Growth, production and consumption of the thalassinid prawn *Upogebia africana* (Ortmann) in the Swartkops estuary

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Populations of large and stunted *Upogebia africana* were regularly and quantitatively sampled in the Swartkops estuary. The growth of these prawns, determined by cohort analyses, was described by von Bertalanffy equations: $Lt = 24{,}4\ (1 - e^{-0{,}0583\ (t\ +\ 1{,}8446)})$ and $Lt = 19{,}0\ (1 - e^{-0{,}0454\ (t\ +\ 4{,}0726)})$ respectively, where Lt = carapace length (in mm) at age t (in months). Eggs were apparently laid after moulting, which occurred primarily during spring and summer. First sexual maturity was attained after 1,5 years, while the estimated life span was 4 years. The annual somatic production and Pg/B ratios of the populations sampled were 1864 and 1093 $kJ.m^{-2}$ and 0,79 and 0,99 respectively. Somatic production of the entire estuarine population was approximately 1077 × 10^6 $kJ.y^{-1}$. An estimated 13, 5 and 2% of this was 'consumed' by birds, fish and man respectively, while the remainder apparently entered the scavenger and detrital food webs.

Kwantitatiewe monsters van normale en verdwergde *U. africana* is met gereelde tussenposes in die Swartkopsgetyrivier geneem. Die groei van hierdie garnale, soos bepaal deur kohort-analise, is deur von Bertalanffy groeivergelykings soos volg beskryf: $Lt = 24{,}4\ (1 - e^{-0{,}0583\ (t\ +\ 1{,}8446)})$ en $Lt = 19{,}0\ (1 - e^{-0{,}0454\ (t\ +\ 4{,}0726)})$ waar Lt karapakslengte (in mm) op ouderdom t (in maande). Eiers is blykbaar na vervelling, wat hoofsaaklik gedurende lente en somer plaasgevind het, gelê. Geslagsrypheid is na 1,5 jaar bereik, terwyl die berekende lewensduur 4 jaar is. Die jaarlikse somatiese produksie en Pg/B verhouding van die gemonsterde bevolkings is onderskeidelik 1864 en 1093 $kJ.m^{-2}$ en 0,79 en 0,99. Somatiese produksie van die hele getyrivier se bevolking is naastenby 1077 × 10^6 $kJ.j^{-1}$. 'n Geskatte 13, 5 en 2% hiervan is onderskeidelik deur voëls, visse en mense verbruik, terwyl die res waarskynlik die aasvreter- en detritus-voedselweb binnegedring het.

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Mud prawns, *Upogebia africana* (Ortmann), are abundant in many East Cape estuaries (Hill 1967; Hecht 1973; du Preez 1978; Hanekom 1980, 1982; Day 1981; Hodgson 1987), where they are a major food source for a variety of fish and bird species (Schramm 1978; Marais 1984; Hanekom, Baird & Erasmus 1988; Martin & Baird 1987; Whitfield 1988; Martin 1991) and are extensively exploited as a bait organism by man (Hill 1967; Hanekom 1980; Martin 1991; Wynberg 1991). Knowledge of their somatic production and consumption would be important in determining conservation measures for these estuaries.

Adult *U. africana* from the lower shore of the lower reaches of the Swartkops estuary have carapaces 1–5 mm longer than those from the creeks and middle reaches. These size variations are due to differences in growth rates, which are apparently influenced by the tidal transport of suspended food material (Hanekom & Erasmus 1988). The growth and somatic production of large and stunted *U. africana* were determined by cohort analyses of regularly sampled populations. This work complements limited growth studies of *U. africana* (Siegfried 1962; Hill 1967) and extensive research of *U. pusilla* (Dworschak 1988), and investigates the impact of birds (Schramm 1978; Martin 1991), fish (Marais 1984) and man (Hill 1967; Wynberg 1991) on the somatic production of the entire estuarine *U. africana* population.

Study site

The Swartkops estuary is situated well within the distributional range of *U. africana* in southern Africa (Figure 1). It has extensive *Spartina* dominated salt marshes (363 ha; Pierce 1979) in the upper intertidal and smaller *Zostera* beds on the lower shore (13–16 ha; Talbot & Bates 1987). The

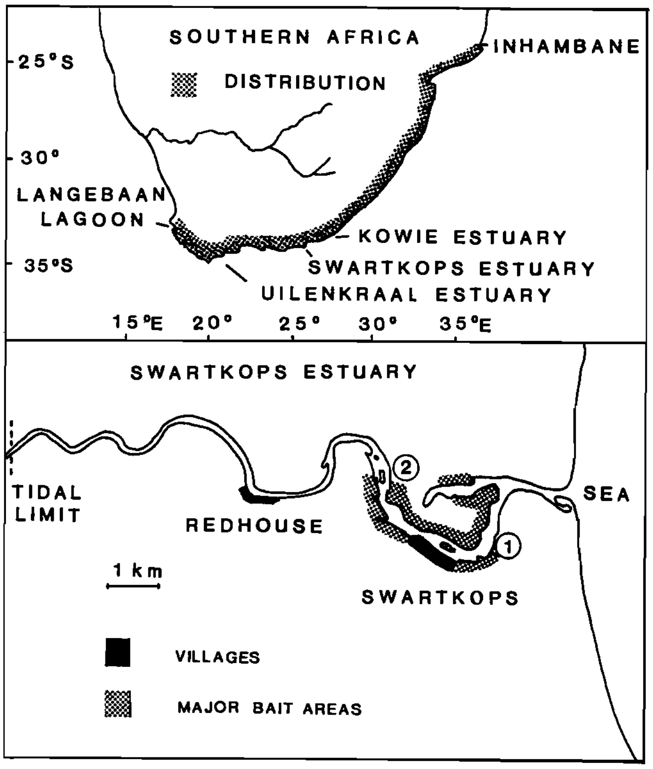

Figure 1 (A) Location of Swartkops estuary and the distribution of *U. africana* (from Hill 1967) in southern Africa. (B) Sampling sites and major bait-collecting areas within the Swartkops estuary.

estuarine mouth is perennial and approximately 57% of the tidal prism of 2,9 × 10^6 m^3 is exchanged per spring tide cycle (Lord & Thompson 1988). Little vertical stratification occurs in the water column, the salinities gradient along its length is usually within 15–35‰ and the annual range in water temperatures is close to 13–28°C (McLachlan & Grindley 1974; Wooldridge 1979; Emmerson 1985a).

Methods

Approximately once a month, between July 1976 and November 1978, the authors, staff of the Port Elizabeth City Engineer (unpubl. data) and Wooldridge (unpubl. data) each independently and on separate days took surface temperature and salinity readings of the water column near Sites 1 and 2 (Figure 1) in a manner described in Hanekom & Erasmus (1989). These readings were pooled and the mean monthly temperatures and salinities were calculated.

U. africana were regularly (*c.* every six weeks) and quantitatively sampled at Sites 1 and 2, where human disturbance was low and populations of large and stunted prawns, respectively, occurred. At each site duplicate samples were taken at 0 cm and 30 cm above the spring low tide mark, tidal levels within which prawn densities were high and variations in maximum prawn size were small (Hanekom 1980). A 50 × 50 cm metal quadrat with a depth of 30 cm, which reached approximately 95% of the prawns within the quadrat area (Hanekom *et al.* 1988), was forced into the substratum. Its contents were removed with a spade and bucket, and hand sieved through a 3-mm mesh sieve. Carapace lengths (CL) of all prawns sampled were measured to the nearest 0,2 mm with vernier calipers. Prawns (CL >10,0 mm) were sexed, pleopods inspected for eggs and the hardness of their integument noted. Because sampling was abrasive, affecting the firmness of the prawns, only very soft individuals were classed as freshly-moulted. These numbers were low, but comparable at both sites, and data from the two sites and study periods were pooled to determine mean monthly percentages of freshly moulted adults (CL > 17,0 mm and 12,0 mm at Sites 1 and 2 respectively, Hanekom & Erasmus 1989) and juveniles.

Length measurements were grouped into 1 mm size classes and size frequency histograms were constructed for each sampling date. Probability paper was applied to identify cohorts (Harding 1949; Cassie 1954), but in certain instances the oldest cohorts were separated by inspection. The modal means were fitted to the von Bertalanffy growth model, generally regarded as the most suitable for expressing fish growth (Pauly 1979 and Hughes 1986 in Mann 1992) and used in decapod studies (Emmerson 1985b; Dworschak 1988). The equation applied was:

$$Lt = L_\infty \ (1-e^{-k\ (t-t_0)}),$$

where constants L_∞ and k were determined from a Walford (1946) plot of Lt + 1,5 (sampling interval = 1,5 months) versus Lt (carapace length in mm at age t) (Ricker 1971), and time of hatching (t_o) from monthly counts of ovigerous females in each population.

Length–dry mass relationships of male and female prawns from each site were determined during summer and winter. Non-ovigerous prawns were measured to the nearest 0,2 mm, oven dried at 95°C for 24 h and weighed to the nearest milligram. The values for each determination were fitted to a regression equation and these equations (in their logarithmic form) were compared in a manner described by Snedecor & Cochran (1973).

Energy determinations of juveniles, adult males and non-ovigerous females were done quarterly, with samples from each group being freeze dried, homogenized and bombed in a bomb calorimeter. Replicates were within 1% of each other.

Somatic production of the populations was determined by the growth method of Crisp (1971) namely: $Pg = \Sigma \Delta Wt.Nt$, where Pg = production by somatic growth, Nt = the mean number of individuals in cohort over time interval t and ΔWt = the change in the mean mass of these individuals over time t. The numbers spawned were estimated by extrapolating numbers (Nt) against time (Crisp 1971).

Results

Corresponding length-mass equations of *U. africana* for the two sexes and seasons were similar ($p > 0{,}05$), but those for Sites 1 and 2 differed ($p < 0{,}025$) from each other (Table 1). Hence, a single length-mass equation was determined for each site, namely: $W = 0{,}0487\ L^{3{,}2889}$ (Site 1) and $W = 0{,}0510\ L^{3{,}2552}$ (Site 2), where W is dry mass (mg) and L is

Table 1a Constants (*a* & *b*), regression coefficient (r^2), numbers of observations (*n*) and significance (*p*) of carapace length (mm) versus dry mass (mg) relationship ($W = aL^b$) for *U. africana*. Key: (S) = summer, (W) = winter, M = male, F = female and ** = p < 0,025

Site	Season	Sex	*a*	*b*	r^2	*n*	*p*
1	S	M	0,0557	3,2391	0,98	93	<0,01
1	S	F	0,0479	3,2953	0,98	90	<0,01
1	W	M	0,0431	3,3405	0,99	47	<0,01
1	W	F	0,0445	3,3107	0,98	83	<0,01
1	S & W	M & F	0,0487	3,2889	0,98	313	<0,01
2	S	M	0,0578	3,2230	0,98	46	<0,01
2	S	F	0,0414	3,3208	0,98	53	<0,01
2	S	M & F	0,0510	3,2552	0,98	99	<0,01

Table 1b Statistical comparisons of the length-mass regression data for the two sexes, seasons and sites

	Residual variance	Slope	Elevation
Sexes			
Site 1 (W) M *v*. F	1,23	0,03	1,19
Site 1 (S) M *v*. F	1,24	0,14	0,04
Site 2 (S) M *v*. F	1,09	0,04	0,04
Seasons			
Site 1 M (S) *v*. (W)	1,19	1,64	1,15
Site 1 F (S) *v*. (W)	1,20	2,14	0,36
Sites			
M (S) Site 1 *v*. Site 2	1,35	4,82**	0,04
F (S) Site 1 *v*. Site 2	1,00	5,96**	1,65

carapace length (mm) (Table 1). These equations were used to determine the mass of individuals in growth and production studies.

Females comprised between 56 to 60% of the prawn populations (CL > 10,0 mm) sampled. Their size frequency distributions generally corresponded to those of males (Figure 2), and to simplify growth and production studies length measurements of the two sexes were pooled. Similarly, although the energy content of adult females was higher than adult males and juveniles (Figure 3), values were pooled and means (juvenile data used for both sites) of 14,303 and 14,680 $kJ.g^{-1}$ dry mass were used to convert prawn mass to energy at Site 1 and 2 respectively.

Percentages of adult male and female *U. africana* freshly moulted were highest between October and February, a period of rising water temperature and increasing solar radiation (Figure 4). Juveniles had an additional moulting peak in autumn, suggesting a shorter intermoult period than adults.

The numbers and size composition of prawns sampled were consistent throughout the study period (Figures 5 & 6), and samples were taken to be representative of the populations studied. Because *U. africana* larvae develop at sea, recruitment to prawn populations occurs through postlarvae entering the estuary with flood tides (Emmerson 1983; Wooldridge 1991). At Site 1, near the mouth of the estuary, recruitment occurred continuously throughout the year, and the juvenile cohorts of January 1977 and 1978 (1 & 0 in Figure 5) comprised recruits from the entire June to April 'breeding' season (Figure 4). Hence, their mean spawning time was in October. Conversely, at Site 2 (in the middle reaches) annual recruitment was dominated by a 'single' (winter) influx of juveniles (Cohorts 1 & 0 in Figure 6), presumably hatched during March of the same year (Figure 4).

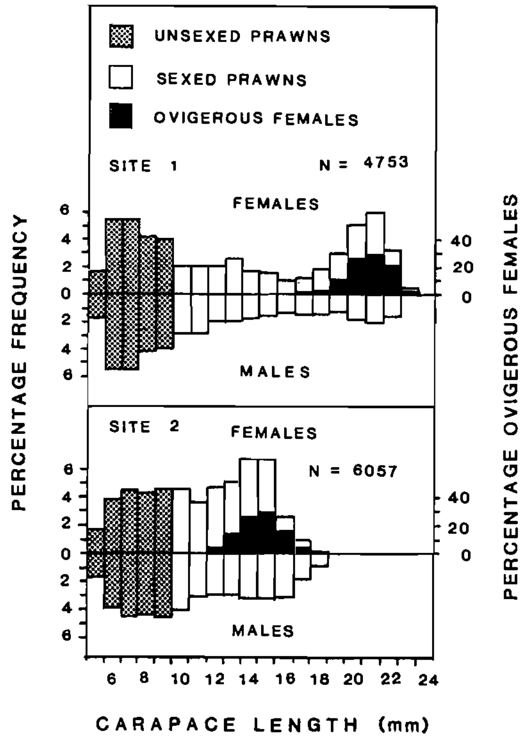

Figure 2 Size frequency distributions of male and female prawns, as well as ovigerous females (scale on right-hand margin) sampled at Sites 1 and 2 over the entire study period.

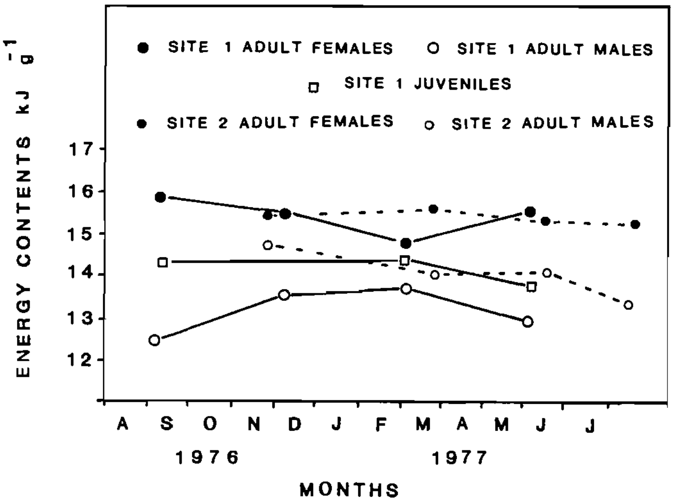

Figure 3 Energy values of adult and juvenile *U. africana* at Sites 1 and 2.

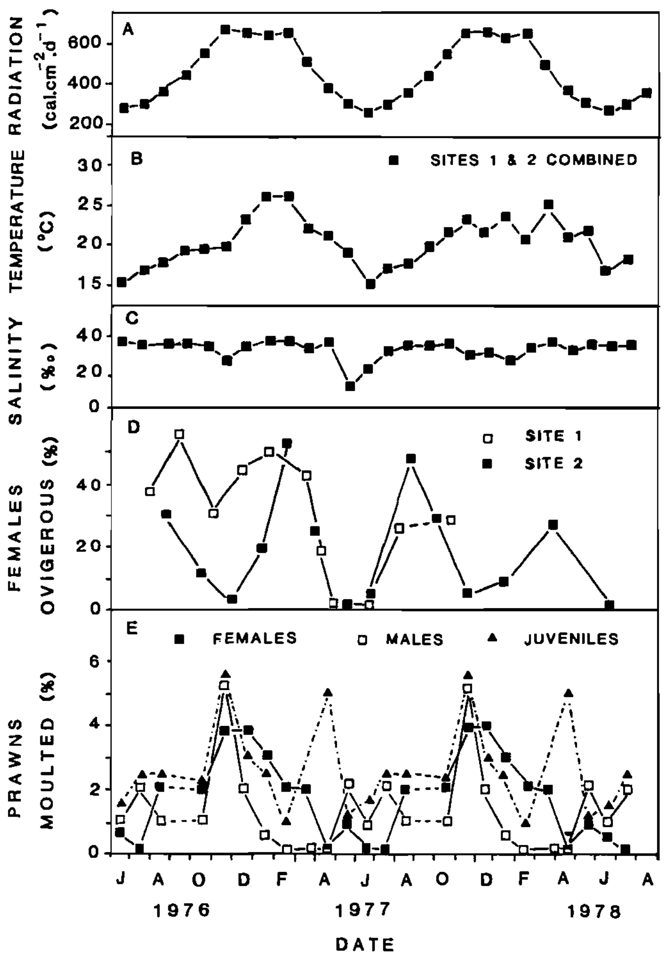

Figure 4 (A) Mean monthly solar radiation measured at ground level at Port Elizabeth (16 km south-west of Swartkops estuary) during 1957/8 (Hill, Kaplan, Scott & Partners 1974); (B) & (C) mean monthly water temperatures and salinities; (D) percentages of adult female *U. africana* ovigerous and (E) combined (Sites 1 and 2) mean monthly percentages of prawns moulted.

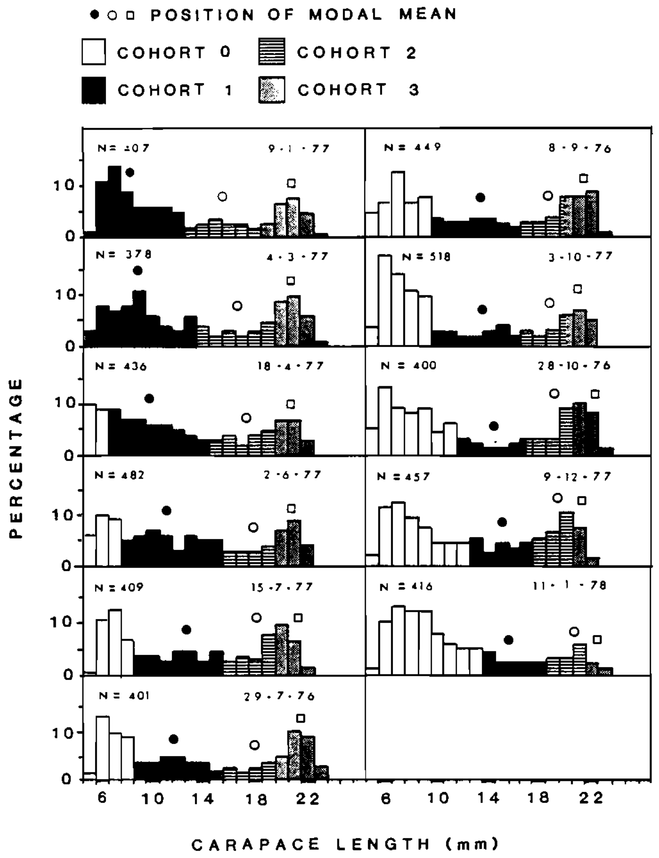

Figure 5 Size frequency histograms of *U. africana* sampled at Site 1 between July 1976 and January 1978, sampling dates and numbers per m^2 are shown.

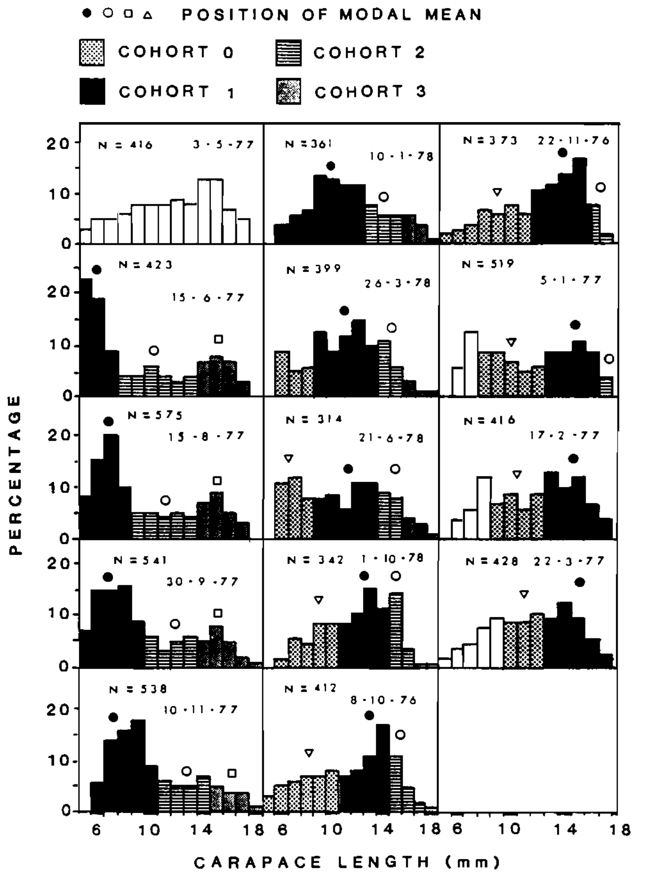

Figure 6 Size frequency histograms of *U. africana* sampled at Site 2 between October 1976 and June 1978, sampling dates and numbers per m^2 are shown.

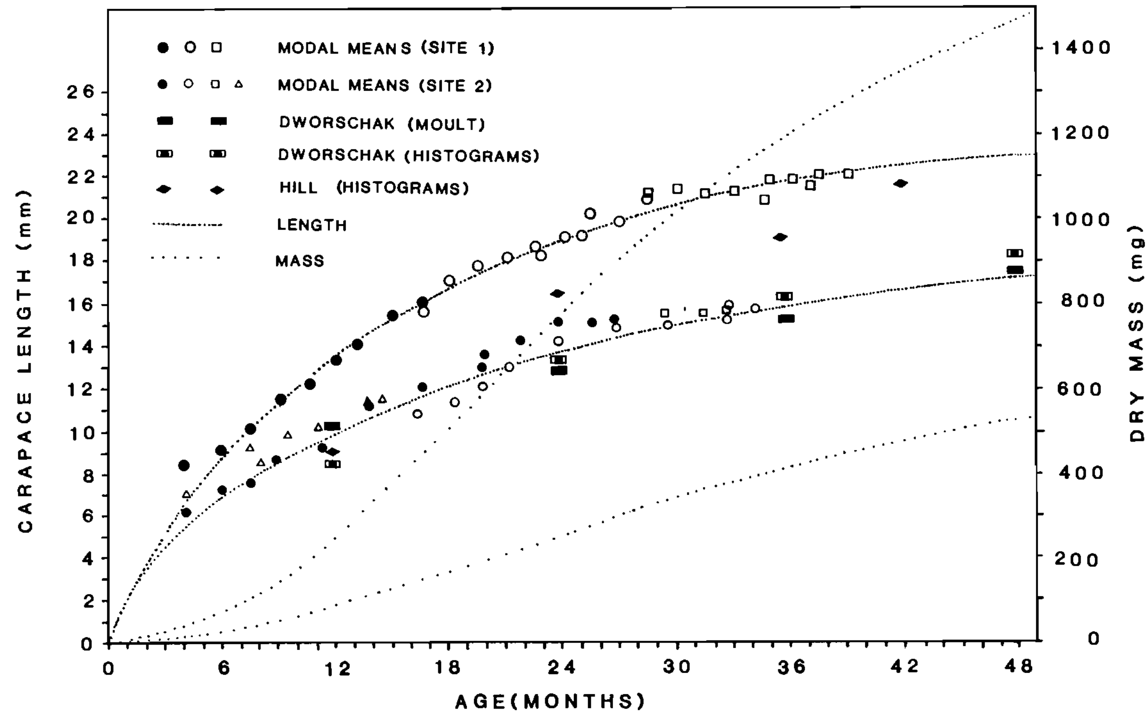

Figure 7 The progression of the modal means of cohorts in Figures 5 & 6 against time, and the resultant growth curve for *U. africana* as determined by von Bertalanffy equations:
$L_t = 24{,}4\,(1 - e^{-0{,}0583\,(t\,+\,1{,}8446)})$ (Site 1) and $L_t = 19{,}0\,(1 - e^{-0{,}0454\,(t\,+\,4{,}0726)})$ (Site 2).
Included are growth rates of female *U. pusilla* from Grado, determined from: (1) moult increments and intermoult durations, and (2) size frequency histograms (Dworschak 1988), as well as rates of *U. africana* from the Kowie estuary, assessed from histograms (Hill 1967).

The progressions of these and other cohorts in Figures 5 and 6 were plotted against time (Figure 7), and the von Bertalanffy growth equations (calculated from the mean modal values for each age group) were:

$Lt = 24{,}4\,(1 - e^{-0{,}0583\,(t\,+\,1{,}8446)})$ (Site 1) and
$Lt = 19{,}0\,(1 - e^{-0{,}0454\,(t\,+\,4{,}0726)})$ (Site 2)

where Lt = carapace length (mm), t = age (months) and e = 2,7183. These equations fitted the observed data adequately (Figure 7) and the calculated L_{∞} (maximum theoretical carapace length attainable) values were similar to the largest carapace lengths recorded at Sites 1 (24,4 v. 24,8 mm) and Site 2 (19,0 v. 19,3 mm).

Most (*c.* 95 %) *U. africana* sampled at Sites 1 & 2 had carapace lengths less than 23,0 and 17,0 mm respectively (Figure 2), and their potential life span was estimated to be four years (Figure 7).

The numbers of prawns in the various cohorts generally decreased steadily over the study period (Figure 8). The annual somatic production (Pg) and production / biomass (P/B) ratios at Site 1 and 2 were calculated to be 1864 and 1093 $kJ.m^{-2}$ and 0,79 and 0,99 respectively, while somatic production for the entire estuary was approximately 1077 × 10^{-6} $kJ.y^{-1}$ (Tables 2–4).

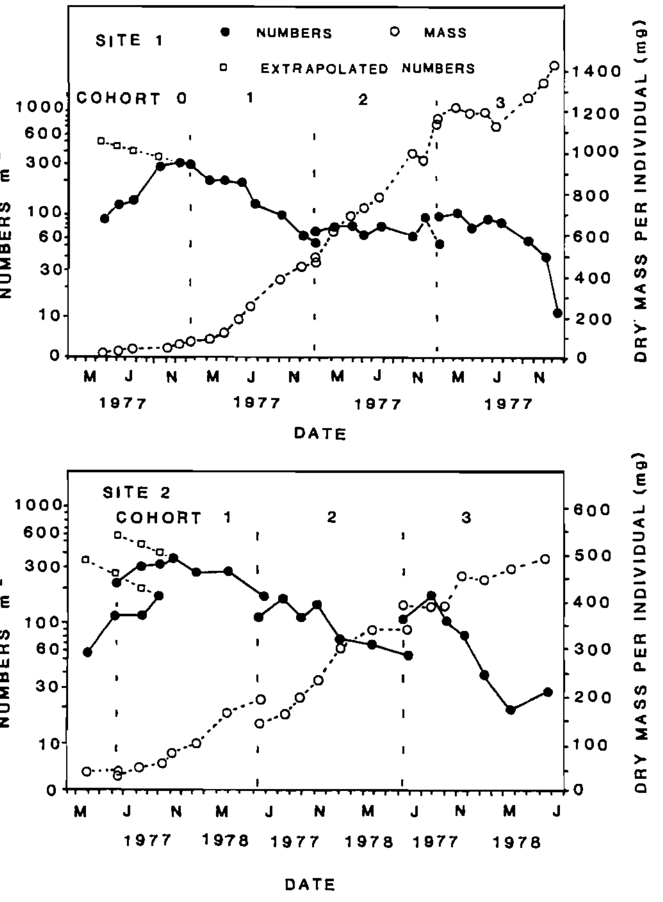

Figure 8 Survivorship plots, showing the number and mean dry mass of the *U. africana* in each cohort sampled at Site 1 and 2 over periods January 1977 to January 1978 and June 1977 to June 1978 respectively. Extrapolation, shown by stippled lines, is to estimate numbers at time of recruitment.

Table 2 Somatic production (g dry mass. m^{-2} & $kJ.m^{-2}$) of the *U. africana* population sampled at Site 1 from January 1977 to January 1978. Values in brackets were determined from extrapolations in Figure 8

Month	Cohort	Numbers in cohort Nt (nos/m^2)	Mean mass per prawn Wt (mg)	Production increment (A) $Nt\Delta Wt$ (g)	Production increment (B) (A)(14,303) (kJ)
Jan. 77	–				
Mar. 77	–				
Apr. 77	0	(460)	16		
Jun. 77	0	(420)	25	3,960	56,640
Jul. 77	0	(400)	37	4,920	70,371
Oct. 77	0	(350)	38	0,375	5,364
Dec. 77	0	306	57	6,232	89,136
Jan. 78	0	300	67	3,030	43,338
Total				18,517	264,849
Jan. 77	1	240	56		
Mar. 77	1	212	72	3,616	51,720
Apr. 77	1	204	98	5,408	77,351
Jun. 77	1	207	154	11,536	164,999
Jul. 77	1	119	219	10,595	151,540
Oct. 77	1	93	286	7,102	101,580
Dec. 77	1	59	352	5,016	71,744
Jan. 78	1	54	444	5,198	74,347
Total				48,471	693,281
Jan. 77	2	65	418		
Mar. 77	2	72	553	9,248	132,274
Apr. 77	2	79	643	6,795	97,189
Jun. 77	2	63	679	2,556	36,558
Jul. 77	2	74	729	3,425	48,988
Oct. 77	2	57	809	5,240	74,948
Dec. 77	2	96	911	7,803	111,606
Jan. 78	2	51	1087	12,936	185,024
Total				48,003	686,587
Jan. 77	3	98	1121		
Mar. 77	3	102	1157	3,600	51,491
Apr. 77	3	74	1121	–3,168	–45,312
Jun. 77	3	92	1139	1,494	21,369
Jul. 77	3	86	1070	–6,141	–87,835
Oct. 77	3	73	1248	14,151	202,402
Dec. 77	3	37	1286	2,090	29,893
Jan. 78	3	11	1424	3,312	47,372
Total				15,338	219,379
Total production (P0, P1, P2, P3):				130,329	1864,096

Discussion

Growth of crustaceans is discontinuous, occurring in steps of successive moults (Passano 1960). Soft, newly moulted *U. africana* were recorded throughout the year, with peak counts (especially in the Uilenkraal estuary) in late spring and early summer (Figure 4; Siegfried 1962). Spring-summer peaks in moulting have been recorded in *U. deltaura* (Tunberg 1986), the lobster *Nephrops norvegicus* (Farmer 1973), as well as decapods *Callianassa kraussi* and *Sesarma catenata* in the Swartkops estuary (unpubl. data; Els 1982). The moulting peaks of *U. africana* coincided with periods of increasing solar radiation (or day length), and rising water temperature (Figure 4), factors capable of inducing moulting

Table 3 Somatic production (g dry mass. m^{-2} and $kJ.m^{-2}$) of the *U. africana* population sampled at Site 2 from June 1977 to June 1978. Values in brackets were determined from extrapolations in Figure 8

		Numbers in cohort	Mean mass per prawn	Production increment	
Month	Cohort	N_t (nos/m^2)	W_t (mg)	(A) $N_t \Delta W_t$ (g)	(B) (A)(14,680) (kJ)
Mar. 78	0	(320)	29		
Jun. 78	0	(220)	31	0,540	7,927
Total				0,540	7,927
Jun. 77	1	(550)	18		
Aug. 77	1	(430)	32	6,860	100,705
Sep. 77	1	(390)	38	2,460	36,113
Nov. 77	1	339	58	7,290	107,017
Jan. 78	1	249	70	3,528	51,791
Mar. 78	1	255	141	17,892	262,655
Jun. 78	1	156	166	5,138	75,426
Total				43,168	633,706
Jun. 77	2	106	118		
Aug. 77	2	132	141	2,737	40,179
Sep. 77	2	108	175	4,080	59,894
Nov. 77	2	124	221	5,336	78,332
Jan. 78	2	72	294	7,154	105,021
Mar. 78	2	69	336	2,961	43,467
Jun. 78	2	59	336	0,000	0,000
Total				22,268	326,894
Jun. 77	3	106	399		
Aug. 77	3	138	390	−1,098	−16,119
Sep. 77	3	108	390	0,000	0,000
Nov. 77	3	75	469	7,229	106,122
Jan. 78	3	40	507	2,185	32,076
Mar. 78	3	20	497	−0,300	−4,404
Jun. 78	3	28	516	0,456	6,694
Total				8,472	124,369
Total production (P0, P1, P2, P3):				74,448	1092,897

in crustaceans (Els 1982; Stephens 1955; Passano 1960).

Although not apparent in this study (Figure 4), moulting in female *U. africana* (Siegfried 1962) and *U. deltaura* (Tunberg 1986) peaked approximately one month earlier than in males. Moreover, using data from these studies, positive correlations were obtained between the proportion of newly moulted females and those in berry [i.e. $r^2 = 0{,}56$; $p < 0{,}025$ (Siegfried 1962) and $r^2 = 0{,}41$; $P < 0{,}07$ (Tunberg 1986) *cf.* $r^2 = 0{,}29$; $p < 0{,}14$ (Site 1)], suggesting that egg-laying occurs shortly after ecdysis.

The smallest ovigerous female *U. africana* recorded at Sites 1 and 2 were in the 17 mm and 12 mm size classes respectively (Figure 2), and sexual maturity was attained after approximately 18–20 months (Figure 7). The reproductive output of these females increased with age (or size), ranging from 0,86 to 20,42 kJ per annum (Hanekom & Erasmus 1989). This output apparently retards female growth (Tucker 1930 & Reverberi 1942 in Dworschak 1988; Hill 1977) and their maximum carapace lengths are generally 1–3 mm smaller than males (Hill 1977; Hanekom & Erasmus 1989; Dworschak 1988). However, few large males were recorded from Sites 1 and 2 (Figure 2) and growth rates determined in Figure 7 approximate those of female *U. africana*.

Table 4 The standing biomass and annual somatic production of populations monitored at Sites 1 & 2, as well as biomass (Hanekom 1980 & Hanekom *et al.* 1988) and production (calculated using Pg/B ratios of Sites 1 & 2) values for the entire estuarine *U. africana* population

	Standing biomass (kJ×10^3)*	Somatic production (kJ×10^3)*	Pg/B ratio
Large prawns			
Site 1	2,345	1,864	0,79
Populations:			
Intertidal	708 384,033	559 623,386	0,79
Subtidal	24 968,844	19 725,387	0,79
Total	733 352,878	579 348,773	0,79
Stunted prawns			
Site 2	1,104	1,093	0,99
Populations:			
Intertidal	375 583,392	371 827,558	0,99
Subtidal	126 985,209	125715,357	0,99
Total	502 568,601	497 542,915	0,99
Large and stunted prawns			
Populations			
Intertidal	1083 967,425	931 450,944	
Total	1235 921,479	1076 891,689	

* Energy content of large and stunted prawns = 14,303 and 14,680 $kJ.g^{-2}$ respectively

The similarity in growth of *U. africana* from Site 2 with that (calculated by integrating data of intermoult intervals and moult increments) of female *U. pusilla* from Grado (Figure 7), suggested that these two species have similar intermoult periods, when experiencing annual mean temperatures of 20,9°C (*SD* = 3,2°C) (Figure 4) and *c.* 14,0°C (*SD* = 6,8°C) (Del Piero, Orel & Specchi 1978 in Dworschak 1987) respectively.

The relative increments in size per moult (as percentage of premoult total length) of *U. pusilla* decreased with increasing body length, ranging from 16,4 to 0,7% (Dworschak 1988). This was similar to the range in (positive) increments recorded between corresponding modal means from consecutive *U. africana* samples taken at Sites 1 and 2 (means of the three largest and smallest increments = 15,4 (*SD* = 1,2) and 0,6 (*SD* = 0,2)% respectively), as well as modal increments noted for *Callianassa kraussi* (*c.* 20–1%; Forbes 1977; Hanekom 1980) and to a lesser extent *C. folholi* (*c.* 9–1%; Devine 1966).

Life spans of 3,5 to 4 years estimated for *U. africana* from cohort analyses (Hill 1967; Figures 5–7), were comparable with those (> 3 years) suggested from size frequency distributions by Gustafson (1934) for *U. deltaura*, as well as by Tucker (1930) and Popovici (1940) for *U. pusilla* (in Dworschak 1988). However, Dworschak (1988) showed that mature *U. pusilla* (CL = 14–18 mm) could live more than three years under laboratory conditions and he calculated a life span of over five years for this species. This suggested that cohort analyses probably underestimate longevity, presumably owing to the difficulty in separating older, slow-growing year classes from each other.

The growth rate of prawns at Site 1 was much greater than at Site 2 (Figure 7), as was the annual somatic production (Pg) of the population (1859 kJ.m^{-2} v. 1093 kJ.m^{-2}). However, the production/biomass (P/B) ratio was lower (0,79 v. 0,93), depressed by a large biomass denominator (Table 4). These production values were higher than determined from Dworschak's (1988) data for a theoretical population of predominantly large, slow growing adult *U. pusilla* (Pg = 134,1 kJ and P/B = 0,32), but comparable with a *C. kraussi* population from the Swartkops estuary (Pg = 1791 kJ.m^{-2}; P/B = 1,41; Hanekom 1980).

U. africana is the dominant macrobenthic species of the non-marshland regions of the Swartkops estuary (Hanekom 1980; Hanekom *et al.* 1988), and approximately 85% of its total somatic production of 1077 × 10^6 kJ occurs within the intertidal region (Table 4). This means it is vulnerable to predation by both birds and fish, as well as exploitation by man (Hanekom *et al.* 1988).

The eleven most important bird species (comprising > 80% of the bird numbers) consume an estimated 136 × 10^6 kJ.y^{-1} of *Upogebia africana* (Martin 1991), or 13% of the annual somatic production (Table 4). Predation is greatest during spring and summer, and large (CL = 11–22 mm), parasitized prawns which surface at low tide are usually taken (Martin 1991). This may account for the rapid decline in prawn numbers recorded in Cohort 3 during spring and summer (Figure 8).

Fish also prey extensively on *U. africana* and estimates, based on gill net catches (Marais & Baird 1980a), stomach analyses (Marais 1984) and feeding rates (du Preez 1987) of the larger fish species of the Swartkops estuary (Table 5), suggest that these fish consume approximately 50 × 10^6 kJ.y^{-1} of *U. africana*. Many of the smaller fish missed by the gill nets also feed on *U. africana* [e.g. *Caffrogobius nudiceps*, *C. multifasciatus* (Whitfield 1988) & *Pomadasys olivaceum* (Day, Blaber & Wallace 1981)] and the consumption estimate was increased to 55 × 10^6 kJ or 5% of the *U. africana* somatic production.

Licensed bait outlets and private fisherman collect about 4 000 kg dry mass — 58 × 10^6 kJ — of *U. africana* per annum (Martin 1991). Although much of this bait is ultimately consumed by fish, a significant proportion (probably 20 × 10^6 kJ) dies and is discarded, or is used in the sea and other estuaries. Moreover, the disturbance caused by high intensity sampling using prawn pumps (e.g. compaction of the substratum and exposure of unharvested prawns to opportunistic predators) can result in a 25% reduction in *U. africana* densities (Wynberg 1991). Assuming a similar annual sampling mortality rate in the major bait collecting areas of the Swartkops estuary (Figure 1), the loss owing to disturbance would be 192 × 10^6 kJ of *U. africana*. Whilst much of this is taken by opportunistic bird predators (Martin 1991; Wynberg 1991), a large proportion (possibly 40%) is probably consumed by scavengers [e.g. 'crabs' *Diogenes brevirostris* (McLachlan, Lombard & Louwrens 1981) and *Cyclograpsus punctatus* (Alexander & Ewer 1969)] or forms

Table 5 An estimation, based on gill net catches, stomach analyses and food intake experiments, of predation on *U. africana* by the larger fish species in the Swartkops estuary. Key: PC = *Pomadasys commersonnii*, GF = *Galeichthys feliceps* MF = *Monodactylus falciformis*, PI = *Platycephalus indicus*, EM = *Elops machnata*, RH = *Rhabdosargus holubi*

		Fish species					
Parameters	Reference	PC	GF	MF	PI	EM	RH
Area of estuary (ha)	1	154	154	154	154	154	152
Effective net area (ha)	2	0,3	0,3	0,3	0,3	0,3	0,3
Areas: estuary /net		513	513	513	513	513	513
Mass caught/net (g)	3	3850	796	80	263	1987	192
Mass in estuary (g)	4	1 975 050	408 348	41 040	134 919	1 019 331	98 496
Mean mass of fish (g)	3	879	561	63	571	1656	88
Intake per fish (kJ/d)	5	89,964	62,251	10,362	63,160	151,227	13,629
% mass intake = prawns	6	44,6	94,1	6,4	5,4	2,1	2,4
Prawns per fish (kJ/d)	7	40,124	58,579	0,663	3,411	3,176	0,327
Prawns: all fish (kJ/d)		90 156	42 639	432	806	1955	366
Prawns: all fish (kJ/y)		32 906 964	15 563 225	157 688	294 148	713 504	133 634
Total consumption of prawns (kJ/y) = 49 769 163							

Ref. 1: Martin (1991).

Ref. 2: The 50 m long gill nets of Marais & Baird (1980a) were assumed to catch all fish in the water column 30 m either side of them, which gave a fish density of 43 kg wet mass.ha^{-1}, compared to 40–50 kg wet mass.ha^{-1} (moisture content = 70%; Marais 1990) for eelgrass beds or marsh ponds in North California and Texas (Marshall Adams 1976; Hellier 1962 & Kjelson, Johnson, Garner & Watson 1973 in Marshall Adams 1976), and a mean angling catch of >2442 kg of *P. commersonnii* per year in the Swartkops estuary (Marais & Baird 1980b).

Ref. 3: Marais & Baird (1980a).

Ref. 4: Fish were assumed to be evenly distributed throughout the subtidal area.

Ref. 5: Food intake of all species was determined using the equation derived for *Pomadasys commersonnii*, namely: Log FI = –0,46 + 0,82log M, where FI = daily *U. africana* intake at 20°C (kJ), M = live body mass (g) (du Preez 1987).

Ref. 6: PC–EM = Marais (1984); RH = Whitfield (1988).

Ref. 7: It was assumed % mass intake = % energy intake.

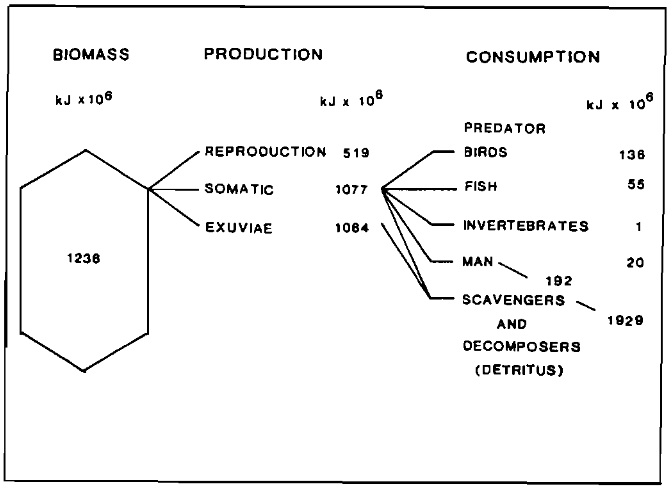

Figure 9 The estimated biomass, production and consumption of the entire estuarine *U. africana* population.

detritus. Similarly, most of the remaining somatic production of *U. africana* (792 × 10^6 kJ) is likely to enter the scavenger and detrital food webs, because, except possibly for the nemertean worm *Polybranchiorhynchus dayi* (Day 1981), no other major predators are apparent in the Swartkops estuary.

Exuviae loss (through moulted exoskeleton) could also make a significant contribution to the detrital component (Hosie & Ritz 1983). Dworschak (1988) estimated that exuviae loss constituted 55% of the total annual production of a population of predominantly large adult *U. pusilla*, compared to 21 and 34% in the isopod *Ligia dilatata* and krill *Nyctiphanes australis* respectively (Willows 1987 and Hosie & Ritz 1983 in Dworschak 1988). An assumed exuviae loss of 40% of the total annual *U. africana* production would contribute 912 × 10^6 kJ.y^{-1} to the detrital food web of the Swartkops estuary. Therefore, although *U. africana* is prey to numerous bird and fish species (Martin 1991; Marais 1984), its greatest contribution to the Swartkops ecosystem is apparently through the scavenger and detritus food web (Figure 9), an aspect that should be studied further.

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