

## Determinations of the reproductive output of populations of a thalassinid prawn *Upogebia africana* (Ortmann) in the Swartkops estuary

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Populations of large and 'stunted' (adult carapace lengths = 17,0–24,0 and 12,0–19,0 mm respectively) *Upogebia africana* were regularly and quantitatively sampled in the Swartkops estuary. At the site with 'stunted' prawns a well-defined spring (July to October) and summer (December to March) breeding cycle was recorded. The 'stunted' female prawns produced two broods of eggs per annum and the brood size ranged from about 305 to 2282 eggs depending on the size of the female. At the site with large prawns the spring and summer breeding cycles tended to merge, forming a longer breeding season, with the adult females apparently producing three broods of eggs per annum. The brood size of these females ranged from about 1304 to 4819 eggs. The calculated reproductive output (Pr) and reproductive biomass ratio (Pr/B) of the latter population were much greater than those of the 'stunted' prawns (1331 kJ m<sup>-2</sup> y<sup>-1</sup> and 0,53 v. 332 kJ m<sup>-2</sup> y<sup>-1</sup> and 0,26).

Bevolkings van normale en 'verpotte' (volwasse karapaks lengtes = 17,0–24,0 en 12,0–19,0 mm respektiewelik) *Upogebia africana* in die Swartkopsgetyrrivier is met gereelde tussenposes kwantitatief gemonster. By die monsternemingspunt met die 'verpotte' garnale is goed gedefinieerde lente- (Julie tot Oktober) en somer- (Desember tot Maart) broeisiklusse waargeneem. Die 'verpotte' wyfie-garnale produseer twee broeisels per jaar en die grootte van die broeisels varieer van ongeveer 305 tot 2282 eiers afhangende van die grootte van die wyfie. By die monsternemingspunt met normale grootte garnale het die lente- en somer-broeisiklusse oorvleuel om 'n langer broeitydperk te vorm en die wyfies het blykbaar drie broeisels per jaar geproduseer. Die broeiselsgrootte van hierdie wyfies varieer van ongeveer 1304 tot 4819 eiers. Die berekende reprodruktiewe produksie (Pr) en die reprodruktiewe biomassa-verhouding (Pr/B) van die laasgenoemde bevolking is baie groter as dié van die 'verpotte' garnale (1331 kJ m<sup>-2</sup> j<sup>-1</sup> en 0,53 v. 332 kJ m<sup>-2</sup> j<sup>-1</sup> en 0,26).

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The mud prawn *Upogebia africana* (Ortmann) is a common macrobenthic species in many southern African estuaries (Day 1981). The genus *Upogebia* is distributed world wide (Hill 1967) and exploited as a bait organism, therefore knowledge of its reproductive potential would be important in the framing of conservation measures.

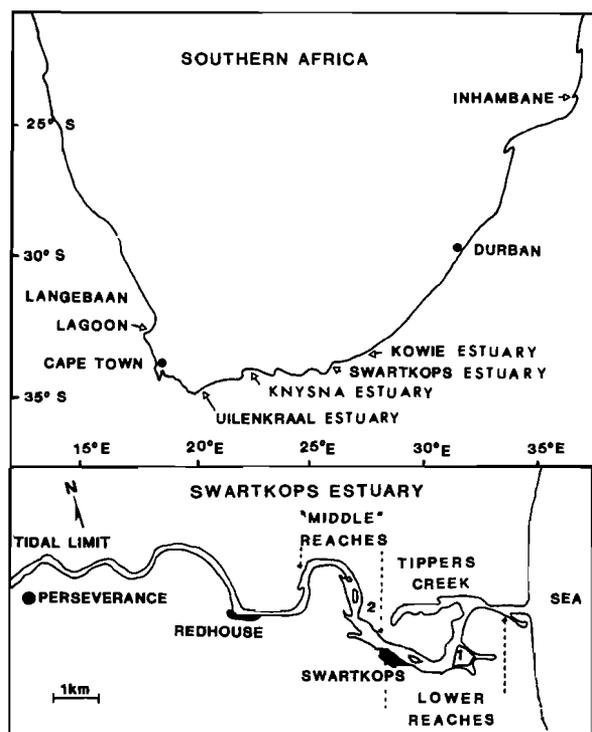
The sizes of adult *U. africana* vary within the Swartkops estuary and adults from the low tide levels of the lower reaches are generally 3–5 mm larger in carapace length than from the 'middle' and creek regions (Hanekom & Erasmus 1988). This paper concentrates on the reproductive energetics of these large and 'stunted' prawns within the Swartkops estuary. It augments the work of Hill (1977), which related breeding seasons, brood sizes and egg production of *U. africana* in three different estuaries to the temperature regimes experienced. Other notable reproductive studies of thalassinid prawns include that of Dworschak (1988) on *U. pusilla* and those of Hailstone & Stephenson (1961), Devine (1966), Forbes (1977) and Hanekom (1980), all of which deal with *Callinassa* species.

The Swartkops estuary is situated in the approximate centre of the distributional range of *U. africana* in southern Africa, which stretches from about Inhambane in the east to Langebaan lagoon in the west (Hill 1967, Figure 1). It has a tidal range of 16 km and extensive intertidal mud flats in the lower reaches. The annual range in the water temperatures of the main channel is approximately 13–28°C, while the salinity gradient

along its length is normally within 15–35‰ and there is little vertical stratification in the water column (McLachlan & Grindley 1974; Wooldridge 1979).

### Methods

Between July 1976 and November 1977 *U. africana* were regularly (*ca.* every six weeks) and quantitatively sampled at Sites 1 and 2 in the Swartkops estuary (Figure 1), where populations of large and 'stunted' prawns occurred respectively. At each site duplicate samples of 0,25 m<sup>2</sup> and 30 cm deep were dug at 0 and 0,25 m above low-water mark of spring tide [tidal levels within which the highest prawn densities occurred and where there was little variation in population structure (Hanekom, 1980)]. Samples were sieved through a 3 mm-mesh sieve in a manner described by Hanekom (1980). The sampling depth used reached about 95% of the *U. africana* within the study area (Hanekom, Baird & Erasmus 1988). Prawns collected (*ca.* 400 per transect) were counted and carapace lengths measured to the nearest 0,2 mm using vernier calipers. Individuals larger than 10,0 mm were sexed and pleopods of females inspected for eggs. Length measurements were grouped into 1 mm size classes and size frequency distributions of ovigerous (egg-bearing) and non-ovigerous prawns collected at each site were determined for the various sampling dates. Prawns having lengths equal to or larger than the smallest ovigerous size class at each site were regarded as sexually mature.



**Figure 1** A map of southern Africa, showing the geographical position of the Swartkops estuary and other areas mentioned in the text, while the lower section illustrates the sampling sites within the Swartkops estuary.

Approximately once a month during the study period the authors, staff of the Port Elizabeth City Engineer (unpubl. records) and Wooldridge (unpubl. data) each independently and on different days recorded temperatures and salinities in the surface layer (0–30 cm deep) of the water column near Sites 1 and 2. The former two groups measured close (1–8 m) to the estuarine bank during spring low tides, while the latter researcher sampled in midstream and generally during neap tides. The data were pooled and monthly means calculated. These data were used to calculate the mean temperature regimes experienced by *U. africana* at Sites 1 and 2, since the populations monitored were inundated by water for most (ca. 70–90%) of the tidal cycle and work by Hill (1967) suggested that when the temperature of the water column is below 25°C, *U. africana* would readily circulate water through its burrow, and the temperature in the latter would correspond almost exactly to that of the overlying water. The approximate incubation times of *U. africana* eggs during the breeding seasons were calculated using the equation of Hill (1977), namely,  $\log Y = -1,881 \log T + 4,0378$ , where  $Y$  = incubation periods (days) and  $T$  = temperature (°C).

The numbers and size composition of the prawns recorded from the samples regularly collected at Sites 1 and 2 were consistent throughout the study period (Hanekom 1980) and these samples were taken as representative of the populations in the above areas. It was assumed that if the sampling intervals corresponded to the incubation times of the eggs, then the ovigerous females recorded in consecutive samples could be

regarded as 'separate' groups of breeding females, because theoretically the ovigerous females recorded in one sample would have spawned by the next and those non-ovigerous females, which subsequent to sampling extruded eggs, would still be carrying them on the next sampling date. The number of ovigerous females per sample was expressed as a percentage of the mature females present. These values were then cumulatively plotted over a period of a year and the final total was used to estimate the number of broods produced (e.g. 100 and 200% = one and two broods per adult female per year respectively).

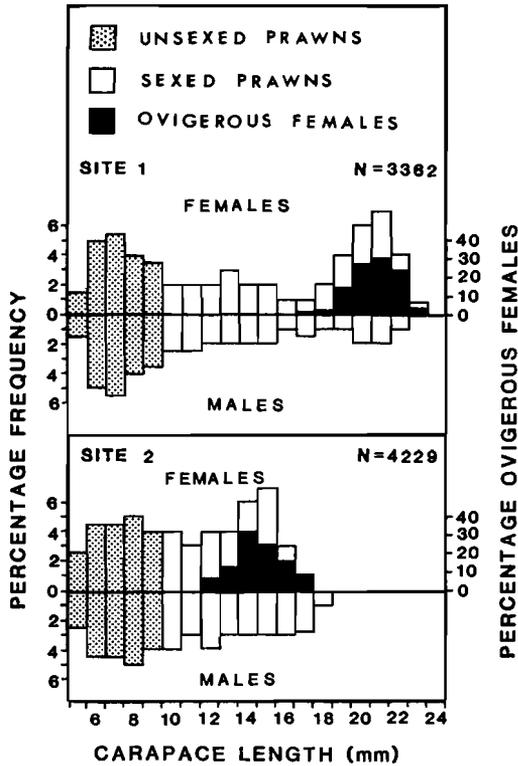
Between November 1976 and March 1977 approximately 45 prawns of varying carapace lengths and which appeared to be carrying a full complement of eggs were collected from each site. These prawns were measured, the egg bearing pleopods dissected off and placed in Gilson's fluid for at least three weeks to help loosen the eggs from the pleopods (Bagenal & Braum 1971). The eggs were then scraped or cut free from the pleopods and washed into a graduated flask. The volume was made up to 100 ml and the sample thoroughly mixed. Two 10-ml subsamples were taken with a wide bore pipette and transferred to separate counting trays. Counts were done using a stereo-microscope and digital counter. Logarithmic values of the carapace lengths of the prawns and the numbers of eggs per brood were determined and regression lines fitted to the data collected from each site. These lines were compared using the method described in Snedecor & Cochran (1973).

Approximately 100 freshly extruded (greenish yellow, non-eyed) eggs were physically removed from the pleopods of prawns from Site 1 and placed on a pre-weighed slide. The eggs were counted under a microscope, oven dried at 60 °C for 24 h, weighed to the nearest 0,01 mg and the mean mass per egg was calculated. The mean of five replicates was taken. A second batch of eggs was freeze dried and bombed in an adiabatic bomb calorimeter. Replicates were within one per cent of each other.

To calculate the annual reproductive output (Pr) of the populations sampled, the numbers of ovigerous females recorded in each size class over the sampling year were determined from size frequency data. These numbers were then multiplied by the dry mass values of the eggs produced by the corresponding size classes. The products were then summed and converted to kilojoules.

## Results

The percentage of prawns (> 10 mm carapace length) at Site 1 which was female, was significantly ( $p < 0,01$ ) larger than at Site 2 ( $\bar{x} \pm SD = 62 \pm 2,3$  v.  $56 \pm 2,5$ ;  $n = 10$  &  $12$  samples respectively), as were the carapace lengths of the ovigerous females ( $21,2 \pm 1,1$  mm v.  $15,1 \pm 1,3$  mm;  $n = 257$  &  $200$  respectively, Figure 2). The smallest ovigerous females found at Sites 1 and 2 were in the 17,0–17,8 and 12,0–12,8 mm carapace length classes respectively and prawns having sizes equal to or larger than these classes were regarded as sexually mature.



**Figure 2** Size frequency distributions of the *U. africana* sampled at Sites 1 and 2 over the entire study period, with the right-hand margin expressing the numbers of ovigerous females as a percentage of their total.

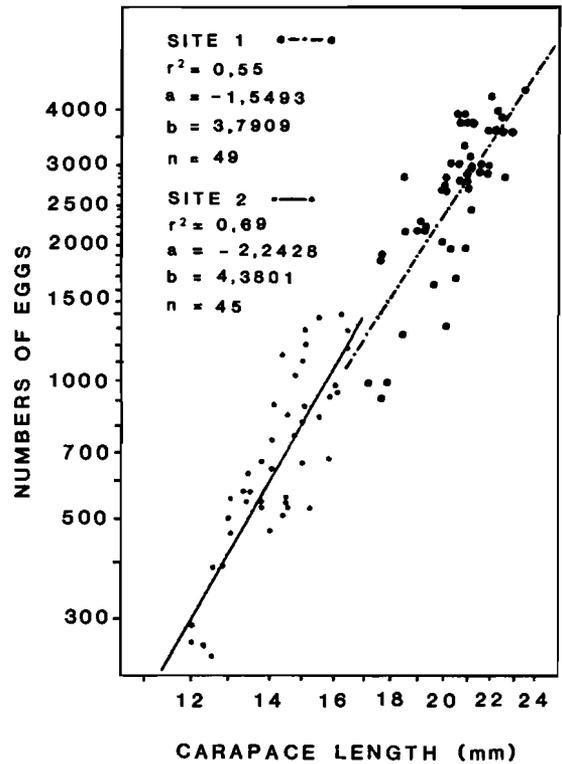
The slope and elevation of the regression line, describing the relationship at Site 1 between the size of the female *U. africana* and the number of eggs per brood, differed significantly from that of Site 2 ( $F = 59$  & 10 respectively;  $df. \approx 1:90$ ;  $p < 0,01$ ). The data from the two sites were therefore treated separately and the regression lines,

$$\log E = 3,7909 \log L - 1,5493 \quad (r^2 = 0,55; p < 0,01) \text{ and}$$

$$\log E = 4,3801 \log L - 2,2428 \quad (r^2 = 0,69; p < 0,01),$$

where  $E$  = number of eggs and  $L$  = carapace length in mm (Figure 3), were used to calculate egg production of the females at Site 1 and 2 respectively. The mean dry mass per egg was  $0,06 \pm 0,001$  mg, while the energy content was  $23,541$  kJ  $g^{-1}$ .

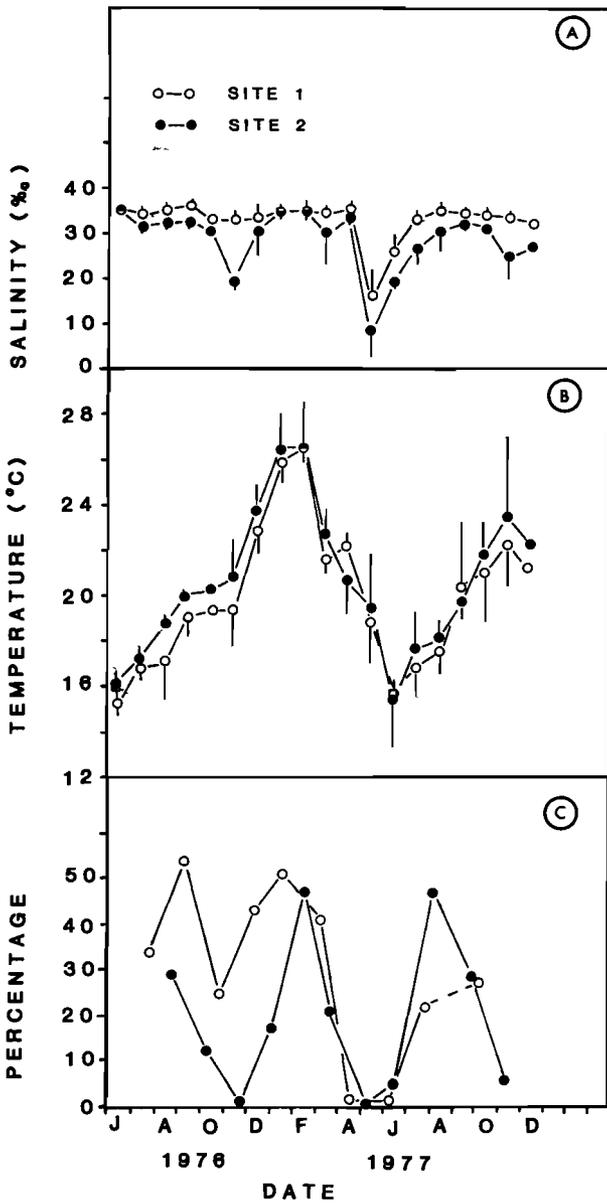
The percentages of adult females recorded as ovigerous at various times of the year at Site 2 indicated a distinct spring (July to October) and summer (December to March) breeding cycle (Figure 4). The spring cycle started as the water temperatures in the estuary began to rise and ended while they were still increasing. After a short latent period (*ca.* 2 months), the summer cycle started and continued till late autumn. At Site 1 this latent period between the two cycles is apparently reduced and the spring and summer breeding seasons tended to merge. At both sites the maximum percentage of mature females recorded as ovigerous at one time was close to 54% (Figure 4). These maximum values are relatively low, partly owing to the fact that the smallest adult size classes, which encompassed only a few



**Figure 3** The relationships between the size of the *U. africana* and the number of eggs per brood at Sites 1 and 2. Included are the regression coefficients ( $r$ ) and the constants of these regression equations ( $\log E = a + b \log L$ , where  $E$  = number of eggs and  $L$  = carapace length in mm).

reproductively active females (Figure 2), were included in the calculations. The salinity regime in the estuary during most of the study period was generally close to 34‰ and when fresh-water flooding did occur in November 1976 and May 1977, the numbers of ovigerous females in the populations were already declining (Figure 4). This made it difficult to assess the effects of reduced salinities on the breeding of *U. africana*.

The results of Figure 4 indicate that the breeding season of *U. africana* at Sites 1 and 2 could be divided into a spring (July to October) and summer (December to March) cycle and the mean incubation times of the eggs during these periods were calculated (Table 1). At Sites 1 and 2 during the summer cycle and at Site 2 during the spring breeding, the sampling intervals were about 1,3 times longer than the incubation periods. This meant that certain prawns could have extruded and hatched eggs all within a sampling interval and these breedings would not have been recorded. To try and correct for this deficit, the numbers of ovigerous females noted during these periods were multiplied by the ratio of the sampling interval to the incubation time (Table 1). The cumulative percentages of mature females recorded as ovigerous over a period of one year at Sites 1 (250) and 2 (165) (Figure 5) then became 315 and 222 respectively, which suggested a production of three and two broods of eggs per adult female per annum respectively. The calculated annual reproductive output ( $Pr$ ) of the



**Figure 4** (A-B) The mean monthly salinity and water temperature values recorded at Sites 1 and 2 over the study period and (C) the percentage adult female prawns, which were ovigerous on each sampling date.

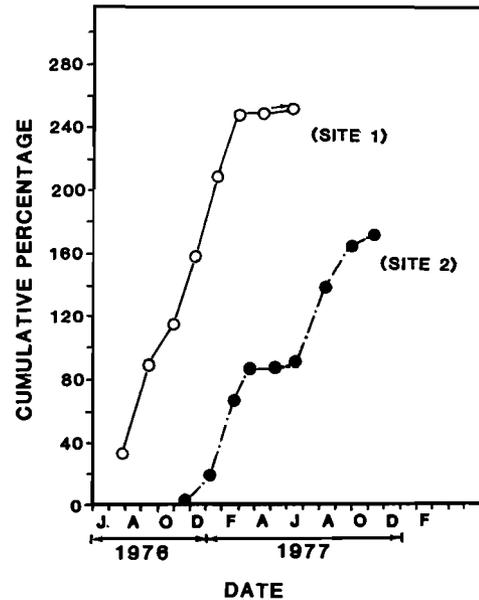
female population at Site 1 was higher than at Site 2 (1331 v. 342 kJ m<sup>-2</sup>, Table 2), as was the reproductive biomass ratio (Pr/B) (0,54 v. 0,26).

**Discussion**

The sizes of adult *U. africana* vary within the Swartkops estuary and Sites 1 and 2 are representative of areas having populations of large and 'stunted' prawns respectively (Hanekom & Erasmus 1988). At the former site the smallest recorded ovigerous female was considerably larger than that of Site 2 (ca. 17 v. 12 mm carapace length), as was the mean size of these females (21,2 ± 1,1 v. 15,1 ± 1,3 mm carapace length). The size frequency distributions of the above populations show distinct modal peaks of adult females (Figure 2), a phenomenon recorded by Hill (1977) for *U. africana*

**Table 1** The calculated mean and standard deviation ( $\bar{x} \pm SD$ ) of the water temperatures, incubation times of prawn eggs and sampling intervals during the spring (July to October) and summer (December to March) breeding cycles

	Site 1 $\bar{x} \pm SD$	Site 2 $\bar{x} \pm SD$
<b>Winter cycle</b>		
Water temperatures (°C)	18,1 ± 1,3	19,0 ± 1,3
Incubation times (days)	47 ± 7	43 ± 6
Sampling intervals (days)	45 ± 7	53 ± 11
<b>Summer cycle</b>		
Water temperatures (°C)	24,1 ± 2,4	24,8 ± 1,9
Incubation times (days)	27 ± 5	26 ± 4
Sampling intervals (days)	40 ± 1	38 ± 7
<b>Entire study period</b>		
Sampling intervals (days)	43 ± 3	44 ± 7



**Figure 5** Cumulative plots of the percentages of adult female prawns, which were recorded as ovigerous over the study periods at Sites 1 and 2.

populations sampled in the Kowie, Knysna and Uilenkraal estuaries. Hill (1977) related these peaks to an accumulation of adult females in certain size classes, as a result of a slowing up in their growth rates owing to increased energy expenditure on reproduction. The adult male prawns were generally larger than the females and did not form well-defined modal peaks [Figure 2 (trend at Site 1 indistinct) and Hill 1977]. The larger size of adult males (ca. 12% by mass, Hill 1977 and Hanekom 1980) and their lower energy content per dry gram body mass (ca. 11%) relative to adult females (Hanekom 1980), suggested a comparatively small reproductive output by males. The male component was therefore ignored in the reproductive calculations.

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**Table 2** The calculated reproductive output of the female *U. africana* populations sampled at Sites 1 and 2 over the period July 1976 to July 1977 and November 1976 to November 1977 respectively

Size class	Numbers of ovigerous females recorded per m <sup>2</sup> A	Dry mass of eggs per brood (g) B	Reproductive output	
			g m <sup>-2</sup> A×B	kJ m <sup>-2</sup> A×B×23,541*
<b>Site 1</b>				
17,0–17,8	4	0,085	0,342	8,045
18,0–18,8	6	0,106	0,634	14,915
19,0–19,8	35	0,129	4,517	106,334
20,0–20,8	92	0,156	14,365	338,175
21,0–21,8	106	0,187	19,844	467,141
22,0–22,8	65	0,223	14,468	340,600
23,0–23,8	9	0,263	2,364	55,652
17,0–23,8	317	1,149	56,534	1330,862
<b>Site 2</b>				
12,0–12,8	16	0,021	0,338	7,954
13,0–13,8	31	0,030	0,919	21,646
14,0–14,8	79	0,041	3,212	75,604
15,0–15,8	85	0,055	4,637	109,158
16,0–16,8	44	0,072	3,162	74,433
17,0–17,8	16	0,093	1,490	35,077
18,0–18,8	3	0,119	0,357	8,401
12,0–18,8	274	0,431	14,115	332,273

\*The determined energy values (kJ/g) for *U. africana* eggs.

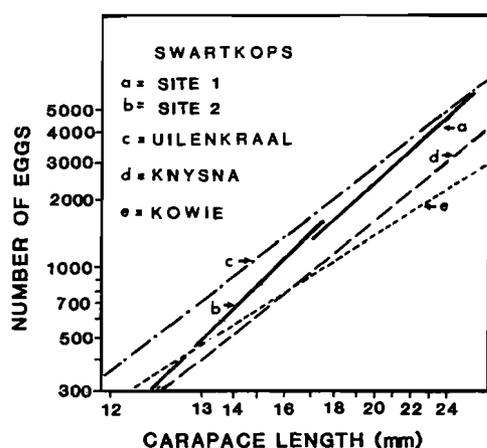
The percentage of the population sampled at Site 1 which was female, was significantly ( $p < 0,01$ ) higher than at Site 2 (62 v. 56%) and that (ca. 50%) from samples taken in the Kowie and Knysna estuaries (Hill 1977). It was, however, comparable with values (ca. 66%) recorded from the Uilenkraal estuary and Knysna heated ponds (Siegfried 1962; Hill 1977). Hill (1977) postulated that the higher ratio of females to males in the heated ponds relative to the estuary at Knysna was a result of warmer temperatures. Data collected from the Swartkops estuary, however, showed no temperature, salinity or size related pattern, since the percentage females recorded from samples (ca. 150–350 individuals) of large prawns (adult carapace length  $\approx$  16–23 mm) taken from nine sites along the length of the lower reaches were similar to those from samples of 'stunted' prawns (adult carapace length  $\approx$  12–18 mm) taken along the slightly warmer (ca. 1°C) and less saline (ca. 1–2‰) 'middle' reaches ( $\bar{x} \pm SD = 55 \pm 4\%$  v.  $54 \pm 7\%$ ;  $t = 0,24$ ;  $p > 0,05$ ; Hanekom 1980 unpubl. data). Similar variations in sex ratios have been noted in the *Callinassa kraussi* and *U. pusilla* populations of the Swartkops estuary and Northern Adriatic Sea respectively, but no determining factors could be discerned (Hanekom 1980; Dworschak 1988).

The recorded breeding season of *U. africana* at Site 2, with a distinctive spring (July to October) and summer (December to March) cycle (Figure 4), is similar to that

noted for the same species in the Kowie estuary (Hill 1977). Conversely, the pattern at Site 1, where the two cycles tended to merge, shows a greater similarity to the breeding season recorded in the Knysna and Uilenkraal estuaries (Siegfried 1962; Hill 1977). In all these areas *U. africana* were reproductively inactive during the months of May and June, after which the numbers of ovigerous females began increasing as the estuarine temperatures started to rise in early spring (Figure 4 and Hill 1977). This suggested that changes in temperature may be important in initiating the breeding cycle. Conversely, salinity appears unlikely to be an initiating factor, since the breeding cycle of the prawns in the Swartkops and Kowie estuaries appears to begin regularly in late winter (Figure 4 and Hill 1977), while heavy falls of rain in these areas occur irregularly (MacNae 1957; Hill 1967) and fresh-water flooding of the former estuary has been recorded throughout the year (Hanekom 1989). Reduced salinities may, however, affect the development and possible premature 'shedding' of eggs, a phenomenon reported by Forbes (1973) for *C. kraussi*.

The size of the adult prawns in the Swartkops estuary tended ( $p < 0,01$ ) to decrease with distance from the estuarine mouth and this reduction in prawn size appeared to be related to the transport of oxygen and food material by tidal currents (Hanekom & Erasmus 1988). The prawns at Site 1, which are larger than at Site 2, would therefore appear to live in a more favourable environment. At this site the spring and summer breeding cycles tended to merge (Figure 4) and the cumulative total of the percentage mature females recorded as ovigerous over a period of a year, was 93 percentage units greater than at Site 2 (315 v. 222, Figure 5). This suggests that at Site 1 there is a faster recovery rate after the spring spawning and the production of an extra (3 v. 2) brood of eggs. Dworschak (1988) calculating the differences in exuviae and somatic productions between male and female *U. pusilla* [whose maximum sizes are similar to those of *U. africana* (Siegfried 1962)], determined that more than two broods of eggs are energetically possible for females having carapace lengths larger than 17,0 mm. He estimated a reproductive output of three broods per adult female per annum for this species in the lagoon of Grado in the Adriatic Sea. This value is well below the maximum number of broods (5 & 7), which Hill (1977) calculated could theoretically have been produced by *U. africana* populations monitored in the Kowie and Knysna estuaries. The latter values were determined by dividing the total duration of the breeding season by the incubation times of the eggs and did not involve the proportion of the population which was ovigerous. If Hill's (1977) data were reworked in the manner described in this survey, the cumulative values of the percentage mature females which were ovigerous over a period of a year, ranged between 200–470 and had a mean and standard deviation of approximately 312 and 92 respectively. The latter suggests that 2–4 broods of eggs are produced per adult female per year, which corresponds to the values of this survey and Dworschak (1988).

The slopes of the regression lines describing the



**Figure 6** Regression lines determined from data collected from the Swartkops (Sites 1 and 2, Figure 3), Uilenkraal, Knysna and Kowie estuaries (Siegfried 1962; Hill 1977) for the relationships between the size of *U. africana* and the number of eggs per brood.

relationships between the size of the prawns and the number of eggs per brood in this study were much steeper than determined by Siegfried (1962) and Hill (1977) for *U. africana* collected from the Uilenkraal, Knysna and Kowie estuaries (Figure 6). The methods used by the latter two researchers, to determine the number of eggs in a brood, differed from this study. This and the fact that there is a large variation in the number of eggs produced by prawns of similar sizes [correlation coefficients ( $r^2$ ) of most of the above lines ranged from 0,48 to 0,69; Figure 3 and Hill 1977] are probably some of the parameters causing these differences in the slopes of the regression lines. Dworschak (1988) has, however, noted marked variations between the number of eggs per brood of *U. pusilla* from different sites within the Adriatic Sea, as well as smaller seasonal differences. The brood sizes of *U. africana* from the Swartkops River might therefore differ significantly from those of the other estuaries studied (Figure 6).

The eggs of *U. africana* are small, having a mean dry mass of 0,06 mg and an energy content of 23,541 kJ g<sup>-1</sup> dry mass and the calculated reproductive expenditure of an adult female prawn in the Swartkops estuary could range from 0,86 kJ per annum (for a 12,0 mm carapace length prawn of Site 2 producing two broods of 305 eggs) to 20,42 kJ per annum (for a 24,0 mm carapace length prawn of Site 1 producing three broods of 4819 eggs). The estimated annual reproductive output (Pr) and reproductive biomass ratio (Pr/B) of the prawn population at Site 1 were much greater than those of Site 2 (1331 kJ m<sup>-2</sup> and 0,53 v. 332 kJ m<sup>-2</sup> and 0,26) indicating a higher egg production per adult individual at Site 1. The calculated annual somatic production (Pg) for these two populations were 1864 and 1093 kJ m<sup>-2</sup> respectively (unpubl. data) and reproduction would therefore appear to constitute approximately 42 and 23% of the respective total (exuviae ignored) production (Pg + Pr) values. Dworschak (1988) extrapolating values determined for

individual *U. pusilla* to a theoretical population, estimated that about 70% of the total production (Pg + Pr) was due to reproduction. This population, however, consisted primarily (ca. 47% v. 25% at Sites 1 & 2) of adult females, whose energy expenditure on somatic growth relative to egg production is small. This would probably account for his higher reproductive estimates.

To conclude, the calculated reproductive output of the average adult female *U. africana* at Site 1 was approximately three times greater than at Site 2. This difference is apparently related primarily to variations in adult prawn size, which in the Swartkops estuary seems to be determined mainly by tidal currents and their transport of food materials (Hanekom & Erasmus 1988), rather than by temperature, as was postulated by Hill (1977) for the Knysna heated ponds.

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