Variations in size compositions of populations of *Upogebia africana* (Ortmann) (Decapoda, Crustacea) within the Swartkops estuary and possible influencing factors

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The size frequencies of various populations of the mud prawn *Upogebia africana* sampled within the Swartkops estuary were determined and the size compositions of these populations varied along the length of the estuary, as well as vertically within the intertidal zone. Ovigerous prawns were recorded from sites representing the extremes in population structures and their mean sizes differed significantly ($P < 0,05$) from each other. The variations in the size compositions were therefore attributed to differences in the growth of the prawns, rather than a spatial separation of adults and juveniles. The mean sizes of the adult prawns from the various stations were determined and plotted against factors such as water temperatures and salinities, nitrogen and organic contents of the substrata, population densities and distances of the populations from the estuarine mouth. The latter factor, which was used to give a relative measure of the exposure (in terms of duration and current velocity) of the populations to the flow of water entering the estuary during flood tides, gave the most significant ($P < 0,01$) correlation with the mean size of the adult prawns and could satisfactorily account for patterns observed.

Die groottefrekwensie van verskillende bevolkings van die moddergarnaal *Upogebia africana* binne die Swartkops-getyrivier is bepaal en die grootte-samestelling van hierdie bevolkings het in die getyrivier op, sowel as vertikaal binne die intergetygebied gevarieer. Eierdraende wyfies is van bevolkings aan die endpunte van die verspreidingsreeks aangeteken en hulle gemiddelde groottes het betekenisvol ($P < 0,05$) van mekaar verskil. Die variasies in die bevolkingstruktuur is dus toegeskryf aan verskille in groeitempo by die betrokke plekke, eerder as aan die ruimtelike verspreiding van volwasse en jong vorms. Die gemiddelde groottes van die volwasse diere van die verskillende monsternemingspunte is bepaal en gekorreleer met faktore soos watertemperature en -soutgehaltes, stikstof en organiese inhoud van die substrata en afstande van die bevolkings vanaf die mond van die getyrivier. Die laasgenoemde faktor, wat gebruik is as 'n relatiewe meting van die blootstelling (in terme van tyd en stroomsterkte) van die bevolking aan die vloei van water wat die getyrivier gedurende vloedgety binnevloei, het die mees betekenisvolle ($P < 0,01$) korrelasie met die gemiddelde grootte van die volwasse garnale gegee en kon die waargenome patrone in die getyrivier bevredigend verklaar.

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The mud prawn *Upogebia africana* (Ortmann) is a filter feeder (Hill 1967; Schaeffer 1970). It is found in sheltered bays and estuaries along the southern African coast, from approximately Langebaan lagoon in the west to Inhambane in the east (Figure 1) and temperature appears to be the factor limiting its geographic distribution (Hill 1967). Hill (1977) compared the size compositions of populations of *U. africana* from a number of southern African estuaries. In most instances, however, samples were collected from a single site within the estuary and little attention was paid to possible intra–estuarine variations. This paper deals with the differences observed in the size compositions of *U. africana* populations within the Swartkops estuary, as well as the nature of the variations namely, whether they are the result of a spatial separation of juvenile and adult forms or a difference in growth rates. Possible factors which could have caused such variations are considered and these include water temperatures and salinities, substrata, population densities and distances from the estuarine mouth.

The Swartkops estuary is situated in the approximate centre of the distributional range of *U. africana* in southern Africa (Figure 1). The estuary is relatively shallow (ca. 2,5 m deep) and has a tidal fetch of about 16 km (Hill, Kaplan, Scott and partners 1974). In the upper and middle reaches it is narrow (ca. 120 m) being confined between muddy banks, usually about a metre in height. These banks flatten out in the lower reaches and extensive intertidal mud flats and salt marshes develop. The estuarine regime is affected by three sets of man-made structures. The Swartkops Power Station cycles about 50 Ml of untreated estuarine water per hour for cooling purposes (Hill *et al.* 1974) and the heated effluent, which is about 3°C above ambient (Malan 1978), enters the estuary just above the Swartkops village (Figure 1). Slight organic pollution occurs from three sources namely, treated sewage released into the river about 9 km above the ebb and flow; domestic effluent from faulty conservancy tanks along the estuarine banks and sea-borne sewage from the Papenskuil untreated outfall (Hill et al. 1974; Watling 1981). Finally, the pylons and embankments of the bridges close to the Swartkops village impede the tidal flow within the estuary (Reddering & Esterhuysen 1982).

Methods

Forty-four intertidal transects were done along the
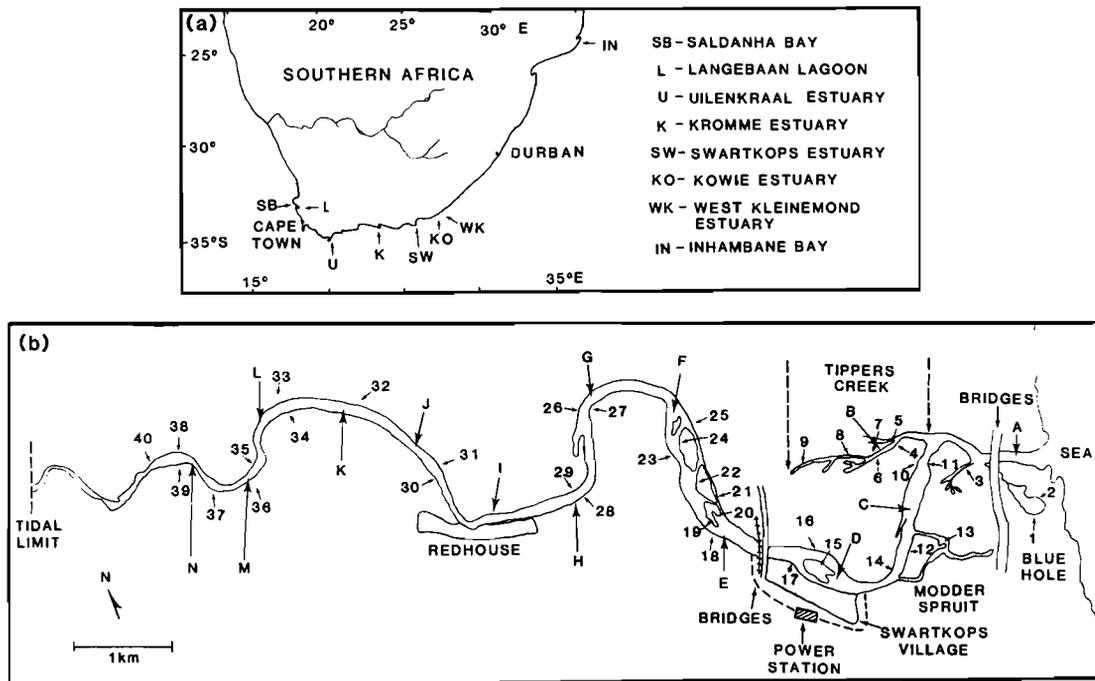
Figure 1 A map of (a) southern Africa, showing the geographical position of the Swartkops estuary and other areas mentioned in the text and (b) the Swartkops estuary, indicating the positions of the sampling sites for macrobenthos (1 – 40) and Wooldridge's (unpubl. data) water analyses (A–N).

length of the Swartkops estuary during the period August 1975 to June 1976 (Hanekom, Baird & Erasmus 1988). Duplicate samples (0,25 m², 30 cm deep and sieved through a 3-mm mesh sieve) were taken in the spring low and mid-tide levels of the major prawn beds (Sites 3–27, Figure 1) and the sampling depth used (30 cm) encompassed about 95% of the *U. africana* within the quadrat area (Hanekom *et al.* 1988). The carapace length (tip of rostrum to hind margin of carapace) of the *U. africana* collected were measured to the nearest 0,2 mm using vernier calipers. These measurements were grouped into 1 mm size classes and size frequency histograms were constructed for the populations sampled at each transect. Sites 12, 13 and 22, which were representative of the lower, creek and 'middle' reaches of the estuary respectively (Figure 1), were resampled during the peak breeding season of the *U. africana* July–February). The prawns collected were measured, sexed and their pleopods examined for eggs. The sizes of the ovigerous (egg-bearing) females recorded from the various tidal levels of the above sites were compared using either Scheffe (1959) group wise test or a *t* test (Snedecor & Cochran 1967). These data and probability paper (Cassie 1954) were respectively used to assess the size ranges and modal means of the adult cohorts in the various prawn populations sampled at Sites 3–27. The values of these modal means were then plotted against factors such as water temperatures and salinities, nitrogen and organic contents of the substrata, population densities and distances from the estuarine mouth.

During the period November 1976 to October 1978, Wooldridge (unpubl. data) took monthly surface and bottom water temperature and salinity readings at 14 sites along the length of the Swartkops estuary (Figure 1). Since tides affect the pattern of dispersal of heated effluent from the Swartkops Power Station within the estuary (Malan 1978), the temperature and salinity readings for the ebb and flood tides were separated and weighted means were calculated for each site. These values were then · extrapolated to the various macrobenthic stations. In the case of the low-tide stations, which were regularly covered (ca. 10 h per day) by water depths greater than 0,4 m, the mean of the surface and bottom water values were used, while for the mid-tide stations surface water values were applied. The mean sizes of the adult prawns from the various stations were then plotted against the corresponding temperature and salinity values and correlation coefficients for these relationships were determined and tested for significance (Snedecor & Cochran 1967).

Ten centimetre deep cores of the substratum were taken in the low-tide region of the major *Upogebia* banks (Sites 3–27). Each core was homogenized and three sets of subsamples were taken. The first (ca. 100 g) was wet-sieved through a series of sieves having phi intervals (1 to – 4) and the median particle size and percentage subsieves were determined (Morgans 1956). The second set was oven dried at 90°C for 24 h and analysed for organic nitrogen using the micro-Kjeldhal, while the third was ashed in a muffle furnance at 500°C for 6 h to determine organic content. Replicates for nitrogen and organic matter were within 5 and 1% of each other respectively and the results were treated in the manner described in the preceding paragraph.

Population densities (nos. m⁻²) and dry biomass values

(g m^{-2}) of *U. africana* recorded at the various stations were taken from Hanekom (1980). Values for only this species were considered, because *U. africana* comprised over 78% of the shell-free dry biomass of macrobenthos sampled at each station, except those of Site 14 (Hanekom 1980). The results were treated as in the temperature and salinity section.

Distance from the estuarine mouth via the main channel was used as a relative measure of the exposure (in terms of duration and current velocity) of the various populations to the flow of water entering the estuary during flood tides. Distances were determined from 1:10 000 orthophotographs and values for the mid-tide stations were doubled, since these stations were inundated with water for only half the tidal cycle. Secondly, the Swartkops estuary branches and the distance measurements were divided into two groups namely, (i) from the mouth to the end of Tippers creek (Sites 3, 4–9, 13 (value for Modderspruit creek included)) and (ii) from the mouth to the end of the 'middle' reaches (Sites 3, 10, 12, 14–27, Figure 1). Site 11 was excluded from the latter group, because it is separated from the main channel by extensive shallows (Hill *et al.* 1974).

Results and Discussion

Size frequency histograms of a number of the *U. africana* populations sampled are shown in Figure 2. It is apparent that the largest prawns from the mid-tide levels tended to be smaller than from corresponding low-tide stations, while those from the lower reaches of the estuary (Sites 3–5, 10–11) were generally bigger than from corresponding tidal levels in the 'middle' (Sites 24–27) and creek (Sites 8–9) regions. The size ranges of the prawns in the various populations, therefore, varied both within the intertidal zone and along the length of the Swartkops estuary.

The mean sizes of the ovigerous *U. africana* sampled from the low tide regions of Sites 13 (creek) and 22 ('middle' reaches of the estuary) were significantly (ANOVA = 191; $P < 0,01$) smaller than from a similar tidal level at Site 12 (lower reaches), while those from the low-tide regions of Site 12 and 22 were significantly ($t = 8,09$; $t = 2,57$; $P < 0,05$) larger than their counterparts from the mid-tide levels (Figure 3). The presence of ovigerous (or mature) females in all these populations and the significant ($P < 0,05$) differences in their sizes indicate that the variations observed in the size compositions of the various populations were primarily a result of differences in the growth of the prawns, rather than a spatial separation of adult and juvenile forms.
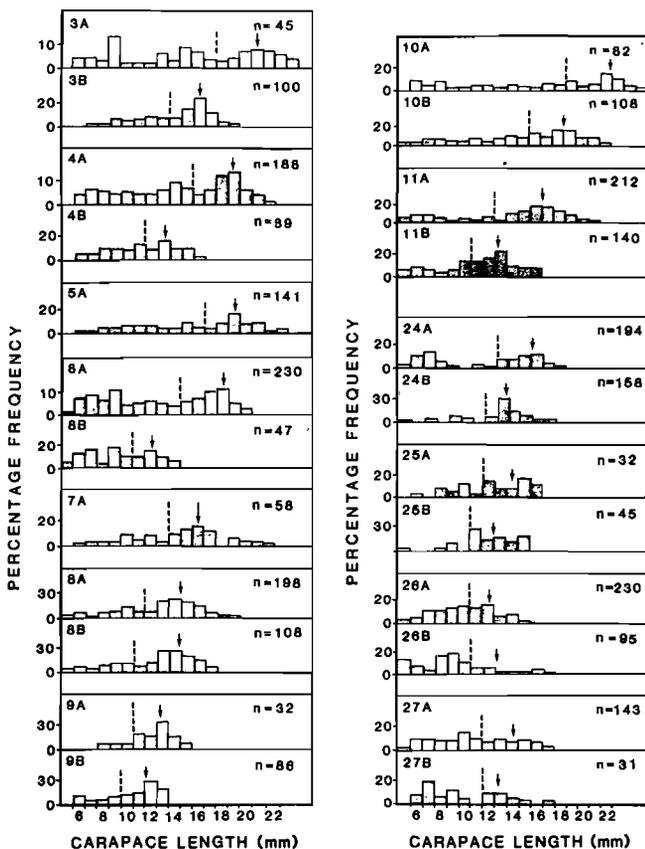
Figure 2 Size frequencies of the *U. africana* populations sampled in the spring low (A) and mid-tide (B) levels of Sites 3 – 11, 24 – 27. Stippled lines and arrows indicate the estimated beginnings and calculated modal means of the adult cohorts respectively, while n shows the numbers of individuals sampled.
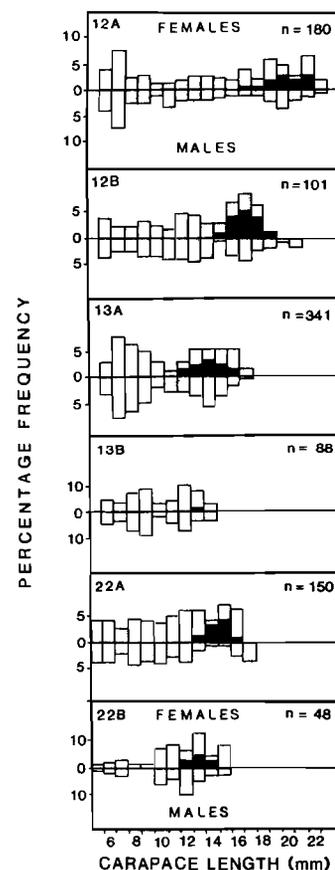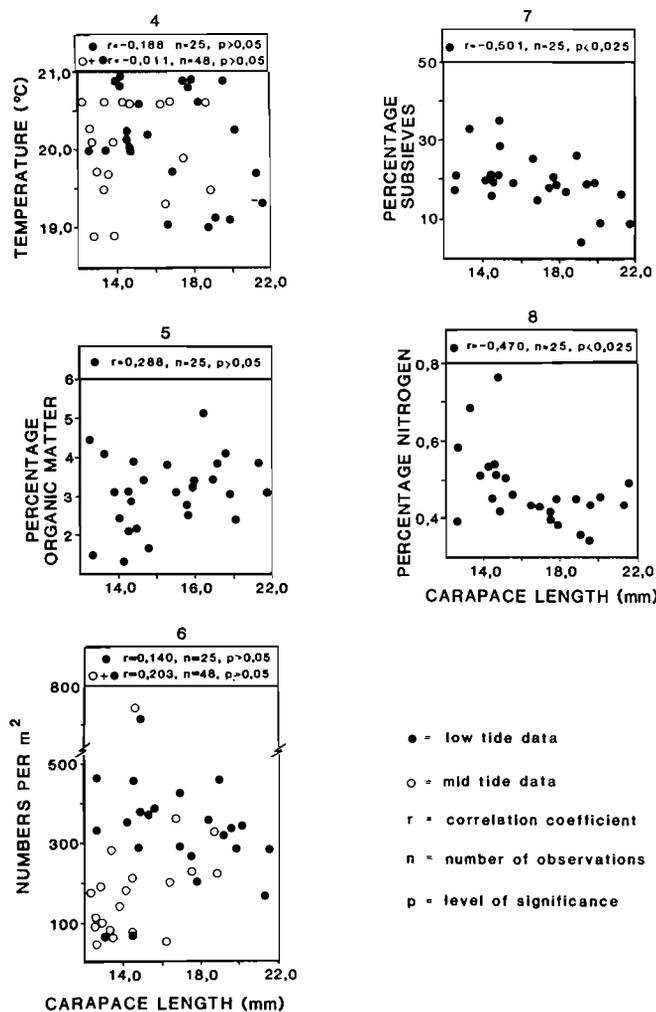

Figure 3 Size frequencies of *U. africana* sampled in the spring low (A) and mid-tide (B) levels of Sites 12, 13 and 22 during the peak breeding season. Dark shading indicates ovigerous females and n the number of individuals sampled.

No significant $(P > 0,05)$ correlations were determined between the mean sizes of the adult *U. africana* sampled at the various stations and the water temperatures, total organic contents of the substrata and population densities recorded at these stations (Figures 4, 5, 6). The latter three factors were therefore assumed to be unimportant in determining the size of adult prawns within the estuary.

The size of the adult *U. africana* tended $(P < 0,025)$ to be larger in substrata having smaller amounts of subsieve sediments (particles < 63 μm) and organic nitrogen (Figures 7–8). These trends and the lack of a significant $(P > 0,05)$ correlation between prawn sizes and organic contents of the substrata (Figure 5) are contrary to the patterns expected if the bacterial and organic materials of the substrata were serving as a major food source for the filter feeding *U. africana* (see Newell 1965; Longbottom 1970; Tunnicliffe & Risk 1977) and thereby influencing its growth (Carefoot 1967; Branch 1974; Swiss & Johnson 1976).

Adult *U. africana* tended $(P < 0,01)$ to be largest in areas having the highest biomasses of prawns (Figure 9).

This trend, together with the lack of a significant $(P > 0,05)$ correlation between prawn sizes and population densities (Figure 6) are contrary to the density dependent growth patterns observed by Branch (1975) and Emmerson & Andrew (1981) in other marine invertebrates and these factors were, therefore, assumed to be unimportant in determining the size variations observed within the estuary.

Significant $(P < 0,01)$ correlations were determined between the sizes of the adult prawns and the salinities of the water column (Figure 10). The variations in the mean carapace lengths of the adult prawns recorded along the length of Tippers and Modderspruit creeks (Sites 4–9, 12–13), as well as vertically within the intertidal zone of most sites were large (0,2–6,0 mm) (Figure 2), but salinity differences within these areas were generally small. For instance, the mean recorded salinity in Tippers creek (Site B $= 33^{\circ}/oo$) was close to those of the main channel of the lower reaches (Sites A, C, D $= 33$–$34^{\circ}/oo$) and the sea ($35^{\circ}/oo$), while values for the surface and bottom waters of these regions were within $2^{\circ}/oo$ of each other (Table 1). It seemed highly unlikely that salinity differences of this magnitude could have caused such large growth variations in *U. africana*, since this species can apparently live in salinities close to $17^{\circ}/oo$ and is capable of hyperosmoregulating between levels of 3–$30^{\circ}/oo$ (Hill 1967, 1971).

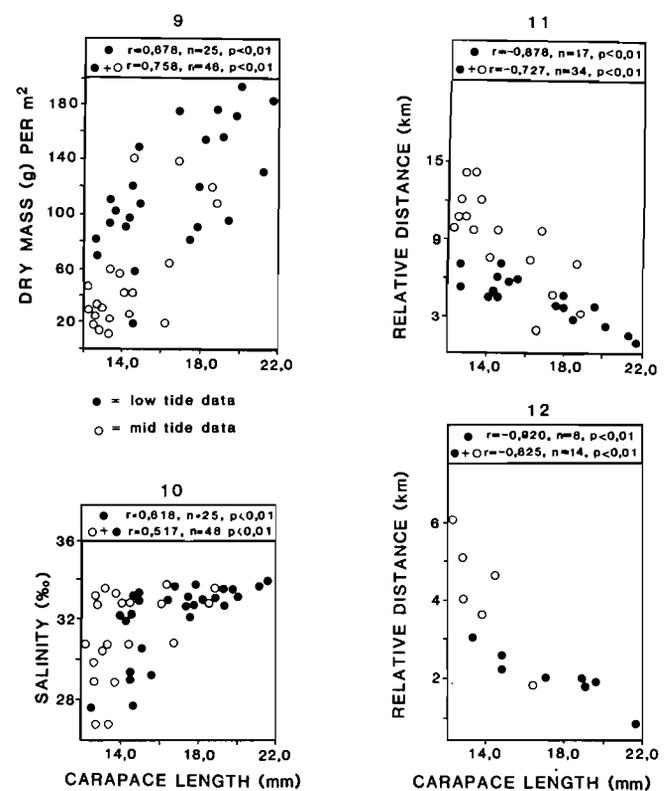The most significant $(P < 0,01; r = 0,7$–$0,9)$ correla-

Figures 4 – 8 Plots of the carapace lengths of modal means of the adult *U. africana* sampled at the various stations against (4) water temperatures, (5) percentage organic contents of the substrata, (6) population densities, (7) percentage subsieves and (8) organic nitrogen of the substrata.

Figures 9 – 12 Plots of the carapace lengths of modal means of the adult *U. africana* sampled at the various stations against (9) population biomasses, (10) salinities of the water column, (11) relative distances of the populations in the main channel and (12) creek systems from the mouth of the estuary. Key given in Figures 4 – 8.

Table 1 The mean of monthly surface and bottom water salinity values recorded by Wooldridge (unpubl. data) over the period November 1976 to October 1978 at Sites A–H along the length of the Swartkops estuary [values for May, 1977 (flood conditions) and April, 1978 (normal conditions) were omitted from calculations, because readings were incomplete]

| Salinities (‰)	Creek	Lower reaches			Middle reaches			
	B	A	C	D	E	F	G	H
Surface (S)	32,9	34,4	33,4	33,0	30,8	28,9	26,7	25,1
Bottom (B)	33,3	34,3	33,0	32,7	31,5	29,5	28,9	27,1
Difference (S – B)	–0,4	0,1	0,4	0,3	–0,7	–0,6	–2,2	–2,0

tions were recorded between the mean sizes of the adult prawns and their relative distances from the estuarine mouth (Figures 11–12). These distance measurements (low-tide stations = actual values, mid-tide stations = twice the actual values) were used to provide a relative measure of the exposure (in terms of duration and current velocity) of the various prawn populations to the flow of water entering the estuary during flood tides. Two possible ways in which this flow could have accounted for the variations observed are as follows. The sea could supply the major food and oxygen input into the estuary during flood tides (Korringa 1956; Odum 1971) and exposure (in terms of duration and intensity) to this supply would decrease towards the head of the estuary and vertically within the intertidal zone. The second possibility is related purely to water movement, in that tidal currents would affect the amount of oxygen and suspended particulate matter transported over the prawn beds.

Emmerson (1985) recorded high oxygen values (ca. 7,2 mg l⁻¹) along the entire length of the Swartkops estuary, as well as significantly ($P < 0,05$) lower mean nitrite (5 v. 29 μg l⁻¹), nitrate (236 v. 820 μg l⁻¹), phosphate (277 v. 3218 μg l⁻¹) and total phoshorus (401 v. 3519 μg l⁻¹) levels at the mouth than at the head of the estuary. Furthermore the ash-free dry masses of particulate matter filtered (using Whatmans microfibre paper) from water collected from the mouth and middle reaches of the estuary on flood tides were similar ($t = 1,05$; $df = 10$; $P > 0,05$) (unpubl. data). These results argue against a decreasing supply of food and oxygen towards the head of the estuary.

Upogebia species actively pump water (ca. 1–30 l h⁻¹) through their burrows (Hill 1967; Dworschak 1981; Koike & Mukai 1983), which are apparently sites of nitrification – denitrification and microbial activity (Aller, Yingst & Ullman 1983). Despite this, there are factors which suggest that tidal currents (or water movement) are important to *U. africana*. Firstly, the closure of the mouth of an estuary, although it might not affect the salinity regime, appears to be deleterious to many invertebrate forms, resulting in high mortality rates and lowered production (Day 1967) and Hill (1967)

noted that although *U. africana* is abundant in most of the open estuaries of southern Africa, it is absent from closed ones. Secondly, two of the factors, besides relative distance from the estuarine mouth, which correlated significantly ($P < 0,025$) with the mean sizes of the adult *U. africana* within the Swartkops estuary (namely, subsieves and organic nitrogen contents of the substrata, Figure 7–8) are also affected by current velocity (Krumbein 1971). Furthermore, the largest standing biomasses of *U. africana* recorded in the Swartkops estuary were at stations bordering the tidal channels of the lower reaches (Hanekom 1980); while prawn densities decreased markedly in the upper reaches of Tippers and Modderspruit creeks (McLachlan & Grindley 1974). These factors indicate a strong likelihood that water movement and its associated transport of oxygen and food materials may influence the growth of *U. africana*. Maximum current speeds recorded in the main channel of the lower reaches (near Site D) of the Swartkpos estuary during a spring tide cycle was about 42% higher (55 v. 32 cm s⁻¹) than in the middle reaches (near Site H) (Baird, unpubl. data). Assuming that these velocities decrease approximately linearly with distance from the estuarine mouth, then this parameter (if it does affect the growth of the prawns) could satisfactorily account for the size differences noted in the adult prawns from the various stations, as well as providing an explanation for the significant ($P < 0,025$) correlations recorded between prawn size and subsieve and organic nitrogen contents of the substrata [both affected by current velocities (Krumbein 1971)] and the salinity of the water column [which decreases towards the less turbulent middle reaches of the estuary (Table 1 and current velocities in text)]. Tendencies for individuals to be larger in more exposed sites have also been noted for the marine filter feeders, *Pyura stolonifera* (van Driel 1978) and *Crassostrea gigas* (de Keyser 1984) and further studies are required to assess the effect of currents on the growth of *U. africana*.

Populations of another thalassinid prawn, *Callianassa kraussi* Stebbing, were also sampled in the Swartkops estuary (Sites 1–2, 14–15, 33–40) by Hanekom *et al.* (1988). The largest *C. kraussi* were generally found in the low-tide levels of areas close to the estuarine mouth, but this pattern was less consistent than in *U. africana* (Hanekom 1980). The size ranges of the ovigerous females recorded from stations representing extremes in the population structures of *C. kraussi*, differed markedly from each other (Figure 13) and the differences in the size compositions of the various populations were, again, taken to be primarily a result of variations in the growth of the prawns, rather than a spatial separation of adult and juvenile forms. The tendency for adult *C. kraussi* to be small in the high-tide levels and upper reaches of the Swartkops estuary (Hanekom 1980) and the fact that Forbes (1973) recorded only stunted prawns (adult carapace lengths < 9 mm) in the temporarily closed West Kleinemond estuary, suggests that tidal currents may also influence the growth of this deposit-feeding species (Forbes 1973).
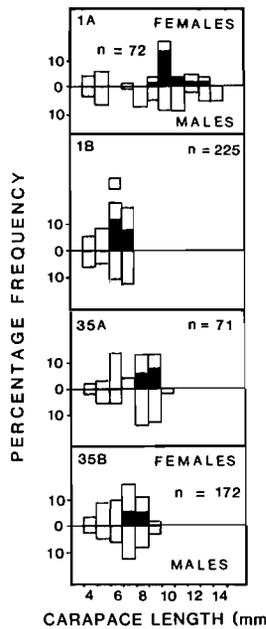
Figure 13 Size frequencies of *C. kraussi* populations sampled in the spring low (A) and high (B) levels of Sites 1 and 35 during the peak breeding season. Dark shading indicates ovigerous females and n the number of individuals sampled. (Data from Hanekom 1980).

The variations recorded in the size compositions of the various prawn populations within the Swartkops estuary appeared to be as great or greater than that noted between the low-tide populations of certain South Coast estuaries (Figure 1). For example, the variation between adult modal means estimated for *U. africana* collected from the Uilenkraal, Knysna and Kowie estuaries were only about 1–3 mm in carapace length (see Hill 1977), whereas within the Swartkops estuary it could be as much as 5–6 mm. In the case of *C. kraussi,* the differences noted within the Swartkops estuary (1–4 mm in carapace length) were as large as those noted between populations from the Kowie and West Kleinemond estuaries (Forbes 1973). Caution should therefore be exercised in the inter-estuarine comparisons of growth and production rates of these prawns.

References

ALLER, R.C., YINGST, J.Y. & ULLMAN, W.J. 1983. Comparative biogeochemistry of water in intertidal *Onuphis* (Polychaeta) and *Upogebia* (Crustacea) burrows: temporal patterns and causes. *J. Mar. Res.* 41: 571–604.

BRANCH, G.M. 1974. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. (3) Growth. *Trans. roy. Soc. S. Afr.* 41(2): 161–191.

BRANCH, G.M. 1975. Intraspecific competion in *Patella cochlear* Born. *J. Anim. Ecol.* 44: 263–282.

CAREFOOT, T.H. 1967. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *J. mar. Ass. U.K.* 47: 565–589.

CASSIE, R.M. 1954. Some uses of probability paper in the analysis of size frequency distribution. *Australian J. Mar. Freshwater Res.* 5: 513–522.

DAY, J.H. 1967. The biology of Knysna estuary, South Africa. In: Estuaries. (Ed.) G.H. Lauff. American Association for the Advancement of Science, Washington. pp. 397–407.

DE KEYSER, J. 1984. The influence of current speed, water depth and packing density on the growth rate of the Pacific oyster, *Crassostera gigas.* B.Sc. (Hons.) project report. Department of Zoology, University of Port Elizabeth.

DWORSCHAK, P.C. 1981. The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea) *J. exp. mar. Biol. Ecol.* 52: 25–35.

EMMERSON, W. D. 1985. The nutrient status of the Swartkops River Estuary, Eastern Cape. *Water S.A.* 11(4): 189–198.

EMMERSON, W.D. & ANDREWS, G. 1981. The effect of stocking density on the growth, development and survival of *Penaeus indicus* Milne Edwards larvae. *Aquaculture* 23: 45–57.

FORBES, A.T. 1973. A study of the burrowing sand prawn, *Callianassa kraussi* Stebbing. (Crustacea: Decapoda: Thalassinidea). Ph.D. thesis, Rhodes University, Grahamstown, R.S.A.

HANEKOM, N. 1980. A study of two thalassinid prawns in the non *Spartina* regions of the Swartkops estuary. Ph.D. thesis, University of Port Elizabeth, R.S.A.

HANEKOM, N., BAIRD, D. & ERASMUS, T. 1988. A quantitative study to assess standing biomasses of macrobenthos in soft substrata of the Swartkops estuary, South Africa. *S.A. J. Mar. Sci.* 6: 163–174.

HILL, B.J. 1967. Contribution to the ecology of *Upogebia africana* (Ortmann). Ph.D. thesis, Rhodes University. Grahamstown, R.S.A.

HILL, B.J. 1971. Osmoregulation by an estuarine and marine species of *Upogebia* (Anomura, Crustacea). *Zool. Afr.* 6: 229–236.

HILL, B.J. 1977. The effect of heated effluent on egg production in the estuarine prawn *Upogebia africana* (Ortmann). *J. exp. mar. Biol. Ecol.* 29: 291–302.

HILL, KAPLAN, SCOTT & PARTNERS, 1974. Report for the Port Elizabeth City Engineer. Swartkops River basin. Vol. 2. Hydrology and hydraulics. 1–73.

KOIKE, I. & MUKAI, H. 1983. Oxygen and inorganic nitrogen contents and fluxes in the burrows of the shrimps *Callianassa japonica* and *Upogebia major.* *Mar. Ecol. Prog. Ser.* 12: 185–190.

KORRINGA, P. 1956. Oyster culture in South Africa. *Investl Rep. Div. Sea Fish. S. Afr.* 20: 288–370.

KRUMBEIN, W.E. 1971. Sediment microbiology and grain size distribution, as related to tidal movement during the first mission of the West German underwater laboratory 'Helgoland'. *Mar. Biol.* 10: 101–112.

LONGBOTTOM, M. R. 1970. The distribution of *Arenicola marina* (L) with particular reference to the effect of particle

size and organic matter of the sediments. *J. exp. mar. Biol. Ecol.* 5: 138–157.

MALAN, D.E. 1978. Preliminary studies on thermal effluent of the Swartkops River. Third year project, Zoology Department, University of Port Elizabeth, R.S.A.

MCLACHLAN, A. & GRINDLEY, J.R. 1974. Distribution of macrobenthic fauna of soft substrata in the Swartkops estuary, with observations on the effects of floods. *Zool. Afr.* 9(2): 211–233.

MORGANS, J.F.C. 1956. Notes on the analysis of shallow water soft substrate. *J. Anim. Ecol.* 28: 367–387.

NEWELL, R.C. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch, *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proc. Zool. Soc. Lond.* 144: 25–45.

ODUM, E.P. 1971. Estuarine ecology. In: Fundamentals of ecology. Third edition, Saunders College Publishers, Philadelphea. pp. 352–361.

REDDERING, J.S. & ESTERHUYSEN, K. 1982. The sedimentary ecology of the Swartkops estuary. R.O.S.I.E. Report No.1. Department of Geology, University of Port Elizabeth, R.S.A. 111 pp.

SCHAEFFER, N. 1970. The functional morphology of the foregut of three species of Decapod Crustacea: *Cyclograpsus punctatus* Milne–Edwards, *Diogenes brevirostris* Stimpson and *Upogebia africana* Ortmann. *Zool. Afr.* 5: 309–326.

SCHEFFE, H. 1959. The analysis of variance. Wiley, New York. 477 pp.

SNEDECOR, G.W. & COCHRAN, W.G. 1967. Statistical Methods, Sixth edition, Iowa State University Press. Amer. Iowa 593 pp.

SWISS, J.J. & JOHNSON, M.G. 1976. Energy dynamics of two benthic crustacea in relationship to diet. *J. Fish. Res. Bd. Can.* 33(11): 2544–2550.

TUNNICLIFFE, V. & RISK, M.J. 1977. Relationship between the bivalve *Macoma balthica* and bacteria in intertidal sediments, Minas Basin, Bay of Fundy. *J. Mar. Res.* 35(3): 499–508.

VAN DRIEL, C.D. 1978. Aspekte van die biologie van *Pyura stolonifera* (Heller) (Tunicata: Ascidiacea) in Algoabaai met spesiale verwysing na die energie metabolisme. Ph.D. thesis, Univ. Port Elizabeth, Port Elizabeth, R.S.A.

WATLING, R.J. 1981. South eastern Cape monitoring programme. Report for the period April 1980 – May 1981. Marine Pollution Group, Zoology Department, University of Port Elizabeth, R.S.A. 111 pp.