An estimation of the standing stock and population structure of *Upogebia africana* (Crustacea: Thalassinidae) in the Knysna Estuary

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Within the Knysna Estuary *Upogebia africana* has an extensive distribution from north of Leisure Isle to the Red Bridge, occupying 62% of the available intertidal zone. Six sites were surveyed within the above distributional range. *U. africana* was found from the high-water level (*Spartina* zone) to the shallow subtidal zone (to about 1.5 m depth). The density, biomass and population structure of the mud prawns were found to be highly variable within the estuary. Only small animals (carapace length $\bar{x}$ = 10.9 mm) were found in the upper estuary at the Red Bridge. Although large animals were present, the Invertebrate Reserve had a low density and biomass of *U. africana* ($\bar{x}$ = 11.7 m^{-2}; 3.9 $g.m^{-2}$ dry weight). By contrast a relatively inaccessible centre mud bank (Oyster Bank) in the middle reaches of the estuary had much larger populations ($\bar{x}$ = 176.5 m^{-2}; 65.3 $g.m^{-2}$ dry weight). This site is, therefore, a natural mud prawn reserve. Within the intertidal zone, mud prawn density (74–76 m^{-2}) and biomass (26–27 $g.m^{-2}$ dry weight) was usually greatest in the *Spartina* and lower *Zostera* zones. Sex ratios throughout the estuary did not deviate significantly from 1:1.

INTRODUCTION

The thalassinid crustacean *Upogebia africana* (Ortmann) (commonly known as the mud prawn) is often the most abundant macrobenthic invertebrate in South African warm temperate, open estuaries (Day, 1981a,b; Hanekom *et al.*, 1988; Hodgson, 1987). In the Swartkops River Estuary, for example, this crustacean was estimated to comprise over 78% of the shell-free biomass of the infaunal macrobenthos (Hanekom, 1980). The presence of *U. africana* is long documented in the Knysna Estuary (Day *et al*, 1952; Day, 1967), these authors providing some estimates of mud prawn density. There are no detailed quantitative studies of the distribution, density, biomass and population structure in the Knsyna Estuary, although Hill (1977) did provide some information on sex ratios and the carapace length of females.

U. africana is one of the main invertebrates exploited for bait by fishermen. These animals therefore represent an important resource within many estuaries. *Upogebia* spp. are also important as "promoter" species (Reise, 1985). Their activities can increase sediment oxygenation and mineralisation (Ott *et al*., 1976; Hines & Jones, 1985), and change the community structure of soft-bottom estuarine habitats, having diverse effects on microalgae, bacteria and meiofauna (Brenchley, 1981; Flint & Kalke, 1986; Posey *et al.*, 1991; Wynberg & Branch, 1994). Hence, disturbance or removal of populations of "promoter" species (e.g. through over-exploitation by bait collectors) could have implications beyond the disturbance of the organism *per se*.

If the Knysna Estuary and its invertebrate resources, such as *U. africana*, are to be managed on a sustainable basis, fundamental information on the standing stocks and population structure are required. The aim of this study was to provide this information and thus establish the "status" of *U. africana* within the Knysna Estuary. The investigation formed part of a broader study on the exploitation of this animal, the results of which are reported upon in the paper which follows (Hodgson *et al.*, 2000).

MATERIALS AND METHODS

Study sites

Upogebia africana have characteristic burrow openings (Zoutendyk & Bickerton, 1988) which made it possible to assess the distributional limits of this species within the estuary by inspection of holes. An observational survey in February 1995 along the Knysna Estuary from the mouth to the Charlesford rapids revealed that *U. africana* was distributed from the northern side of Leisure Isle to the Red Bridge (Figure 1). Within this distributional range, six sites were chosen to assess the standing stocks and the population structure of mud prawns. The sites not only varied in distance from the mouth but also in the intensity of bait collection at them (R. Cretchley, pers. obs.). The site lowest down the estuary was the Invertebrate Reserve, an area in which bait collecting is prohibited (Figure 1). Adjacent to this reserve, a popular collecting site on the northern side of Leisure Isle was chosen to serve as a comparison. Two sites in the lower middle reaches of the estuary (Ashmead and Thesen Island) were also observed to be regularly exploited by bait collectors and therefore these sites were surveyed. The Ashmead site is a protected shallow channel east and north of Thesen Island, whereas the Thesen Island site is on the main channel of the estuary (Figure 1). In the middle reaches of the estuary, above the railway bridge, a central bank (Oyster Bank) was chosen for sampling as such sites are only accessible by boat and rarely exploited for bait (R. Cretchley, pers. obs.). Finally, the Red Bridge site in the upper reaches of the estuary was sampled as this region represented the upper limits of the distribution of *U. africana*.

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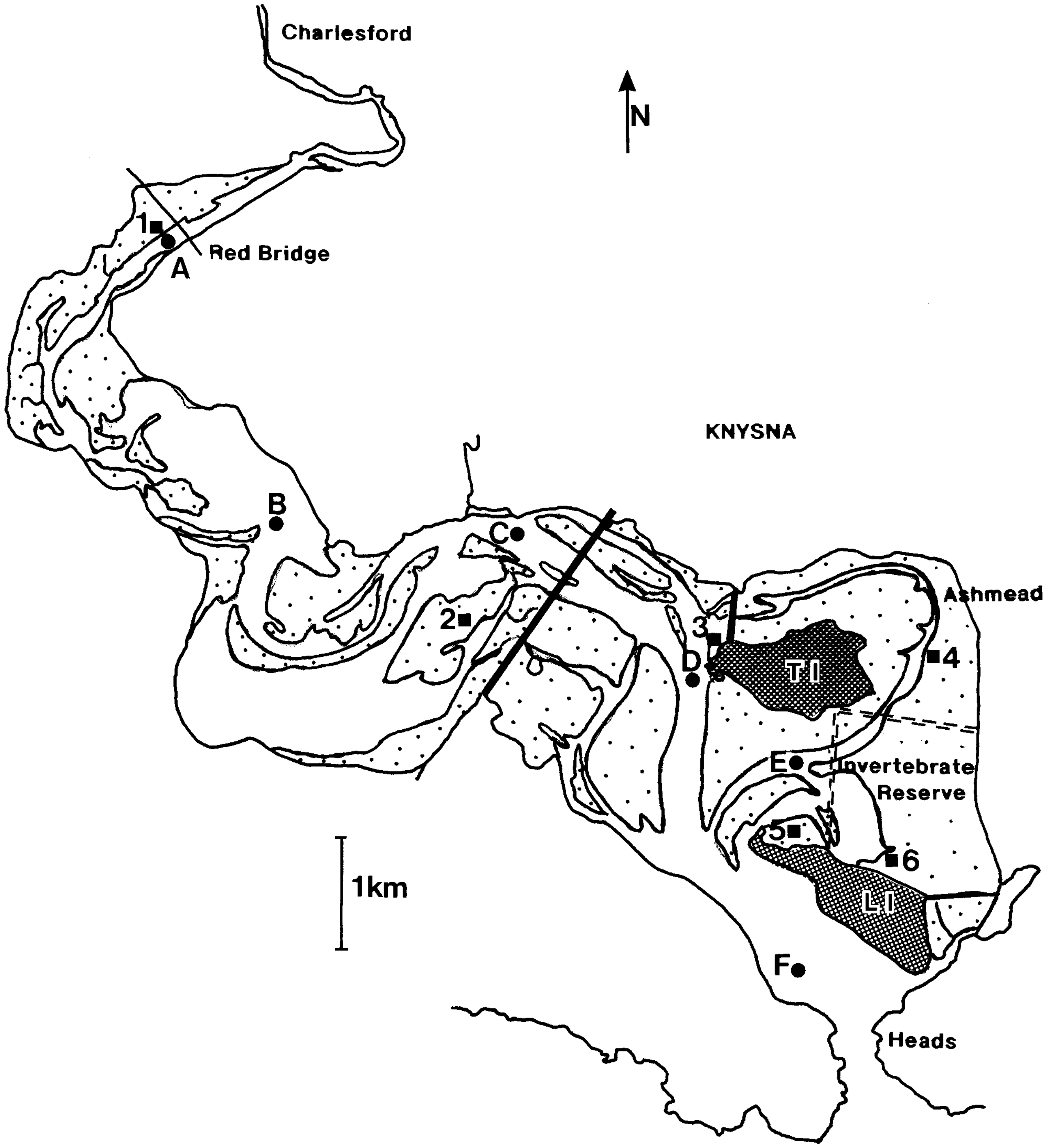


Figure 1. The Knysna Estuary showing (in light stipple) the distribution of the main mud banks (including saltmarsh areas), the locations of the sites sampled for physical data (A–F) and *Upogebia africana* (1–6). 1, Red Bridge; 2, Oyster Bank; 3, Thesen Island; 4, Ashmead; 5, Leisure Isle; 6, Invertebrate Reserve. LI, Leisure Isle. TI, Thesen Island. = = = boundary of the Invertebrate Reserve.

Physical characteristics of the sites

Sediment samples were collected from all sites. At each site the sediment within the *Spartina*, upper *Zostera* or sand, and lower *Zostera* zones were sampled with a corer (0.1 m PVC pipe) to a depth of 0.3 m. The sediment from each core was dried to constant weight at 55°C. Subsamples of 500–1000 g were disaggregated using a pestle and mortar and weighed to the nearest 0.01 g. Samples were shaken through a series of Endecott sieves (whole phi unit intervals) for 10 minutes and the fraction of material remaining in each sieve was collected and weighed to 0.01 g. In addition, the organic content of the sediment was determined by firing pre-dried samples (30–50 g) in a muffle furnace at 400°C for 12 hours. The ash produced was weighed to 0.001 g.

Temperature and salinity were measured every month at the six sites from May 1995 to April 1996. Both parameters were measured from the surface waters (0–0.5 m), temperature with a mercury thermometer and salinity with an optical refractometer. Sampling commenced at the start of the ebb tide at the Red Bridge and continued throughout the ebb tide to the mouth. The temperature and salinity near to the mouth of the estuary was measured as the water here was indicative of the sea conditions.

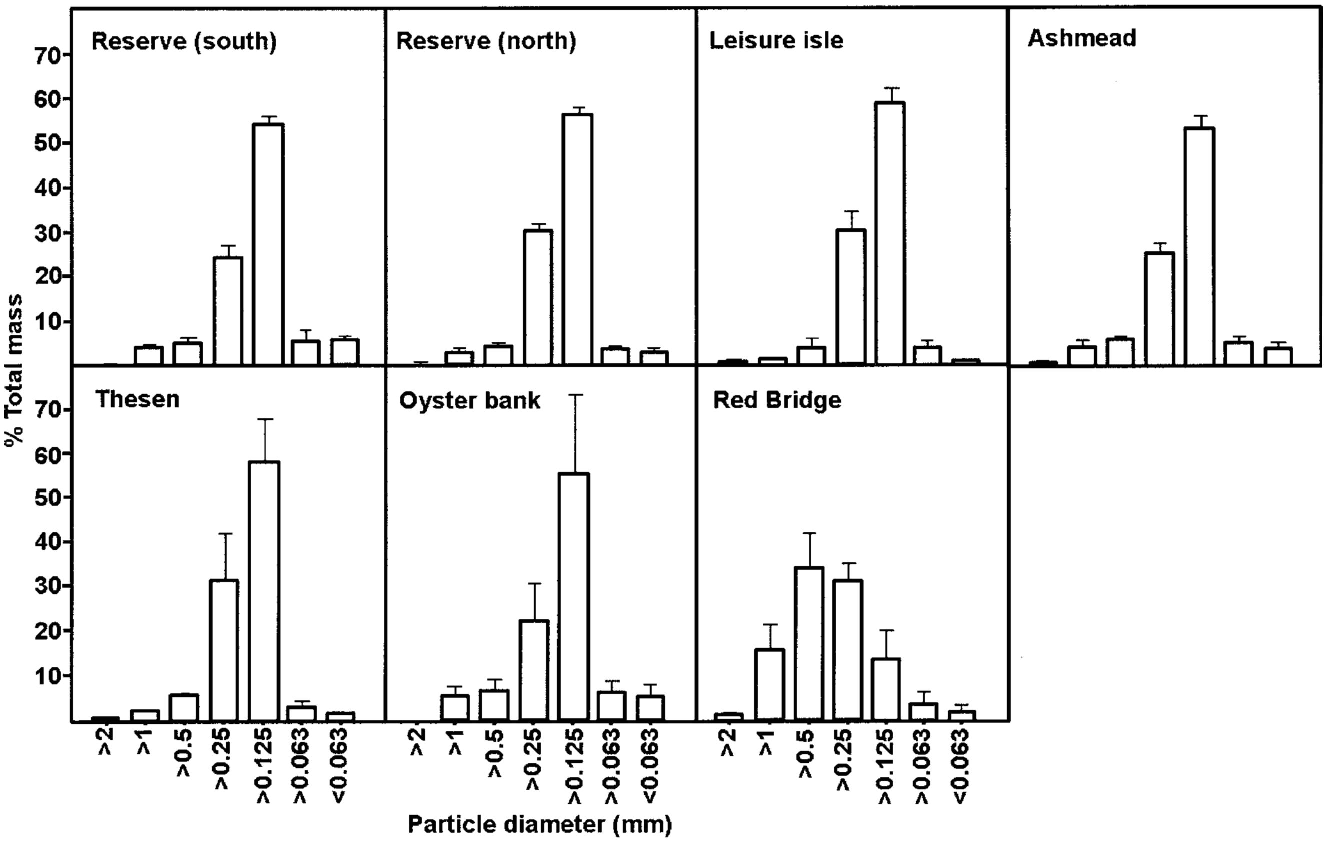


Figure 2. Particle size distribution of sediment where the mass of material (as a percentage of the total mass) is plotted as a size fraction coarser than each size. Size classes are based on whole phi units.

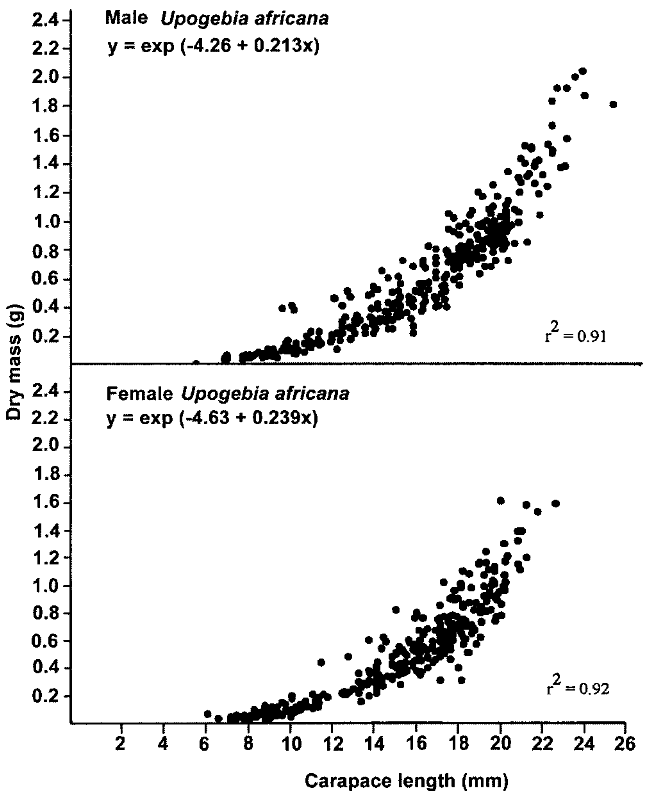


Figure 3. Exponential regressions of the dry mass (g) of male and female *Upogebia africana* against carapace length (mm) used to convert mud prawn lengths into biomass.

Distribution, density and biomass of *U. africana*

Five habitat zones could be identified at each site: the high saltmarsh, *Spartina* zone, upper *Zostera* or sand zone, lower *Zostera* zone, and the subtidal zone below low-water springs. Observations of *U. africana* burrows revealed that animals were distributed from within the *Spartina* zone to the shallow subtidal zone. At the Red Bridge site, *Juncus* replaces *Spartina* and the mud prawns were found from just below the *Juncus* zone to the subtidal zone. Sampling of *U. africana* was undertaken over two spring-tide periods; the Leisure Isle, Red Bridge and Thesen Island sites were sampled between 6 and 8 November 1995, and the remaining sites on 4 and 5 April 1996.

Within each zone in the intertidal region in which *U. africana* occurred, five 0.25 m^2 quadrats were dug to about 0.5 m. Hanekom *et al.* (1988), from depth-stratified sampling, found that 89% of *U. africana* were found in the top 0.25 m of substratum and that a sampling depth of 0.3 m was therefore adequate. In each quadrat the upper 0.1 m of mud was removed first and sieved through a 1 mm mesh to capture small juveniles and newly settled larvae. The remainder of the sample was sieved through a 3 mm mesh. All the mud prawns were retained for later analysis.

Subtidal zone densities of *U. africana* were assessed by scuba-diving. A weighted line was placed perpendicular to the shore and every 5 m the number of burrow openings in ten 0.0625 m^2 quadrats were counted and the water depth recorded. A ratio of 2:1 (holes:mud prawns) was suggested for *U. africana* by Wynberg & Branch (1991) and this conversion factor was used in this study. Subtidal zone counts were carried out from the spring low-water level to the distributional limit of the burrows.

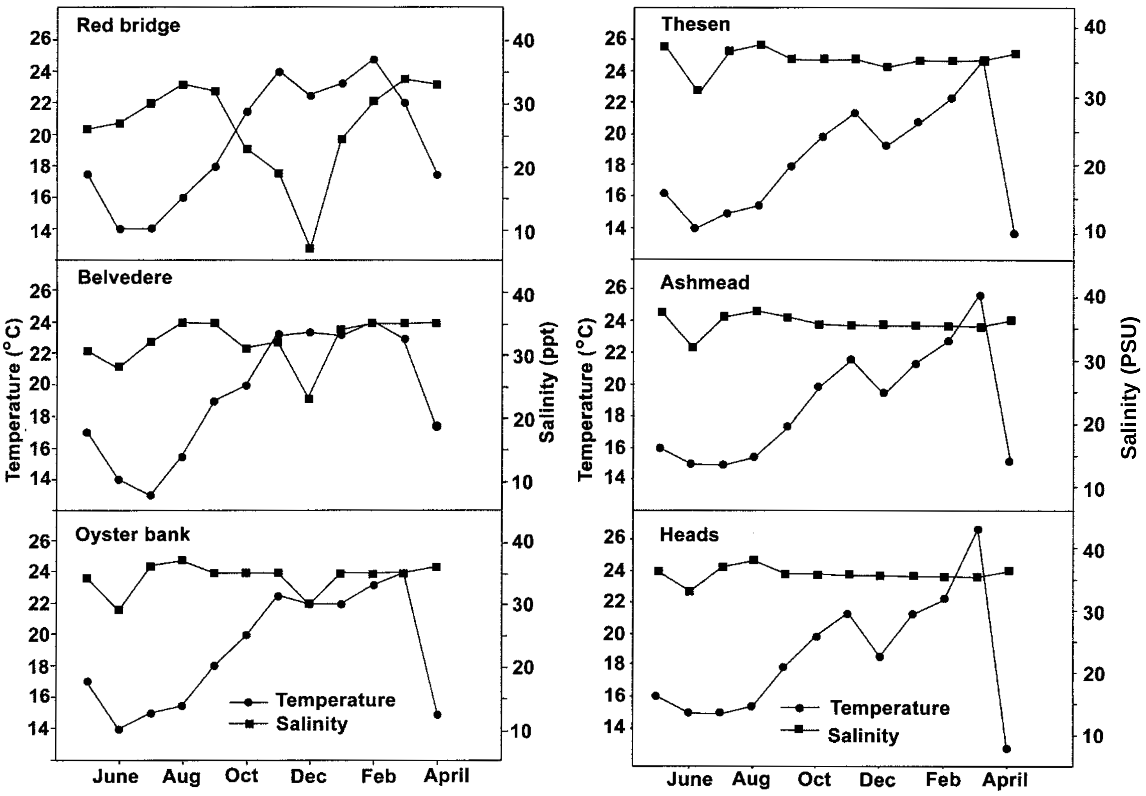


Figure 4. Water temperature and salinity at six sites (A to F on Figure 1) over 12 months from May 1995 to April 1996.

To express *U. africana* densities as dry biomass, 700 mud prawns were collected and measured (to nearest mm) from the tip of the rostrum to the hind margin of the carapace using Vernier callipers (Hill, 1967; Hanekom & Erasmus, 1988). To convert all mud prawn sizes into dry mass, wet masses of the 700 animals were recorded (to nearest 0.01 g), the animals dried to constant weight at 55°C, and reweighed. The relationship of carapace length vs. dry mass was plotted for male and females and the regression equations derived used to convert all mud prawn sizes to dry mass (Figure 2).

Population structure

All mud prawns collected from the quadrats were sexed. Animals of <10 mm carapace length were classed as juveniles, the smallest ovigerous females being recorded previously for the 10 mm size class (Hill, 1977). The carapace lengths of the mud prawns were grouped into 1 mm size classes and size frequency histograms were constructed for each zone and each site.

Table 1. A. Results of an Analysis of Variance to determine whether there are any significant differences in the percentage subsieve sediment between zones (over all sites) and between sites sampled (over all zones). **B.** Results of a Scheffe's Multiple Range Analysis to determine whether there are any significant differences in the percentage subsieve particles between the seven sites sampled. X's in same columns indicate no significant difference.

A

Variation	Sum of squares	d.f.	Mean square	F-ratio	Sig. Level
MAIN EFFECTS					
Zone	12.30	3	4.10	2.925	0.0772
Site	62.23	6	10.37	7.402	0.0017
RESIDUAL	16.81	12	1.40		
TOTAL	99.40	21			

B

Site	n (samples)	Mean ± s.e %	Homogenous groups	
Leisure Isle	3	0.98 ± 0.25	X	
Thesen Island	4	1.07 ± 0.39	X	
Red Bridge	3	1.72 ± 1.30	X	X
Reserve (north)	3	2.42 ± 1.10	X	X
Ashmead	3	3.94 ± 1.30	X	X
Oyster Bank	3	4.82 ± 2.70	X	X
Reserve (south)	3	5.61 ± 1.0		X

Table 2. A. Results of an Analysis of Variance to determine whether the percentages of combustible (organic) material are significantly different between zones (over all sites) and between sites (over all zones). **B.** Results of a Scheffe's Multiple Range Analysis to determine whether the percentages of combustible material are significantly different between sites (over all zones). X's in same column indicate no significant difference.

A

Variation	Sum of squares	d.f.	Mean squares	F-ratio	Sig. Level
MAIN EFFECT					
Zone	2.14	3	0.71	1.626	0.2354
Site	7.95	6	1.32	3.015	0.0491
RESIDUAL	5.27	12	0.44		
TOTAL	15.87	21			

B

Site	n (samples)	Mean ± s.e. %	Homogenous groups	
Leisure Isle	3	0.79 ± 0.06	X	
Reserve (north)	3	0.83 ± 0.11	X	
Thesen Island	4	0.87 ± 0.33	X	
Ashmead	3	0.92 ± 0.04	X	
Reserve (south)	3	1.00 ± 0.31	X	
Oyster Bank	3	1.53 ± 0.31	X	
Red Bridge	3	2.62 ± 1.78		X

Data analysis

All statistical analyses were undertaken using Statgraphics version 7.0.

RESULTS

Physical characteristics of the habitat

At all sites studied, except Red Bridge, the sediment structure was very similar with a modal particle size of 0.125 mm–0.250 mm diameter (Figure 3). The sediment at Red Bridge was coarser than that of other sites, with a modal particle size of 0.5–0.1 mm (Figure 2). At each site there was no significant difference between the percentage of subsieve particles (<63 µm) in the *Spartina*, upper and lower *Zostera* zones (p>0.05, MANOVA). The data from these three zones at each site were therefore pooled. The only significant differences in percentage of subsieve particles between sites were between the Invertebrate Reserve south ($\bar{x}$ = 5.61%), and the Leisure Isle ($\bar{x}$ = 0.98%) and Thesen Island ($\bar{x}$ = 1.07%) sediments (Table 1).

There was no significant difference in the organic content of the sediment of the *Spartina*, upper and lower *Zostera* zones at each site (Table 2) and therefore the results for each site were pooled. The Red Bridge sediment had a significantly higher organic content ($\bar{x}$ = 2.62 ± 1.78%) than that of the other five sites ($\bar{x}$ = 0.99–0.19%) which were not significantly different from one another (Table 2).

The annual range in water temperature at all sites was similar (13–25°C, Figure 4). On some occasions upwelling caused rapid declines (up to 10°C in a few hours) in water temperature (e.g. April 1996) at The Heads, Ashmead and Thesen Island (see also Schumann, 2000). Above the railway bridge, in the middle and upper reaches, temperatures did not fluctuate markedly and remained above 15°C (Figure 4). The Red Bridge and Oyster Bank sites experienced the greater fluctuations in salinity (9–34 and 23–35 respectively, Figure 4), with sites below the railway bridge rarely declining below 35.

Distribution, density and biomass of *U. africana*

At all sites sampled the density and biomass of *U. africana* within the intertidal zone was highly variable. Mean densities and biomass in the intertidal zone ranged from <20 m^{-2} and 5 $g.m^{-2}$ (dry mass) in the Invertebrate Reserve to >200 m^{-2} and >60 $g.m^{-2}$ at the Oyster Bank (Table 3). Both the density and biomass of mud prawns at the central Oyster Bank were significantly higher (p<0.0001, MANOVA) than at the heavily exploited Leisure Isle, which in turn had a significantly greater density and biomass than at the other four sites (p<0.0001, MANOVA).

Table 3. Mean (± s.e.) density and biomass (dry weight) of *Upogebia africana* in three zones at six sites in the Knysna Estuary. For site location refer to Figure 1.

	Density (no. m^{-2})			Biomass ($g.m^{-2}$)		
	Spartina **(or *Juncus*)**	**Upper *Zostera* or sand**	**Lower *Zostera***	***Spartina*** **(or *Juncus*)**	**Upper *Zostera* or sand**	**Lower *Zostera***
Invertebrate Reserve	8.26 ± 4.34	4.34 ± 6.52	22.65 ± 20.86	4.30 ± 3.07	1.23 ± 1.54	6.92 ± 4.61
Leisure Isle	105.09 ± 13.04	67.40 ± 47.82	113.13 ± 38.26	49.23 ± 12.61	33.07 ± 27.69	48.61 ± 7.53
Ashmead	10.86 ± 8.69	20.34 ± 9.56	75.21 ± 22.17	3.23 ± 3.38	10.61 ± 5.53	26.15 ± 7.69
Thesen Island	70.43 ± 16.08	0	41.56 ± 20.00	32.00 ± 8.15	0	13.84 ± 13.84
Oyster Bank	203.34 ± 43.04	140.01 ± 36.95	186.56 ± 35.21	62.30 ± 16.15	62.31 ± 14.92	69.69 ± 12.30
Red Bridge	52.17 ± 30.86	0	13.4 ± 10.86	4.00 ± 2.30	0	0.92 ± 0.77

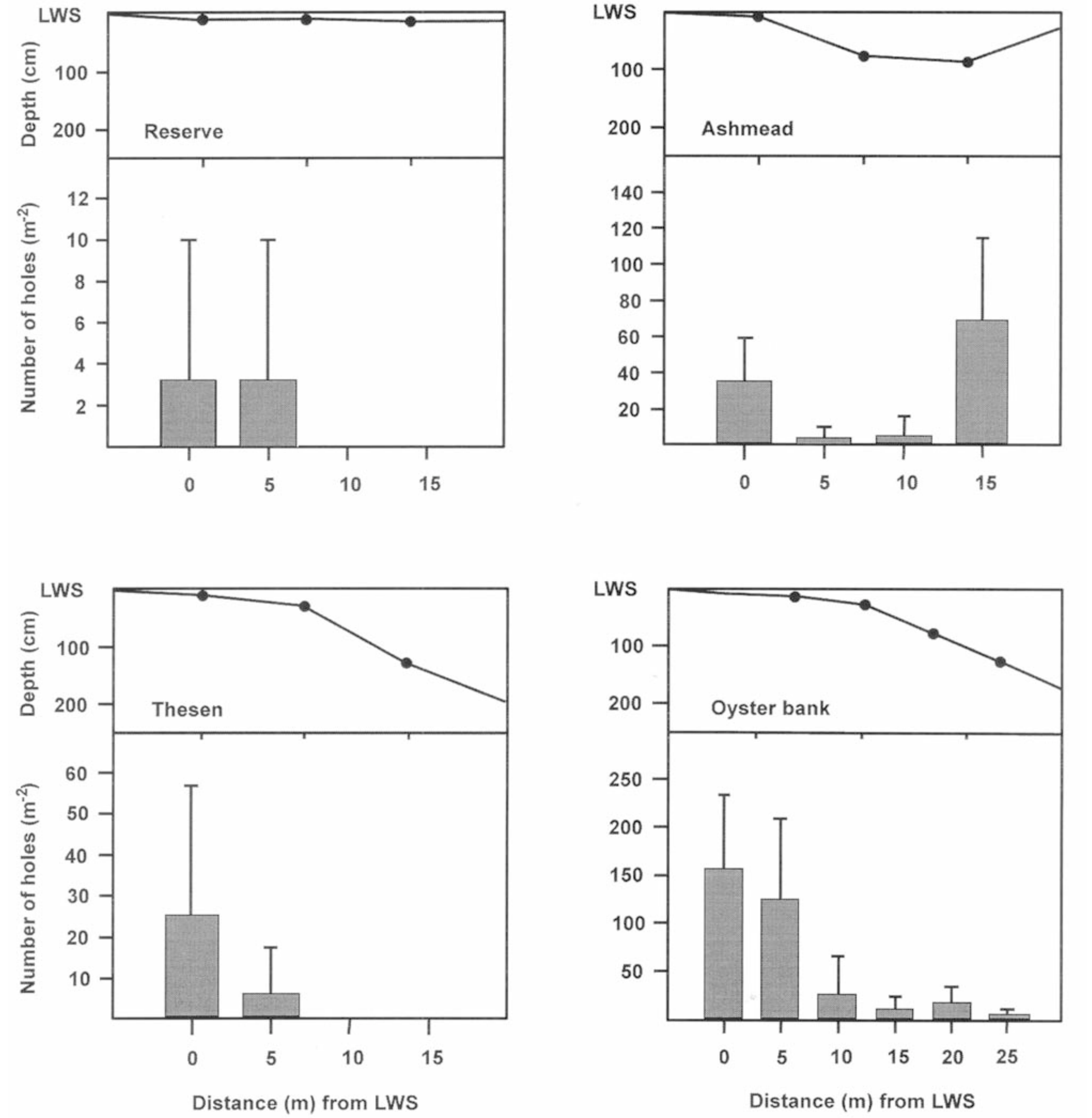


Figure 5. Mean number (± s.e.) of mud prawn holes at 5 m intervals from low-water spring (LWS) at four sites (Leisure Isle and Red Bridge have no mud prawns subtidally). Above each histogram is the bottom profile.

There was no consistent trend in the relationship between the intertidal density and biomass of *U. africana* and height above LWS (Table 3). At the Invertebrate Reserve and Ashmead, density increased in the lower intertidal zones (*Zostera* zones), while at Thesen Island and the Oyster Bank sites, density was highest in the *Spartina* zone. When the data from all sites were combined and compared using a Multifactor Analysis of Variance, the mean density and mean biomass were significantly lower ($p<0.0001$ and $p<0.005$ respectively) in the upper *Zostera/*sand zone (39.2 m^{-2} and 17.5 $g.m^{-2}$) than in the *Spartina* zone above it (74.3 m^{-2} and 26.1 $g.m^{-2}$) and the lower *Zostera* zone below (76.3 m^{-2} and 27.9 $g.m^{-2}$).

Subtidal zone densities were highest in the shallow areas within 5 m of LWS (Reserve, Thesen Island, Oyster Bank) and in the shallow regions of the Ashmead Channel (0 and 15 m along the transect line) (Figure 5). These areas can be uncovered at equinox spring tides. The subtidal zone within 10 m of LWS at the Oyster Bank had densities of 60–75 m^{-2} and up to 35 m^{-2} were recorded subtidally within 5 m of LWS in the shallow channel at Ashmead. At all sites, as the depth and the distance from LWS increased, densities declined (Figure 5). No mud prawn burrows were found below LWS at Leisure Isle and Red Bridge.

Population structure

Although there was some variation in the ratio of males, females and juveniles between sites (Table 4), there was no significant difference in the percentages of males and females ($p>0.05$ at all sites, Chi-square statistic). The percentage of mud prawns less than 10 mm carapace length at Red Bridge (69.51%) was significantly higher than at the other 5 sites ($p<0.005$, Chi square statistic).

Sizes of adult *U. africana* varied significantly between some of the intertidal zones and between some sites within the estuary

Table 4. The percentages of males, females and juvenile prawns at six sites (see Figure 1 for site location).

Site	n	Male	Female	Juvenile
Reserve	19	38.67	52.00	9.33
Leisure Isle	63	39.69	48.68	11.62
Ashmead	499	42.42	47.72	9.85
Thesen Island	96	44.68	34.75	20.57
Oyster Bank	377	39.47	41.97	18.56
Red Bridge	111	19.51	10.98	69.51

(Table 5). Whereas there was no significant difference between the mean size of mud prawns of the *Spartina* and lower *Zostera* zones, and between the upper and lower *Zostera* zones, mud prawns from the *Spartina* zones were significantly smaller than those from the upper *Zostera* zones. The mud prawns at the Red Bridge (10.9 mm carapace length) site were significantly smaller than those from other sites lower down the estuary (14.4–15.9 mm carapace length) (Table 5). At all sites sampled, more juvenile prawns were found in the *Zostera* zones than higher up the shore (Figure 6). At some sites, e.g. Leisure Isle, Thesen Island, Oyster Bank and Red Bridge, the *Spartina* zone contained more large adults (>20 mm carapace length) than the *Zostera* zones.

When the length frequency data for each site were combined (Figure 7), at the sites in the lower reaches, the mud prawns can be seen to range in size from 3 mm to 24 mm carapace length. The largest animals at Red Bridge were less than 12 mm carapace length.

DISCUSSION

There is considerable information on the density of *Upogebia africana* in South African estuaries. Although maximum densities recorded in this study were not as great as those found in studies on the Kowie, Swartkops, and Kariega estuaries (Day, 1981b; Hodgson, 1987; Hanekom *et al*., 1988), the density range is similar to that reported for many South African estuaries (see Hodgson, 1987; de Villiers & Hodgson, 1999) including the Knysna Estuary (Day *et al*., 1952; Day, 1967).

U. africana was found to be distributed throughout the muddy intertidal zones of the lower, middle and upper reaches of the Knysna Estuary. Animals were absent from areas near the mouth (south of Leisure Isle) and above the Red Bridge. With the use of GIS maps and aerial photographs, the total area of mud bank (sand flats and high saltmarsh were excluded) in the estuary was estimated to be 567 ha and the area occupied by *U. africana* 347 ha. From these estimations *U. africana* inhabits about 62% of the intertidal mud bank.

A number of physical and biological factors have been suggested to limit the distribution of *U. africana*. The importance of substratum composition in limiting the distribution of estuarine macrobenthic organisms is well established (Macnae, 1957a,b; McLachlan & Grindley, 1974). In the Swartkops Estuary where salinity is usually similar to that of the sea, McLachlan & Grindley (1974) found that substratum was by far the most important factor influencing the distribution of the macrobenthos, imposing limits on burrow construction. *U. africana* constructs permanent burrows lined with silt (Hill, 1967). The strong tidal currents, resulting in unstable clean sandy sediments in the main channels and south of Leisure Isle,

Table 5. **A.** Results of an Analysis of Variance to determine whether the sizes of adult *U. africana* are significantly different between the three zones sampled and between the six sites sampled. **B.** Results of Scheffe's Multiple Range analysis to determine whether there are any significant differences in size of adult *U. africana* between the three zones and six sites sampled. X's in same column indicate no significant difference.

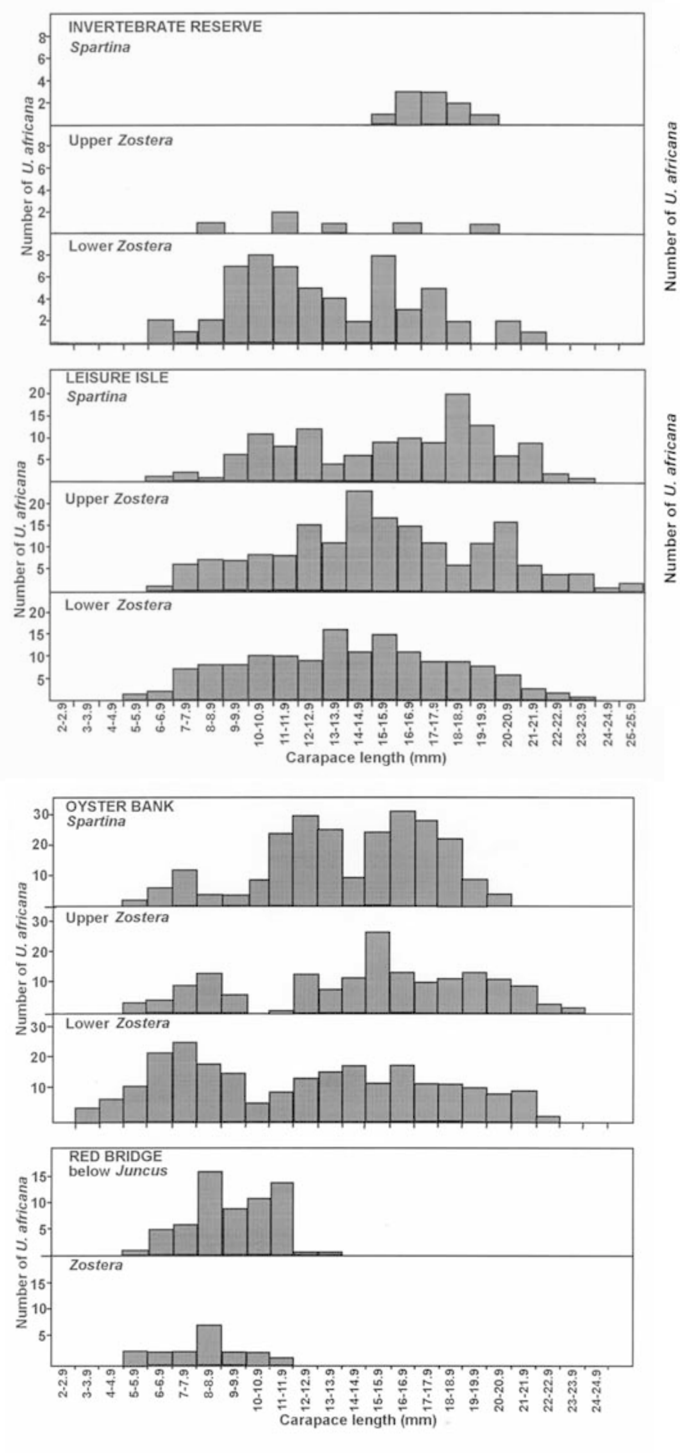
A

Variation	Sum of squares	d.f	Mean square	F-ratio	Sig. Level
MAIN EFFECTS					
Zone	100.60	2	50.30	5.2990	0.005
Site	505.04	5	101.01	10.641	<0.0001
RESIDUAL	10983.11	1157	9.49		
TOTAL	11631.00	1164			

B

Zone	n	Mean size (mm)	Homogeneous groups	
Spartina	440	14.22	X	
Lower *Zostera*	405	14.75	X	X
Upper *Zostera*	320	14.95		X

Site	n	Mean size (mm)	Homogeneous groups	
Red Bridge	19	10.90	X	
Reserve	63	14.41		X
Oyster Bank	499	15.39		X
Ashmead	96	15.57		X
Leisure Isle	377	15.67		X
Thesen Island	111	15.91		X



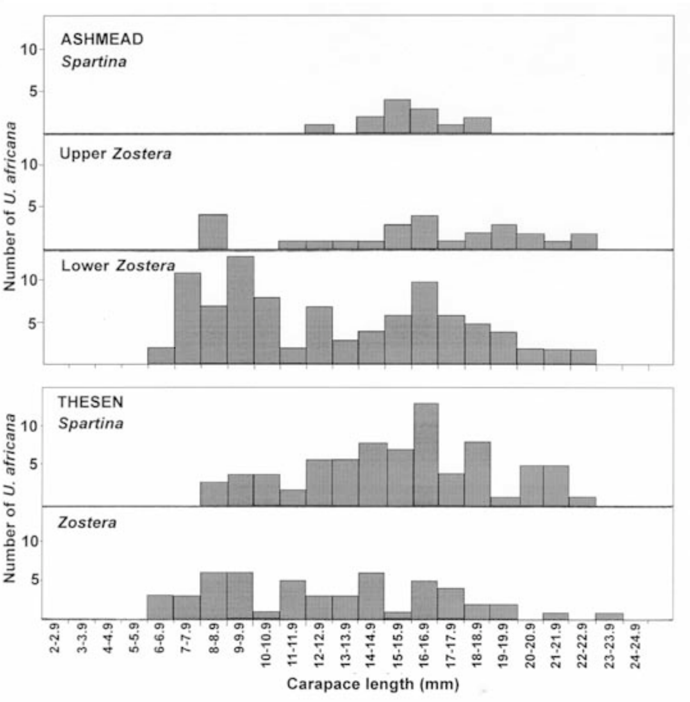


Figure 6. Length frequency distributions of populations of *Upogebia africana* from the three intertidal zones at each site. At Thesen Island and Red Bridge no animals were found in the upper *Zostera* zone.

undoubtedly prevent mud prawn colonisation. Similarly above Red Bridge the sediment is coarse due to a significant component of river sand.

Within its distributional range, the density biomass and population structure of *U. africana* varies within the Knysna Estuary and with vertical height on each shore. *U. africana* has been found to be abundant in sediments that contain a relatively high percentage of subsieve particles (<63 μm). Densities between 50 and 250 m^{-2} are common in mud with 3–20% of silt and clay (Wooldridge, 1968). In sediments with more than 20% subsieve particles mud prawns are not as common (McLachlan & Grindley, 1974; Day, 1981a). In this study the percentage subsieve particles of the sediments from the six sites sampled ranged from between 1 and 8%, values which therefore fall within the recorded range of *U. africana*. Despite this, mud prawn biomass differed significantly between sites. This suggests that the percentage of subsieve sediment does not influence intertidal prawn biomass in the Knysna Estuary and that some other factors are involved.

At each site studied, mud prawn densities were highest in the lower *Zostera* zone just above the spring low-tide water level, and decreased with depth below this point. The subtidal sediment changes from muddy sand to coarser sandier sediments (Reddering & Esterhuysen, 1984). At Ashmead, however, the channel is shallow, currents are not strong and the subtidal sediment remains muddy and fine. Mud prawns were found throughout this channel. A similar distribution pattern was found in the Swartkops Estuary, animal density being reduced in the subtidal zone where there were strong currents, but in sheltered creeks mud prawns are distributed throughout the subtidal zone (Wooldridge, 1968; Hanekom *et al*., 1988). Both the Knysna and Swartkops estuaries have a similar subtidal zone density of mud prawns (39 ± 50 m^{-2} and 51 ± 37 m^{-2} respectively). These animals are generally inaccessible to bait collectors and may represent a small, but important, protected stock.

Hanekom & Erasmus (1988) found significant differences in the size ranges of adult mud prawns at different tidal heights in the intertidal zone along the length of the Swartkops Estuary. Adult mud prawn size tended to be larger in the lower intertidal zones and to decrease with distance from the estuary mouth. The intertidal size-gradient of adult *U. africana* in the Knysna Estuary was not as marked. Although mud prawns from the *Spartina* zone were significantly smaller than those from the upper *Zostera* zone, there was no significant difference in the size of animals in the *Spartina* and lower *Zostera* zones. There was also little variation in the size of *U. africana* along the Knysna Estuary, with adult mud prawns from the Red Bridge site only being significantly smaller than those from the other five sites. The four sites with the larger adult mud prawns (Thesen Island, Leisure Isle, Ashmead and Oyster Bank) tended to have the highest density and biomass of prawns. A similar positive relationship between biomass and mud prawn size has

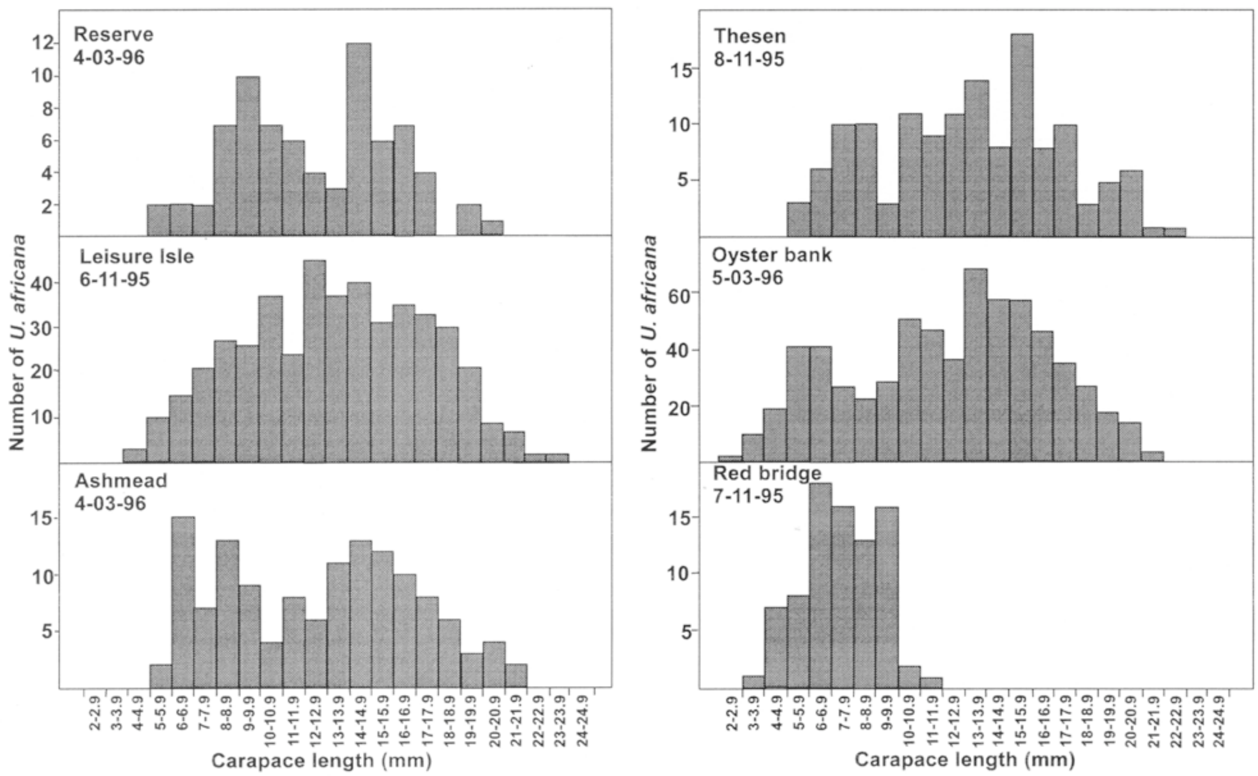


Figure 7. Length frequency distributions of *U. africana* populations from six sites in the Knysna Estuary.

also been recorded in the Swartkops River Estuary (Hanekom & Erasmus, 1988). Hanekom & Erasmus (1988) have suggested that the significant differences in the sizes of ovigerous females from the different regions in the Swartkops River Estuary were a result of differences in growth rate.

The percentage of females (52.1%) in the Knysna Estuary population of *U. africana* is similar to that found by Hill (1977) for the Knysna (50.4%) and Kowie estuaries (50.0%). These percentages are slightly lower than those found in the Swartkops (56–62% female) and Uilenkraal estuaries (65.3% female) (Hill, 1977; Hanekom & Erasmus, 1989; Hanekom & Baird, 1992). The reason(s) for these differences are unknown but may in part reflect different sampling protocols.

The variability in the density and biomass of *U. africana* in the Knysna Estuary and the peak in abundance at the Oyster Bank could be due to the presence of a more favourable habitat, and/or the inaccessibility of this site to bait collectors. Factors contributing to the favourability of the habitat at the Oyster Bank may include water temperature, which was less variable at this site when compared to sites in the lower reaches. In addition, the salinity in the middle reaches was less variable than higher up the estuary and the percentages of subsieve sediment and organic matter of the sediment were slightly higher. Hanekom & Erasmus (1988) found a significant positive correlation between the salinity of the water column and mean adult mud prawn size, but found that temperature and population density had no significant effect in the Swartkops Estuary. Nutrient content of the water may influence mud prawn biomass in the Knysna Estuary. Korringa (1956) suggested that oyster spat and older oysters might thrive above the railway bridge in the middle reaches of the estuary because of the high food content of the water. This suggestion is supported by data which show that this area has a higher chlorophyll-*a* concentration (see Allanson *et al.*, 2000). Filter-feeders such as *U. africana* may benefit from this as well as from the particulate detritus produced by the oysters.

The total area of intertidal mud bank inhabited by *U. africana* can be used to estimate the mud prawn stocks of the Knysna Estuary. If the mean density and mean biomass of the six sites sampled (63.26 individuals m^{-2} and 23.85 g m^{-2}) are taken as representative of the entire estuary, the mud prawn stock is estimated to be 2.19×10^8 individuals which would have a dry mass of about 82 tonnes. Finally, from the density and biomass values obtained in this study it is clear that the Invertebrate Reserve, although it supports high densities of other invertebrates (R. Cretchley & A.N. Hodgson, pers. obs.), does not conserve large stocks of *U. africana*. The Oyster Bank, however, acts as a natural bait reserve as it supports the highest biomass of mud prawns in the Knysna Estuary.

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