	1.1	2.3	5.0

**Table 2**  
Shrimp catch rates (mean  $\pm$  SE) and total biomass by depth stratum estimated from the bottom trawl surveys undertaken during the Northeast Monsoon (NEM) and Southeast Monsoon (SEM) season in Malindi-Ungwana Bay, Kenya. A dash means that no catch was recorded.

Depth (m)	Area (nm <sup>2</sup> )	Northeast Monsoon survey (NEM)			Southeast Monsoon survey (SEM)		
		Hauls (n)	Catch rate (kg/h)	Biomass (kg)	Hauls (n)	Catch rate (kg/h)	Biomass (kg)
0–10	137.3	7	6.34 $\pm$ 1.72	59,519	7	16.85 $\pm$ 3.80	158,834
10–20	234.1	16	0.66 $\pm$ 0.45	11,284	19	5.19 $\pm$ 2.43	87,358
20–40	136.3	13	0.36 $\pm$ 0.26	3766	10	0.56 $\pm$ 0.50	5511
40–100	38.7	5	–	–	–	–	–
Overall	546.4	41	1.45 $\pm$ 0.49	74,570	36	6.17 $\pm$ 1.73	251,703

**Table 3**  
Results of 2-way ANOVA showing significant differences in shrimp catch rates (kg/h) and biomass (CPUA, kg/nm<sup>2</sup>) between seasons, depth strata and the interaction of season and depth stratum, in Malindi-Ungwana Bay, Kenya.

Factors	Df	Error Df	Catch rate (kg/h)		Biomass (kg/nm <sup>2</sup> )	
			F	p-value	F	p-value
Season	1	23	9.138	<b>0.006</b>	8.531	<b>0.008</b>
Depth stratum	2	23	4.397	<b>0.024</b>	3.872	<b>0.036</b>
Season $\times$ depth stratum	2	23	1.748	0.197	1.670	0.210

*semisulcatus* was strongly correlated to deeper water depths and less turbid waters, and the rest of the shrimp species were negatively correlated to these environmental variables. *P. japonicus* was correlated with chlorophyll-a (Chl-a) and water temperature, *P. monodon* with dissolved oxygen (DO), and *M. monoceros* with nitrates.

### 3.3. Shrimp gonad stages, size at first maturity and sex ratios

Large proportions (generally >0.4) of *M. monoceros*, *F. indicus* and *P. semisulcatus* females had immature or developing gonads (stages I or II) during both the NEM and SEM surveys (Fig. 5). In *P. monodon*, the bulk of female gonads were ripe (stage IV; 0.43) during the SEM survey and spent by the NEM survey (stage V; 0.38) (Fig. 5), and during this period their mean carapace length (CL) increased from 34.0 to 45.2 mm (Fig. 6). Most *M. monoceros* females had immature or developing gonads during the SEM survey (stages

I and II; 0.73), but by the NEM survey these were more mature (stages III–V; 0.56) (Fig. 6). Again this pattern was consistent with an increase in mean CL, from 23.9 mm during the SEM to 31.3 mm during the NEM survey (Fig. 6). *P. semisulcatus* captured during the NEM survey were significantly smaller than those caught during the SEM survey (*t*-test =  $-2.17$ ,  $p = 0.03$ ) in area A (Fig. 6), and a similar pattern was observed in area B, although the difference in mean CL was not significant. More females had spent gonads during the SEM survey (Fig. 5). *F. indicus* captured during the NEM survey were also significantly smaller than those caught during the SEM survey (*t*-test =  $-5.32$ ,  $p < 0.0001$ ).

*Metapenaeus monoceros* samples were dominated by females (56%), and *F. indicus* by males (64%;  $\chi^2$ -tests,  $p < 0.001$  in both cases), but no significant deviation from parity was observed in the other species ( $p > 0.05$  in all cases) (Fig. 6). The size at first maturity ( $L_{50}$ ) differed according to species (Fig. 7). *P. monodon* recorded the largest  $L_{50}$  of 41.9 mm within a sampled range of 23–72 mm CL. This

**Table 4**  
Environmental variables (mean  $\pm$  SE) by area and depth stratum measured during the Northeast Monsoon (NEM) survey in Malindi-Ungwana Bay, Kenya, (data not available for Southeast Monsoon, SEM survey). Measurements are for bottom water, except for turbidity (Secchi depth, m). Area A = offshore of Sabaki River; Area B = offshore of Tana River. Df = 2 for areal analyses. Df = 3 for depth analyses.

Environmental variable	Area and depth categories			ANOVA	
	Area A	Area B	A & B offshore	F	p-Value
Water depth (m)	34.0 $\pm$ 6.2	8.4 $\pm$ 1.0	26.4 $\pm$ 3.9	13.160	<b>0.0001</b>
Water temp. ( $^{\circ}$ C)	27.9 $\pm$ 0.2	28.1 $\pm$ 0.3	27.1 $\pm$ 0.2	6.250	<b>0.005</b>
Salinity (‰)	36.3 $\pm$ 0.3	36.4 $\pm$ 0.2	36.4 $\pm$ 0.1	0.090	0.914
Secchi depth (m)	13.8 $\pm$ 1.6	2.1 $\pm$ 0.5	11.3 $\pm$ 0.7	31.690	<b>0.000</b>
Dissolved oxygen (mg/l)	5.4 $\pm$ 0.2	5.5 $\pm$ 0.1	5.6 $\pm$ 0.1	0.100	0.320
Chlorophyll-a ( $\mu$ g/l)	0.24 $\pm$ 0.1	0.32 $\pm$ 0.1	0.29 $\pm$ 0.0	0.010	0.821
(Nitrate + nitrite)-N ( $\mu$ M)	1.2 $\pm$ 0.4	1.7 $\pm$ 0.3	1.2 $\pm$ 0.1	0.690	0.201
Phosphates-P ( $\mu$ M)	1.4 $\pm$ 0.4	1.1 $\pm$ 0.1	0.9 $\pm$ 0.1	1.410	0.259
BOD <sub>5days</sub> (mg/l)	4.4 $\pm$ 0.4	4.7 $\pm$ 0.11	4.2 $\pm$ 0.1	2.060	0.145

Environmental variable	Area and depth categories				ANOVA	
	0–10 m	10–20 m	20–40 m	40–100 m	F	p-Value
Water temp. ( $^{\circ}$ C)	27.7 $\pm$ 0.2	27.2 $\pm$ 0.3	27.7 $\pm$ 0.2	27.3 $\pm$ 0.2	1.000	0.408
Salinity (‰)	36.3 $\pm$ 0.2	36.4 $\pm$ 0.2	36.2 $\pm$ 0.1	37.0 $\pm$ 0.6	1.900	0.151
Secchi depth (m)	1.5 $\pm$ 0.2	8.6 $\pm$ 0.7	12.7 $\pm$ 1.2	14.0 $\pm$ 1.2	19.22	<b>0.000</b>
Dissolved oxygen (mg/l)	5.5 $\pm$ 0.1	5.7 $\pm$ 0.0	5.4 $\pm$ 0.1	5.7 $\pm$ 0.2	3.050	<b>0.043</b>
Chlorophyll-a ( $\mu$ g/l)	0.2 $\pm$ 0.0	0.3 $\pm$ 0.1	0.3 $\pm$ 0.1	0.3 $\pm$ 0.1	0.557	0.647
(Nitrate + nitrite)-N ( $\mu$ M)	1.8 $\pm$ 0.4	1.3 $\pm$ 0.1	1.2 $\pm$ 0.2	0.8 $\pm$ 0.2	1.084	0.370
Phosphates-P ( $\mu$ M)	1.1 $\pm$ 0.2	0.9 $\pm$ 0.1	1.1 $\pm$ 0.1	1.2 $\pm$ 0.6	0.839	0.482
BOD <sub>5days</sub> (mg/l)	4.7 $\pm$ 0.2	4.6 $\pm$ 0.1	4.1 $\pm$ 0.2	3.5 $\pm$ 0.1	5.885	<b>0.003</b>

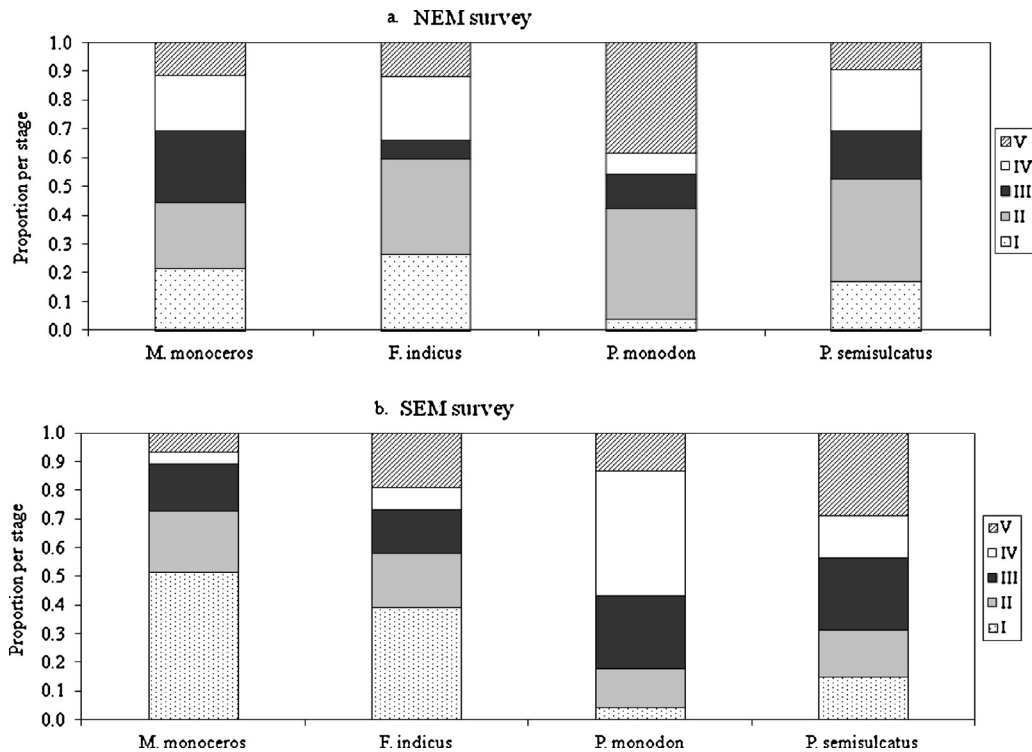


Fig. 5. Proportions of female gonad maturity stages by shrimp species caught in Malindi-Ungwana Bay, Kenya, during (a) Northeast Monsoon (NEM) and (b) Southeast Monsoon (SEM) surveys. Maturity stages were categorised as: I – immature, II – developing, III – maturing, IV – ripe and V – spent.

was followed by *F. indicus* ( $L_{50} = 37.4$  mm; 12–48 mm), *M. monoceros* ( $L_{50} = 36.0$  mm; 9–46 mm) and *P. semisulcatus* ( $L_{50} = 33.4$  mm; 17–58 mm).

#### 4. Discussion

The distribution of shallow-water penaeid shrimps in Malindi-Ungwana Bay was restricted to the Sabaki and Tana areas (A and B respectively, Fig. 1), and no shrimps were caught further offshore of these areas. The species composition and abundance patterns differed between the two areas: all five shrimp species were recorded at the Tana area in both the NEM and SEM seasons, whereas only three species (*P. semisulcatus*, *M. monoceros* and *P. monodon*) were recorded at the Sabaki area during the SEM. Although some clear patterns in species composition and abundance were observed in this study, it should be taken into account that data from only two surveys were available. Therefore inferences relating to these patterns should be viewed as indicative only.

*Fenneropenaeus indicus* was the most abundant species at the Tana area, coinciding with the more turbid environment. Turbid waters in Maputo Bay, Mozambique also coincided with areas of high *F. indicus* catches by commercial trawlers, and turbidity also affected the distribution of *F. indicus* and *M. monoceros* at Saco da Inhaca (Macia, 2004). Juvenile *F. indicus* and *M. monoceros* inhabited turbid waters with reduced visibility to escape predators (Macia, 2004; de Freitas, 2011). *F. indicus* in the present study was not recorded in the less turbid and deeper Sabaki area.

*Penaeus semisulcatus* dominated shrimp catches in the Sabaki area, and previous studies from the Western Indian Ocean (WIO) region showed that this species prefers low turbidity, muddy substrates and deeper water, where it is often associated with sea grass meadows (Macia, 2004; Forbes and Demetriades, 2005; de Freitas, 2011). *P. semisulcatus* is a naturally burrowing species during daytime, but feeds during the night when it can be fished more successfully (Hughes, 1966; Vance et al., 1994; de Freitas,

1986, 2011). Post-larval and young adult *P. semisulcatus* are often associated with submerged macrophytes, especially in estuarine backwaters, and adults prefer deeper waters (3–20 m) in large bays and offshore shelf areas (de Freitas, 1986, 2011). Macia (2004) observed that *P. semisulcatus* preferred deeper water bays compared to *F. indicus*; our findings agree with this observation. *P. monodon*, *M. monoceros* and *P. japonicus* inhabited both Tana and Sabaki areas, suggesting that they have a broader tolerance to factors that may limit *F. indicus* distribution in the bay. Forbes and Demetriades (2005) also suggested that *M. monoceros* can inhabit diverse habitats, from areas with submerged macrophytes to deeper reaches of mangrove swamps in low salinity environments.

The relatively shallow depth associated with sandy bottom and high turbidity, especially during the SEM season, favoured the existence of higher shrimp biomass at the Tana, compared to the Sabaki area. Fulanda et al. (2011) and Munga et al. (2012) also reported higher shrimp catch rates at the Tana area during the SEM than NEM season, using longer term commercial bottom trawl data. Similar seasonal variation in shrimp catch rates was also reported for the Tanzanian commercial bottom trawl and artisanal shrimp fisheries (Semese et al., 1998; Teikwa and Mgaya, 2003).

Size frequency and gonad maturity data can be used to define shrimp seasonal life cycles, which are often species-specific (Garcia and le Reste, 1981; Dall et al., 1990). For example, a preponderance of small shrimps on nearshore banks may suggest a recent recruitment event, larger shrimps with mature gonads would suggest a spawning season, and large shrimps with spent ovaries would suggest that spawning had recently taken place. In a best-case scenario, a series of monthly samples spanning at least a year would be required to describe the annual cycle of recruitment, growth to maturity and reproduction. However, given the cost of bottom trawl surveys, and the spatial heterogeneity of shrimp populations, far fewer samples are generally available, and inferences are somewhat speculative.

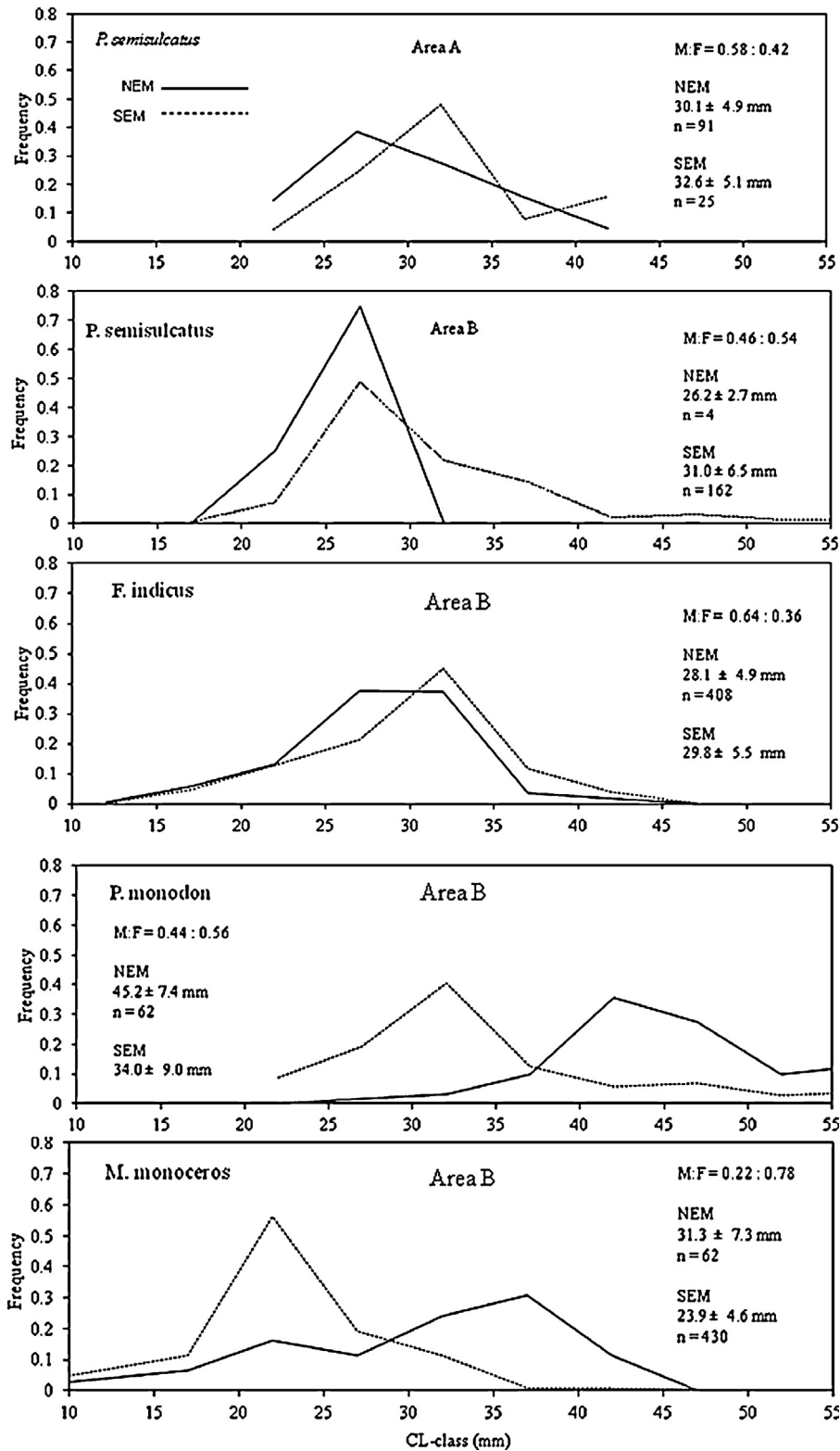


Fig. 6. Spatio-temporal size-frequency distributions, mean carapace lengths, and sex ratios (seasons combined) for the most abundant penaeid shrimp species sampled during the Northeast Monsoon (NEM) and Southeast Monsoon (SEM) surveys in Malindi-Ungwana Bay, Kenya. Only *P. semisulcatus* was abundant in area A (Sabaki).

*Fenneropenaeus indicus* in south-eastern Africa generally spawns throughout the year, with a peak around September to February (Benfield et al., 1989; de Freitas, 2011). Demetriades and Forbes (1993) showed that small *F. indicus* dominated catches in January to June on the Tugela Bank in South Africa, suggesting that juveniles then move out of estuaries onto offshore banks. Similarly,

*F. indicus* caught in Kenya was slightly smaller during January and February (NEM survey) than in May and June (SEM survey). A fundamental difference between these two areas is that the rainy season off eastern South Africa is between October and January (Demetriades and Forbes, 1993), corresponding to the dry NEM season in Kenya. The seasonal pattern in Kenya was difficult to



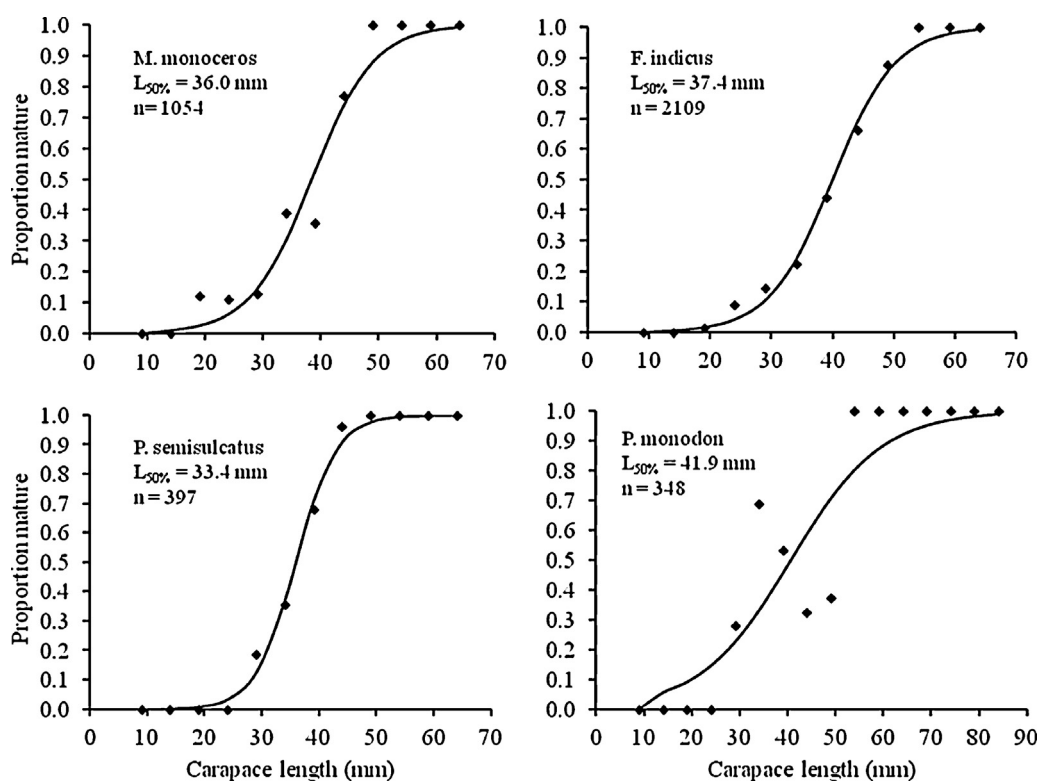


Fig. 7. Maturity ogives showing  $L_{50}$  estimates of penaeid shrimps (sexes combined) caught in the bottom trawl surveys in Malindi-Ungwana Bay, Kenya.

discern from only two surveys, especially if some spawning occurred throughout the year, and more regular annual sampling during NEM and SEM seasons will be required to clarify the seasonal cycle of *F. indicus* in this area.

The mean sizes of *M. monoceros* and *P. monodon* sampled in the SEM survey were much smaller than in the NEM survey, and a larger proportion of gonads were either ripe or spent in the latter samples (Figs. 5 and 6). This suggests that young adults of both species move away from the nearshore areas of the estuaries early in the year, during the SEM season, and grow to maturity during the dry NEM, towards the end of the year, or the beginning of the following year. It therefore appears that most *P. monodon* females spawned between the two surveys (between June and January), possibly at the end of the rainy season (SEM) or beginning of the dry season (NEM), when movement of post-larvae back to estuaries would presumably not be affected by swollen rivers. Assuming similar growth rates to maturity, and based on female gonad condition and shrimp size frequencies, it is therefore suggested that young *P. monodon* and *M. monoceros* in Kenya move out of the Sabaki and Tana estuaries onto offshore sandbanks during the wet SEM season (but possibly earlier than this), where they mature and spawn at a much larger size prior to, or during the dry NEM season. It should be noted that small *M. monoceros* (Fig. 6) and some immature *P. monodon* (Fig. 5) are also present on these banks during the NEM, suggesting that at least some recruitment from estuaries take place then. Demetriades and Forbes (1993) found a peak in catch rates of small *M. monoceros* in July to September off the Tugela Bank, and de Freitas (2011) found small *P. monodon* in Mozambique to migrate out of estuarine backwaters onto offshore banks from May onwards, with mean size on offshore banks increasing towards November. The seasonal patterns observed for *M. monoceros* and *P. monodon* in Kenya in the present study and in Mozambique (de Freitas, 2011) and South Africa (Demetriades and Forbes, 1993) therefore appear to be broadly similar, despite the different rainy seasons.

The size at first maturity ( $L_{50}$ ) is commonly evaluated for wild shrimp populations as a point of biological reference, especially spawning activity (Niamaimandi et al., 2008). The  $L_{50}$  of the four most common species in the present study differed substantially, suggesting that they start spawning at different sizes. *P. monodon* achieved  $L_{50}$  at the largest size, and *P. semisulcatus* at the smallest size. The estimates in the present study were within the range of those obtained by Teikwa and Mgaya (2003) off Tanzania, and by Niamaimandi et al. (2008) in the Persian Gulf. These authors also found  $L_{50}$  to depend on sex, being somewhat larger in females, whereas our study aggregated data for both sexes.

In conclusion, shrimp abundance in Malindi-Ungwana Bay is concentrated near the outflows of the Sabaki and Tana rivers, and these two areas have distinct species compositions, with *F. indicus* dominating in the Tana area and *P. semisulcatus* in the Sabaki area. Species-environment associations showed that *P. semisulcatus* abundance was strongly correlated to deeper less turbid waters, and that the other penaeid shrimp species were negatively correlated to these variables. Total biomass decreased with increasing depth, and was higher during the SEM than the NEM season. Seasonal recruitment and spawning cycles were species-specific, but more regular samples are required to confirm suggested patterns.

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