Afr. J. mar. Sci. 25: 275–282
2003

SPATIAL VARIABILITY IN THE MUDPRAWN *UPOGEBIA AFRICANA* ON THE SOUTH-EAST COAST OF SOUTH AFRICA

O. DUBULA and T. A. LASIAK†*

A nested sampling design was used to examine the variability in density, biomass, sex ratio and size of the estuarine mudprawn *Upogebia africana* in six estuaries on the south-east coast of South Africa. The objectives were to test the general hypothesis that there is variability in these variables at the scales of regions, estuaries, banks and tidal levels, and then to determine at which spatial scales these were most variable. Nested analyses of variance revealed significant differences in the mean size of mudprawns at the scale of regions, in mean size and sex ratio at the scale of banks, and in all four variables at the scale of tidal levels. The greatest variability in all four variables was at the smallest spatial scale examined. The likely causes of this spatial variability are discussed.

Key words: density, sex ratio, size, South Africa, spatial variability, *Upogebia africana*

Physical factors, such as salinity, turbidity, type of substratum, oxygen concentration, water depth and movements, are believed to determine the large-scale distribution patterns of benthic organisms in estuaries (Barry and Dayton 1991, Little 2000). Some of these factors also exert an influence at smaller spatial scales; water movements, for example, can affect the supply of food, oxygen, sediments and larvae at the scale of millimetres (Morrisey *et al.* 1993). The way in which benthic organisms respond to their physical environment is modified by biological factors, such as food supply, competition, predation, behavioural preferences and adult-larval interactions (Thrush 1991, Little 2000). The spatial scale over which biological factors exert an influence also varies; although some have large-scale effects, most operate at small spatial scales (Legendre *et al.* 1997). Meaningful hypotheses about the relative importance of these factors can only be formulated by understanding the distribution patterns that exist at different spatial scales.

Several analytical procedures have been used to identify scales of spatial pattern. Techniques such as block sampling and spatial autocorrelations, which examine variability as a continuous function of scale, require large numbers of regularly spaced sampling units (Greig-Smith 1964, Cliff and Ord 1973, Pielou 1974). An alternative, less labour-intensive approach involves the use of a nested sampling design in which small numbers of independent units are sampled at each of a series of inclusive scales. Estimates of the magnitude of variability at different spatial scales, which are independent of the other spatial scales examined, can then be obtained by subjecting the data collected to nested analyses of variance (Underwood 1997). This approach has been used to identify spatial patterns in abundance in both inter- and subtidal organisms (Green and Hobson 1970, Jones *et al.* 1990, Morrisey *et al.* 1992a, Lindegarth *et al.* 1995, Underwood and Chapman 1996).

The present study uses this procedure to investigate spatial variation in the density, biomass, sex ratio and size composition of the estuarine mudprawn *Upogebia africana* on the south-east coast of South Africa. The objectives of this pilot study were (i) to test the general hypothesis that there is variability in these population-level attributes at the scale of regions, estuaries, banks, and tidal levels and (ii) to determine the spatial scale at which these attributes were most variable. *U. africana* is a major source of food for fish and wading birds (Marais 1984, Martin and Baird 1987) and is also utilized extensively by recreational anglers as bait. This study was prompted by the concerns that have been expressed about the impact of bait-collecting (Hill 1967, Hanekom 1980). A sound understanding of spatial variability in mudprawn populations is needed to design and interpret studies on the impact of bait collecting and other anthropogenic disturbances.

MATERIAL AND METHODS

Sampling was conducted in six permanently-open estuaries on the south-east coast of South Africa, at Qora, Shixini and Nqabara in southern Transkei and at Umtata Mouth, Mdumbi and Mtakatye in central Transkei

* Department of Zoology, University of Transkei, Private Bag X1 Unitra, Umtata 5117, South Africa. E-mail: O_dubula@hotmail.com
† Formerly Department of Zoology, University of Transkei; now Centre for Research into Ecological Impacts of Coastal Cities, Marine Ecology Laboratories, A11, University of Sydney, NSW 2006, Australia. E-mail: tlasiak@bio.usyd.edu.au

Manuscript received January 2002; accepted August 2002

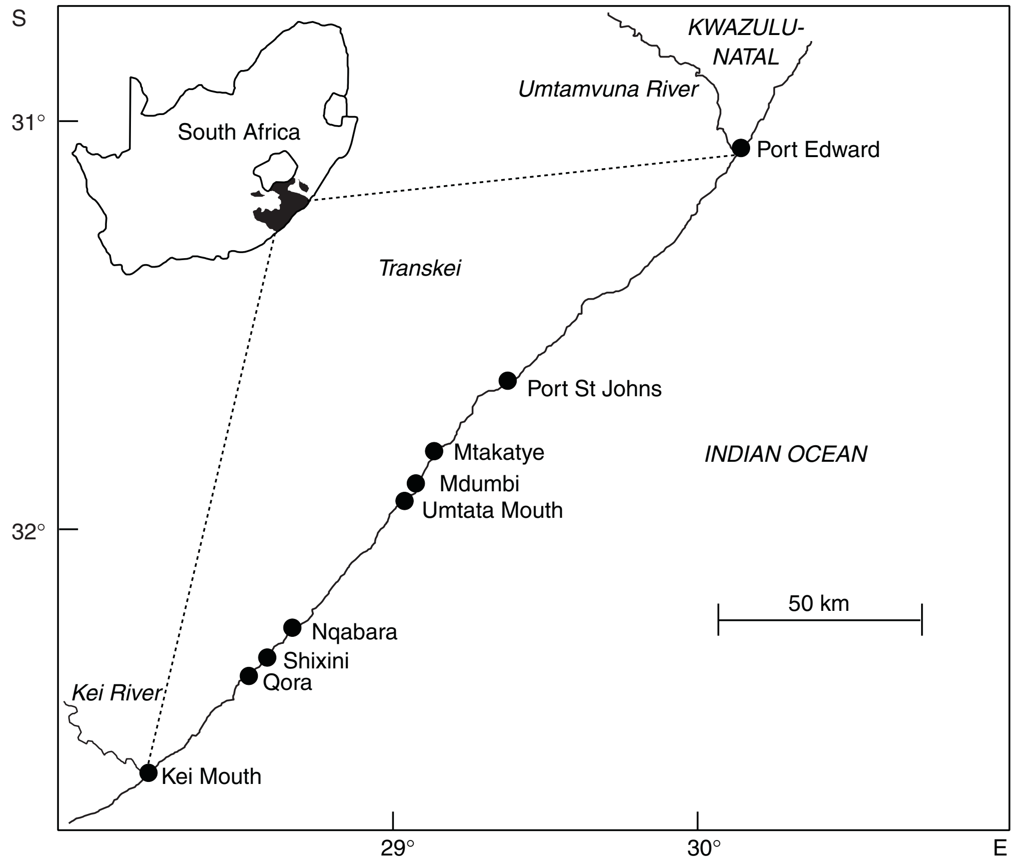

Fig. 1: Map showing the location of the study sites on the Transkei coast of South Africa

(Fig. 1). Samples were collected over a six-week period between 12 September and 29 October 2000. Two mud banks located in the lower reaches of each estuary were sampled. Sampling was restricted to the lower reaches of these estuaries, because previous work had shown that the size composition of mudprawns varies along the length of an estuary (Hanekom and Erasmus 1988). Three levels, representing low, mid and upper tide levels, were selected as sampling sites on each mud bank. At each of these levels, mudprawns were collected from five 0.1 m^2 quadrats positioned randomly along a transect line laid out parallel to the waterline. The prawns were extracted by digging out the quadrat to a depth of 30 cm and then sorting through the mud by hand. Although the burrows of this species can extend 40–50 cm below the surface, previous studies indicate that most prawns occur within the top 25 cm of the substratum (Hill and Bok 1978). The prawns removed from each quadrat were counted, and the sex and the carapace length (measured from the tip of the rostrum to the posterior margin of the carapace) of 10 randomly-selected individuals were determined. The biomass of all the prawns extracted from each quadrat was determined to the nearest 0.001 g after oven-drying for 24 h at 60°C.

Nested analyses of variance were used to assess the significance of differences in the mean density, biomass, sex ratio (male to female) and mean size of prawns between the southern and central regions, among estuaries within regions, between banks within estuaries, among levels within banks and also, in the case of mean size estimates, among replicate quadrats.

Table I: Number, biomass, mean carapace length and sex ratio of *U. africana* caught per estuary ($n = 30 \times 0.01$ m^2 quadrats)

Estuary	Total number	Total biomass (g)	Carapace length (mm)	Male:female
Qora	457	73.80	14.0	1:2.06
Shixini	509	43.50	12.0	1:2.85
Nqabara	442	78.04	12.9	1:2.09
Umtata	404	29.34	10.4	1:2.75
Ndumbi	597	33.72	10.9	1:2.75
Mtakatye	521	46.52	11.5	1:2.33

The various sources of variation were then partitioned in order to determine the significance of the variation among the replicate units nested in each region (Underwood 1997). Prior to these analyses, Cochran's C-test was used to test the data for heterogeneity of variances. In the case of density, biomass and sex ratio, heterogeneity was removed by subjecting the data to a logarithmic transformation. The restricted maximum likelihood method (REML) was used to estimate the variance components attributable to each spatial scale (Searle *et al.* 1992, Statsoft 2001). Untransformed data were used for these analyses, as recommended by Underwood (1997).

RESULTS

The total number of prawns caught per estuary varied from 404 at Umtata Mouth to 597 at Ndumbi, and the overall biomass varied from 29.3 g at Umtata Mouth to 78.0 g at Nqabara. The mean carapace length varied from 10.4 mm at Umtata Mouth to 14 mm at Qora and the sex ratio (male to female) varied from 1:2.06 at Qora to 1:2.85 at Shixini (Table I).

There was a significant difference in the mean size of mudprawns in the two regions, but not in any of the other variables measured (Table II). Prawns in the southern region were, on average, 2 mm larger than those in the central region (Figs 2, 3). No significant differences were evident in any of these variables among rivers within regions. At the scale of banks, significant differences were evident in the mean size of prawns and the sex ratio. However, when the variation at this spatial scale was partitioned, the only significant difference was in biomass and sex ratio among banks in the southern region. All four variables showed significant differences at the scale of levels on the bank. Partitioning of the variation at this spatial scale revealed significant differences in the density, biomass and mean size of prawns in both regions and sex ratio in the southern region. Figures 1 and 2 indicate that, on half the banks studied, the biomass and mean size of prawn decreases up shore.

Table II: Results of nested analyses of variance based on estimates of the density, biomass, mean size and sex ratio of *U. africana*

Source of variation	Density	Biomass	Mean size	Male:female
Region	ns	ns	*	ns
River	ns	ns	ns	ns
River – south	ns	ns	ns	ns
River – central	ns	ns	ns	ns
Bank	ns	ns	*	*
Bank – south	ns	*	ns	*
Bank – central	ns	ns	ns	ns
Level	***	***	***	*
Level – south	*	***	***	**
Level – central	***	***	***	ns
Quadrat			**	
Quadrat – south			*	
Quadrat– central			***	

ns = Not significant ($p > 0.05$)
* = $0.01 < p < 0.05$
** = $0.001 < p < 0.01$
*** = $p < 0.001$

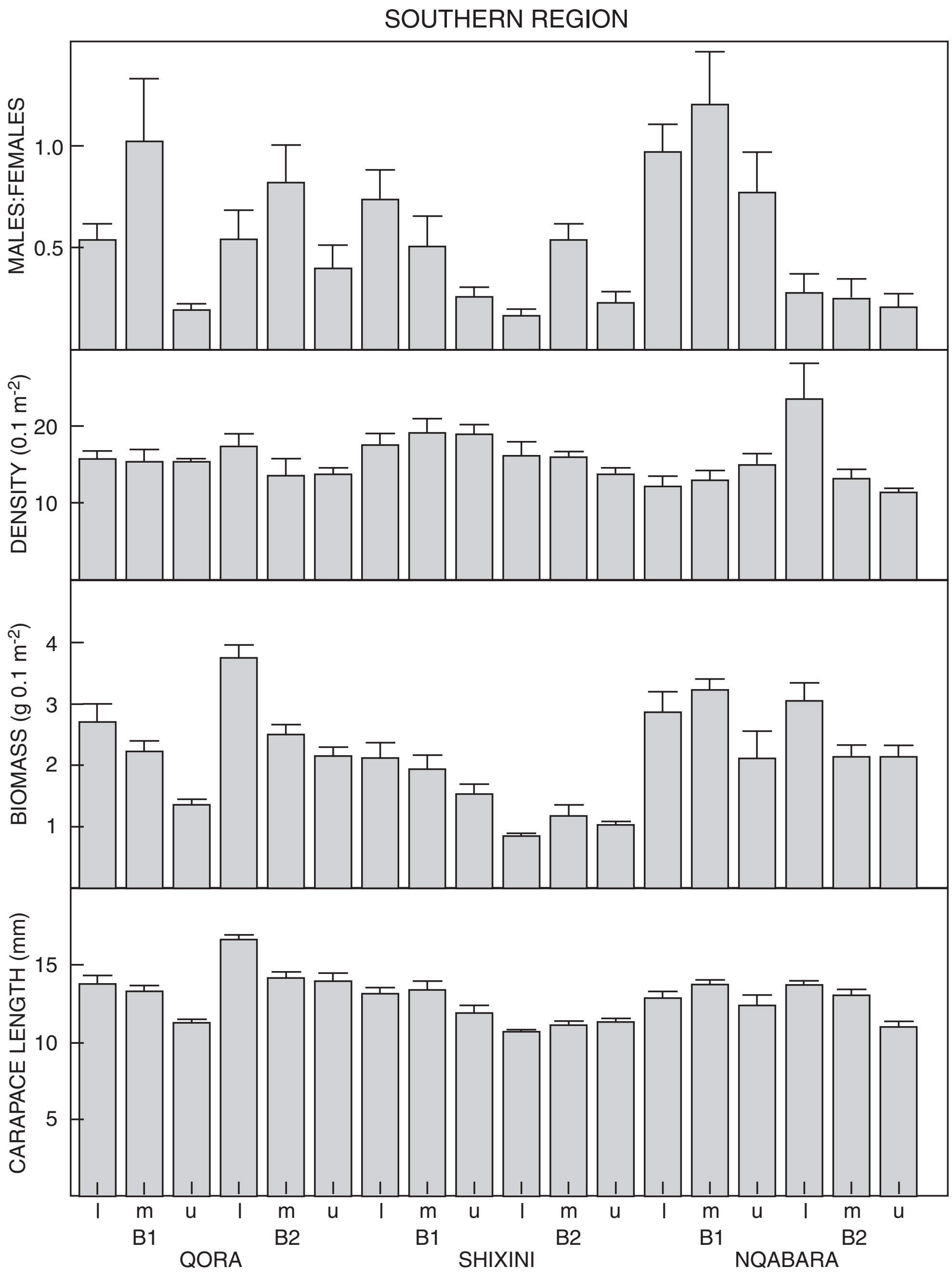

Fig. 2: Spatial differences in the mean (+1 *SE*) carapace length, biomass, density and sex ratio of mudprawns in the southern region at Qora, Shixini and Nqabara (B1 = Bank 1, B2 = Bank 2, l = lower, m = middle and u = upper tidal level)

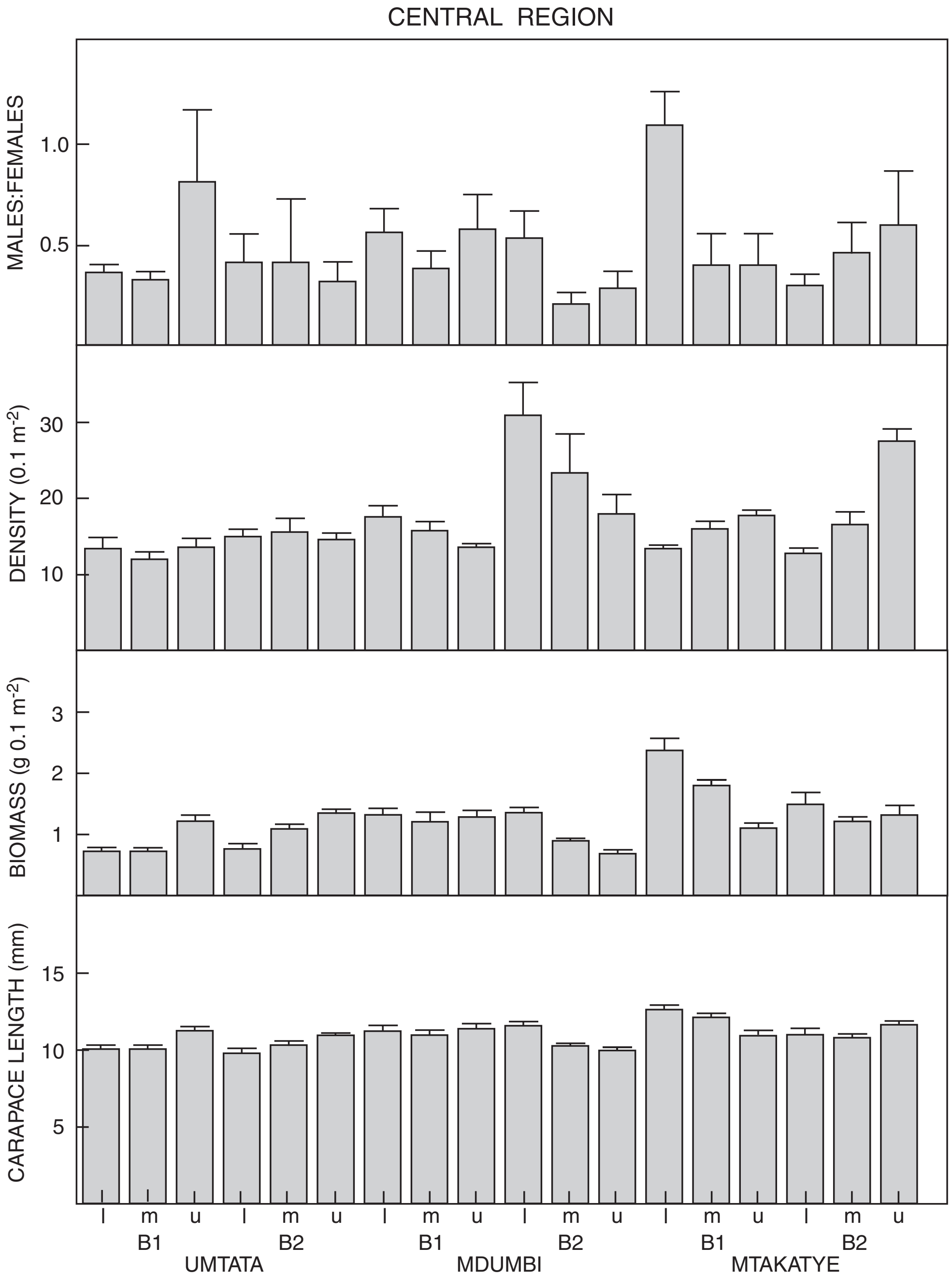

Fig. 3: Spatial differences in the mean (+1 *SE*) carapace length, biomass, density and sex ratio of mudprawns in the central region at Umtata Mouth, Mdumbi and Mtakatye (B1 = Bank 1, B2 = Bank 2, l = lower, m = middle and u = upper tidal level)

Table III: Contribution of various spatial scales to the variance in density, biomass, mean size and sex ratio of *U. africana*

Measure	Spatial scale					
	Region	River	Bank	Levels	Quadrats	Replicates
Biomass	0.374	0.175	0.06	0.181*	0.189*	
Density		0.283	4.168	9.399*	21.447*	
Mean size	1.781	0.259	0.472	0.684*	0.214*	5.001*
Males:females			0.018	0.028	0.135*	

* indicates components with variances that are significantly different from zero

The analyses based on carapace length indicated that there were also significant differences at the scale of quadrats, in both regions.

Although differences between regions appeared to make the greatest contribution to the variance in biomass, asymptotic tests of the significance of the REML variance components indicated that only the variances attributable to the scales of levels within mud bank and quadrats were significantly different from zero (Table III). The greatest variance in density, mean size and sex ratio of mudprawns was at the smallest spatial scale examined. In the case of density and size, there was also significant variance at the scale of levels within mud banks and among quadrats respectively.

DISCUSSION

U. africana lives in burrows in sheltered bays and estuaries stretching around the southern African coast from Langebaan in the Western Cape to Inhambane, Moçambique (Hanekom and Erasmus 1988). Its sedentary habit suggests that processes that influence its recruitment probably play a major role in determining its spatial distribution. Mudprawns have a complex life cycle incorporating an obligate marine larval development phase. Export of larvae to the marine environment is enhanced by maximal release of larvae at crepuscular high water and the aggregation of newly released larvae near the surface, where ebb current velocities are greatest (Wooldridge and Loubser 1996). While at sea, larvae pass through three further developmental stages. The post-larvae aggregate in the surf zone at night, and most re-invade estuaries when low water coincides with sunset. The recruitment of prawns into permanently open estuaries is consequently likely to depend on the supply of larvae, larval behaviour, tidal currents favouring the transport of post-larvae into estuaries, successful settlement and subsequent survival of juveniles.

Hill (1977) noted that mudprawns at localities to the east of the current study area (i.e. in KwaZulu-Natal) were significantly smaller and had a more protracted breeding period than those found to the south-west in the Cape Province. He attributed this to differences in the relative amounts of energy diverted into growth and reproduction in the two regions. The smaller size of mudprawns noted here, as well as in central Transkei and KwaZulu-Natal (Hill 1977), may also be related to the quantity of silt suspended in these subtropical rivers and the adverse clogging effect of these fine particles on the organs and appendages of filter-feeders (De Villiers *et al.* 1999). Differences in the overall structure of estuarine benthic assemblages and in the strength of interactions among species in warm temperate and subtropical regions of South Africa may also be relevant. Warm temperate estuaries are dominated by filter-feeders and deposit-feeders, whereas subtropical estuaries are dominated by detritivorous and deposit-feeding brachyurans (De Villiers *et al.* 1999). Estuaries along the Transkei coast tend to be of intermediate status; they support subtropical and tropical deposit-feeding crabs, such as *Uca* and *Macrophthalmus* spp., in addition to warm temperate species (Branch *et al.* 1994). The activities of deposit-feeders may increase the amount of re-suspended material in the water column (Rhoads and Young 1970), which may, in turn, have an adverse effect on the feeding appendages of filter-feeding organisms. Manipulative experimental investigations of interactions between burrowing crabs and *U. africana* are needed to test this model.

Differences in the abundance, biomass and/or size composition of *U. africana* along the length of individual South African estuaries as well as along vertical intertidal transects have been recorded previously (Hodgson 1987, Hanekom and Erasmus 1988, Hanekom *et al.* 1988). Although none of those authors commented specifically on vertical trends in abundance, their kite diagrams all indicate that mudprawns are less abundant at the top of the mud banks. Hanekom and Erasmus (1988) pointed out that the largest prawns collected from the mid-tidal level tended to be smaller than those from the corresponding low-tide stations. Differences in the biomass and mean size of *U. africana* among levels within mud banks probably reflect differences in the duration of exposure to tidal currents and the ability to filter-feed. Mudprawns obtain food and oxygen by pumping water through their U-shaped burrows and are thus dependent on the tidal flow overhead to replenish these resources. Animals occupying burrows on the lower part of the mud bank are consequently able to feed longer and, as a result, grow faster than those living higher up the bank.

The considerable variability in density, biomass and sex ratio of prawns observed among replicate quadrats suggests that there is also patchiness within levels on the mud bank. The variability at this small spatial scale is probably attributable to the influence of small-scale water movements on larval supply, availability of food and oxygen, sediment type, disturbance by predators, activities of other benthic animals and the presence of various biogenic structures (Morrisey *et al.* 1993).

To the authors' knowledge, there have been no previous attempts to assess whether the spatial distribution patterns of infaunal species in South African estuaries are a general phenomenon. This is probably because previous studies on benthic macrofauna have generally been restricted to one particular estuarine system (Blaber *et al.* 1983, Hodgson 1987, Hanekom and Erasmus 1988, Owen and Forbes 1997, Mackay and Cyrus 1999). It is important to note that the spatial patterns identified in the present study are unlikely to persist over time. This is because the time courses of the various processes influencing benthic populations are likely to vary from place to place and from one spatial scale to another (Morrisey *et al.* 1992a, b). Sampling regimes that incorporate several nested temporal and spatial scales are needed to gain a better understanding of the variability in the population-level attributes of organisms (Underwood 1992). A sound understanding of natural temporal and spatial variability in undisturbed *U. africana* populations is needed to determine the extent to which populations have been impacted by bait collecting and other anthropogenic factors.

ACKNOWLEDGEMENTS

We thank the National Research Foundation for their financial support, Profs A. H. Dye (formerly University of Transkei) and A. Whitfield (South African Institute for Aquatic Biodiversity) for their comments on the initial draft manuscript and our colleagues Messrs E. Makhanandana and T. Situnda for their assistance in the field.

LITERATURE CITED

BARRY, J. P. and P. K. DAYTON 1991 — Physical heterogeneity and the organization of marine communities. In *Ecological Heterogeneity.* Kolasa, J. and S. T. A. Pickett (Eds). New York; Springer: 270–320.

BLABER, S. J. M., KURE, N. F., JACKSON, S. and D. P. CYRUS 1983 — The benthos of South Lake, St Lucia, following a period of stable salinities. *S. Afr. J. Zool.* **18**(4): 311–319.

BRANCH, G. M., GRIFFITHS, C. L., BRANCH, M. L. and L. E. BECKLEY 1994 — *Two Oceans. A Guide to the Marine Life of Southern Africa*. Cape Town; David Philip: 360 pp.

CLIFF, A. D. and J. K. ORD 1981 — *Spatial Autocorrelation*. London; Pion Ltd: 266 pp.

DE VILLIERS, C. J., HODGSON, A. N. and A. T. FORBES 1999 — Studies on estuarine macroinvertebrates. In *Estuaries of South Africa.* Allanson, B. R. and D. Baird (Eds). Cambridge; University Press: 167–207.

GREEN, R. H. and K. D. HOBSON 1970 — Spatial and temporal structure in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca) *Ecology* **51**: 999–1011.

GREIG-SMITH, P. 1964 — *Quantitative Plant Ecology*. London; Butterworth: 256 pp.

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: 252 pp.

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

HANEKOM, N. and T. ERASMUS 1988 — Variations in size compositions of populations of *Upogebia africana* (Ortmann) (Decapoda, Crustacea) within the Swartkops Estuary and possible influencing factors. *S. Afr. J. Zool*. **23**(4): 259–265.

HILL, B. J. 1967 — Contribution to the ecology of *Upogebia africana* (Ortmann). Ph.D. thesis, Rhodes University, Grahamstown: 201 pp.

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

HILL, B. J. and A. BOK 1978 — Commercial exploitation of the prawn *Upogebia africana* (Ortmann) in the Kowie Estuary. Internal report, Cape Department of Nature and Environmental Conservation: 16 pp.

HODGSON, A. N. 1987 — Distribution and abundance of the macrobenthic fauna of the Kariega Estuary. *S. Afr. J. Zool.* **22**(2): 153–162.

JONES, G. P., FERRELL, D. J. and P. F. SALE 1990 — Spatial pattern in the abundance and structure of mollusc populations in the soft sediments of a coral reef lagoon. *Mar. Ecol. Prog. Ser.* **62**: 109–120.

LEGENDRE, P., THRUSH, S. F., CUMMINGS, V. J., DAYTON, P. K., GRANT, J., HEWITT, J. E., HINES, A. H., McARDLE, B. H., PRIDMORE, R. D., SCHNEIDER, D. C., TURNER, S. J., WHITLATCH, R. B. and M. R. WILKINSON 1997 — Spatial structure of bivalves in a sandflat: scale and generating processes. *J. expl mar. Biol. Ecol.* **216**: 99–128.

LINDEGARTH, M., ANDRE, C. and P. R. JONSSON 1995 — Analysis of the spatial variability in abundance and age structure of two infaunal bivalves, *Cerastoderma edule* and *C. lamarcki*, using hierarchical sampling programs. *Mar. Ecol. Prog. Ser.* **116**: 85–97.

LITTLE, C. 2000 — *The Biology of Soft Shores and Estuaries.* Oxford; University Press: 252 pp.

MACKAY, C. F. and D. P. CYRUS 1999 — A review of the macrobenthic fauna of the Mhlatuze estuary. Setting the ecological reserve. *S. Afr. J. aquat. Sci.* **24**: 111–129.
MARAIS, J. F. K. 1984 — Feeding ecology of major carnivorous fish from four Eastern Cape estuaries. *S. Afr. J. Zool.* **19**(3): 210–223.
MARTIN, A. P. and D. BAIRD 1987 — Seasonal abundance and distribution of birds on the Swartkops Estuary, Port Elizabeth. *Ostrich* **58**(3): 122–134.
MORRISEY, D. J., HOWITT, L., UNDERWOOD, A. J. and J. S. STARK 1992a — Spatial variation in soft-sediment benthos. *Mar. Ecol. Prog. Ser.* **81**: 197–204.
MORRISEY, D. J., UNDERWOOD, A. J., HOWITT, L., and J. S. STARK 1992b — Temporal variation in soft-sediment benthos. *J. expl mar. Biol. Ecol.* **164**: 233–245.
MORRISEY, D. J., UNDERWOOD, A. J. and L. HOWITT 1993 — Scales of spatial patchiness in the distribution of marine soft sediment faunas. In *Proceedings of the Second International Temperate Reef Symposium.* Battershill, C. N., Schiel, D. R., Jones, G. P., Creese, R. G. and A. B. MacDiarmid (Eds). Wellington, New Zealand; NIWA Marine: 107–113.
OWEN, R. K. and A. T. FORBES 1997 — Salinity, floods and the infaunal macrobenthic community of the St Lucia Estuary, Kwazulu-Natal, South Africa. *Sthn Afr. J. aquat. Sci.* **23**: 14–30.
PIELOU, E. C. 1974 — *Population and Community Ecology: Principles and Methods.* New York; Gordon & Breach: 424 pp.
RHOADS, D. C. and D. K. YOUNG 1970 — The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. mar. Res.* **28**(2): 150–178.
SEARLE, S. R., CASELLA, G. and C. E. McCULLOCH 1992 — *Variance Components*. New York; Wiley: 501 pp.
STATSOFT 2001 — Statbook Electronic textbook *http//www.statsoft/textbook/stathome.html.*
THRUSH, S. F. 1991 — Spatial patterns in soft-bottom communities. *Trends Ecol. Evol.* **6**: 75–79.
UNDERWOOD, A. J. 1992 — Beyond BACI: the detection of environmental impacts on populations in the real, but variable world. *J. expl mar. Biol. Ecol.* **161**: 145–178.
UNDERWOOD, A. J. 1997 — *Experiments in Ecology: their Logical Design and Interpretation Using Analysis of Variance.* Cambridge; University Press: 504 pp.
UNDERWOOD, A. J. and M. G. CHAPMAN 1996 — Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* **107**: 212–224.
WOOLDRIDGE, T. H. and H. LOUBSER 1996 — Larval release rhythms and tidal exchange in the estuarine mudprawn *Upogebia africana*. *Hydrobiologia* **337**: 113–121.