Distribution, biomass and production of *Ceratonereis erythraeensis* (Fauvel) and *Ceratonereis keiskama* (Day) at the Berg River Estuary, South Africa

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Population dynamics of the polychaetes *Ceratonereis keiskama* and *C. erythraeensis* were studied at the Berg River estuary, South Africa, from December 1987 to April 1989. There was marked size-related depth stratification of both species, with small worms being concentrated in the upper layer of the substratum and larger ones deeper down. Reproduction of both species occurred in summer. Three cohorts were distinguished in both populations. Recruitment of *C. keiskama* peaked in December whereas that of *C. erythraeensis* varied between years and sites (December–April). The population biomass of *C. keiskama* peaked in midsummer and was lowest during the spring and winter. *C. erythraeensis* maintained a high population biomass during winter and reached its lowest biomass during January–February. The total annual production of *C. keiskama* in the restricted area of the estuary where it occurred was 7,58 g m^{-2} y^{-1}, with a mean annual biomass of 4,11 g m^{-2} making P/B = 1,84. Total annual production of *C. erythraeensis* for the whole estuary was 14,42 g m^{-2} y^{-1}, mean annual biomass was 7,59 g m^{-2}, and P/B = 1,90.

Die populasie-dinamika van die polychaete *Ceratonereis keiskama* en *C. erythraeensis* by die Bergrivier strandmeer, Suid Afrika, is van Desember 1987 tot April 1989 bestudeer. 'n Opvallende grootteverwante diepte-stratifikasie is vir beide spesies waargeneem, met kleiner wurms gekonsentreer in die boonste laag van die substraat en met die groter wurms dieper af. Reproduksie vind by albei spesies in die somer plaas. Drie kohorte is in beide populasies onderskei. Rekrutering van *C. keiskama* het 'n piek in Desember getoon terwyl dit in *C. erythraeensis* van jaar tot jaar en tussen lokaliteite gevarieer het (Desember–April). Die bevolkingsbiomassa van *C. keiskama* het in die middel van die somer 'n maksimum bereik en was die laagste in die winter. Die biomassa van *C. erythraeensis* het 'n hoë vlak in die winter gehandhaaf en was die laagste gedurende Januarie–Februarie. Die totale jaarlikse produksie van *C. keiskama*, in die beperkte gebied van die strandmeer waar dit voorgekom het, was 7,58 g m^{-2} j^{-1}, met 'n gemiddelde jaarlikse biomassa van 4,11 g m^{-2}, en 'n P/B van 1,84. Die totale jaarlikse produksie van *C. erythraeensis* vir die hele strandmeer was 14,42 g m^{-2} j^{-1}, die gemiddelde jaarlikse biomassa was 7,59 g m^{-2}, en P/B 1,90.

Studies of the production and biomass of estuarine benthic communities are essential in establishing energy budgets for these systems. The importance of macrobenthos in the production of intertidal areas has been well studied in the northern hemisphere but there are very limited data available south of the equator. Several studies have been made in South African estuaries but these are concerned largely with composition, abundance, biomass and distribution of benthic macrofauna, rather than with their production. A brief report on the production of the most important components of macrobenthic fauna exist in South Africa for Langebaan Lagoon (Puttick 1977) and the Swartkops estuary (I. Muller 1984, unpublished; Baird 1988). There are, however, no detailed studies of the seasonal production of estuarine intertidal invertebrates in South Africa. Such information is essential when interactions between prey populations and their predators are considered. Although shorebirds (Aves: Charadriiformes) are the most conspicuous secondary consumers in the estuaries there are no published studies to date which demonstrate a relationship between them and their prey populations on a seasonal basis.

Twenty-five benthic invertebrate species have been recorded from intertidal mudflats at the Berg River estuary, South Africa (32°47′S/18°10′E) (Kalejta & Hockey 1991). Of these, polychaetes of the family Nereidae are the most important prey of shorebirds (Kalejta 1992) which feed in high densities at the estuary, particularly during the austral summer.

Three species of nereid worms occur in the estuary: *Ceratonereis erythraeensis* Fauvel (1919), *C. keiskama* Day (1953) and *Perinereis nuntia* subsp. *vallata* Grube (1857). The last of these species is confined to an area near the mouth of the river, where it is scarce. The two *Ceratonereis* species are abundant in the estuary and their distribution is correlated with sediment characteristics. *Ceratonereis erythraeensis* is most abundant in coarse sediments, whereas *C. keiskama* is confined to fine sediments (Kalejta & Hockey 1991).

This paper forms part of an intensive research of the interactions between predatory shorebirds and their prey populations at the Berg River estuary. The aim of this particular study was to investigate seasonal patterns in the demography and biomass of *Ceratonereis* species, and to determine their annual production.

Study site and Methods

Four study Sites (A, B, C and D), were established at decreasing distances from the river mouth (Figure 1). Each month, between December 1987 and April 1989, ten randomly-positioned core samples were taken to a depth of 300 mm at each site. The core was 69 mm in diameter and was divided into two sections, 0–50 mm and 50–300 mm, to determine depth distribution of nereids and their availability to predators. Samples were washed through a 500 μm sieve and all nereids retained were preserved in 10% formalin. All samples were taken at low tide.

The bodies of the nereids were often damaged during the

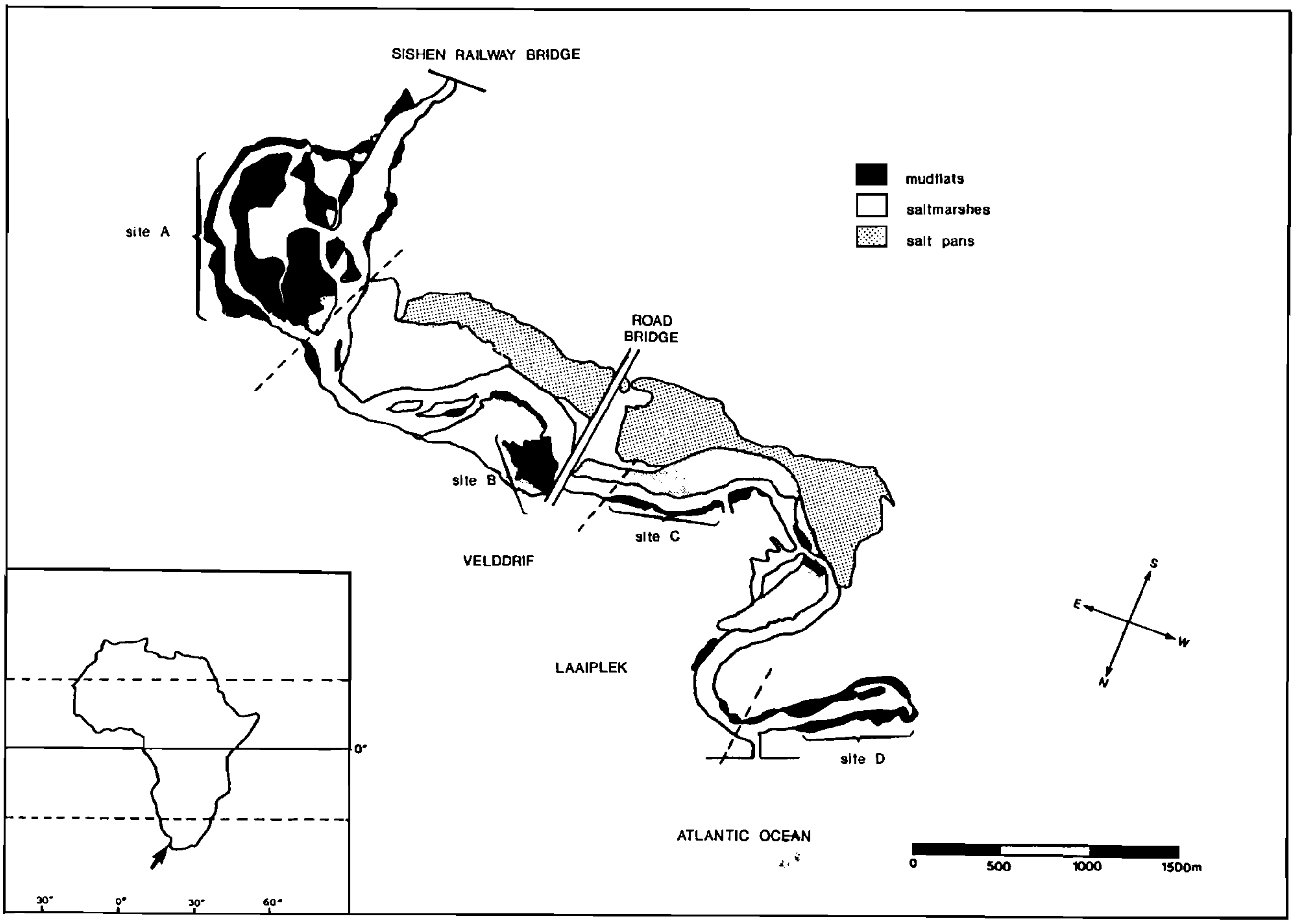

Figure 1 Map of the study area.

sieving process and consequently only their jaws were measured using a binocular microscope and graticule. Jaw lengths were converted to dry body mass and body length using the following conversion equations, calculated from intact worms collected specifically for this purpose.

Ceratonereis erythraeensis:
Body length (mm) = 60,63 jaw length (mm) – 11,31
(r = 0,82; n = 35)
Dry mass (mg) = 4,57 × 10^{-3} jaw length $(mm)^{2,29}$
(r = 0,72; n = 20)

C. keiskama:
Body length (mm) = 24,51 jaw length (mm) – 2,15
(r = 0,91; n = 30)
Dry mass (mg) = 1,70 × 10^{-3} jaw length $(mm)^{2,31}$
(r = 0,82; n = 22)

The size cohorts of the populations were separated from each other by using probability paper (Harding 1949; Cassie 1954). Production of both *Ceratonereis* species was estimated using mean numbers and weight increment of each cohort as described by Crisp (1971). Production was calculated separately for each cohort in each month for the whole study period (17 months). The total annual production was determined by taking an average of those months which were sampled in more than one year (December–April) and summing the production in each month over the 12-month period. The mean annual biomass was calculated in the same way. Both biomass and production are expressed in dry grams. The following months are included in each season: December, January and February — summer; March, April and May — autumn; June, July and August — winter, and September, October and November — spring.

Results

Life cycle and population structure

Ceratonereis keiskama occurred only at Sites A and B. Three cohorts were present at both sites during the study period (Figures 2 & 3). Cohort 1 was present at the beginning of the study period and contained old individuals, assumed to have originated from a major spawning peak during summer of the previous year. A second cohort, of young animals, was also present at the start of the study and remained through the winter until the following summer when a third cohort, consisting of small individuals, appeared.

Ceratonereis erythraeensis occurred at all four study sites, but recruitment patterns differed at each site. Cohorts at Sites B and D could not be separated because small animals were present throughout the year and the whole population decreased in numbers towards the end of the study period. This decrease indicates either emigration or death of

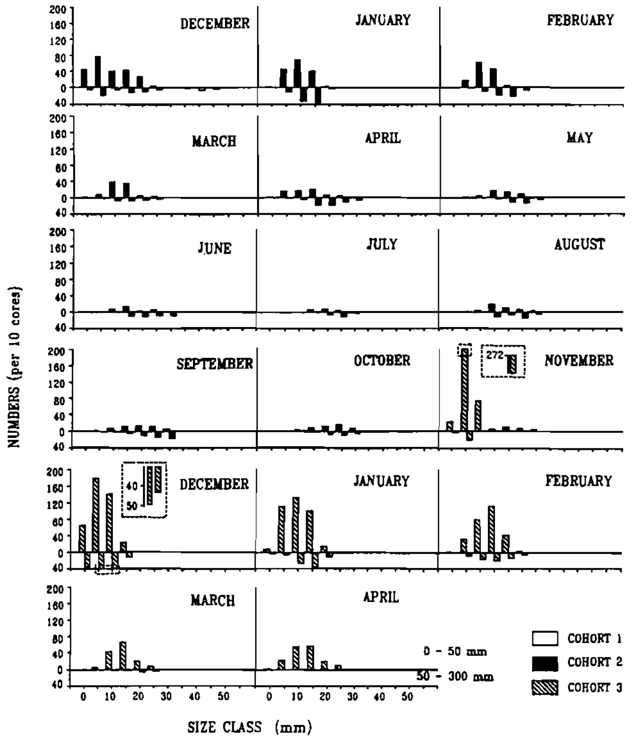

Figure 2 Size distribution of *Ceratonereis keiskama* at 0–50 and 50–300 mm depths at Site A from December 1987 to April 1989.

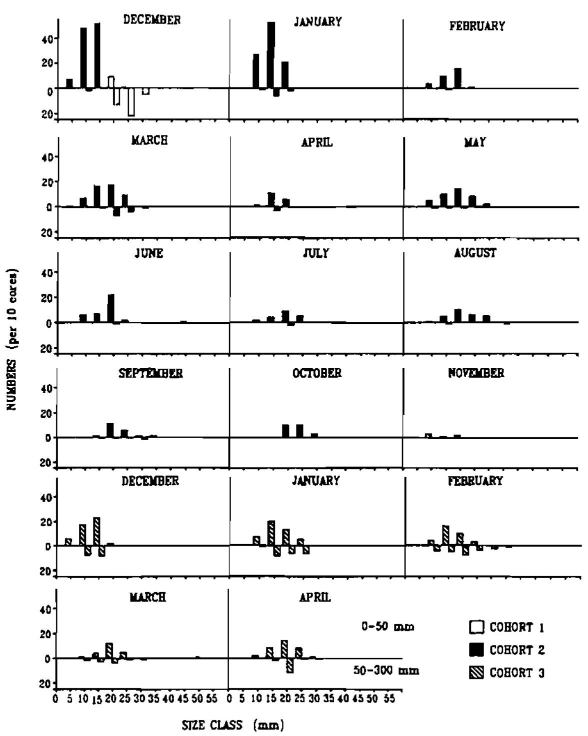

Figure 3 Size distribution of *Ceratonereis keiskama* at 0–50 and 50–300 mm depths at Site B from December 1987 to April 1989.

old individuals, but which of these took place is unknown. Populations of *C. erythraeensis* at the other two Sites, A and C, were represented by three cohorts during the study period (Figures 4 & 5). Cohort 1 contained old individuals and was

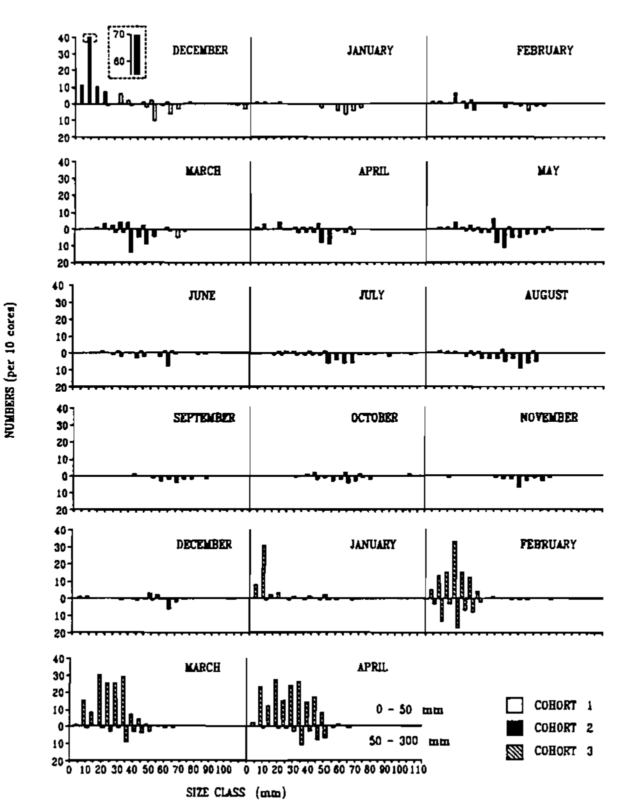

Figure 4 Size distribution of *Ceratonereis erythraeensis* at 0–50 and 50–300 mm depths at Site A from December 1987 to April 1989.

present through the summer and autumn of 1988. Cohort 2 was present at the start of the study period at Site A and appeared one month later at Site C, remaining until the following summer. By this time, newly-settled individuals of Cohort 3 entered the population. Recruitment was spread over the period January to April at Site C in both years. There was a difference in the recruitment pattern at Site A between years with a later recruitment peak in the summer of 1988/89 (April) than in 1987/88 (December) (Figures 4 & 5). Despite these differences, all recruitment was consistently concentrated in summer and early autumn (December–April).

Density

The average density over two study sites of *C. keiskama* varied between 6258 ± 1958) (*SE*) m^{-2} in December 1987 and 789 m^{-2} ± 93 in July 1988. The highest density of 14 897 m^{-2} was reached in December 1988 at Site A. The density of Cohort 2 decreased steadily at Site A and more rapidly at Site B, where 60% of the December 1987 stock had disappeared by February 1988 (Figure 6a). An increase in density at both sites in summer 1989 was due to newly recruiting individuals of Cohort 3.

The average density of *C. erythraeensis* over the whole estuary (including Sites B and D) varied between 5088 ± 809 (*SE*) m^{-2} in December 1987 and 1585 ± 483 m^{-2} in December 1989. The highest density of 7034 m^{-2} was recorded at Site B in December 1987. At Site C, Cohort 2 was numerically dominant throughout the study period (Figure 7a). After a peak in abundance in April, the popula-

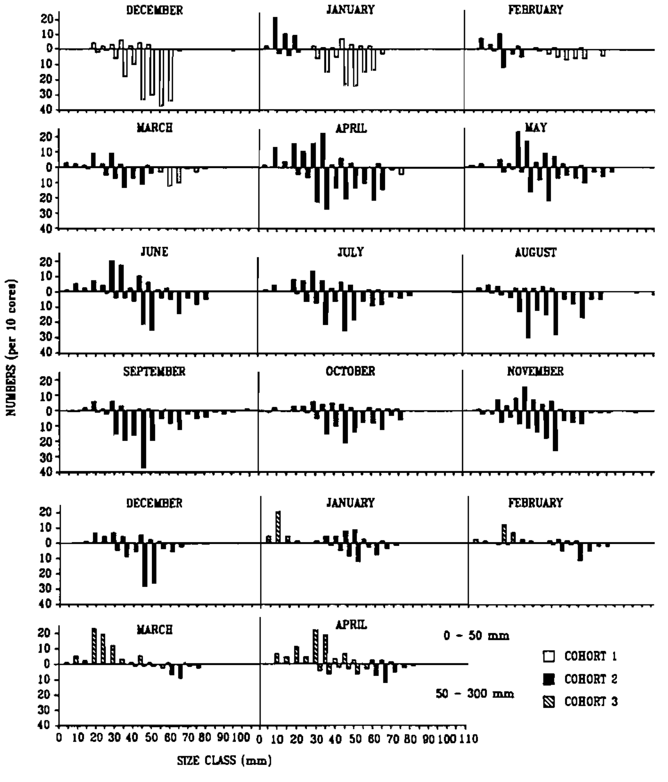

Figure 5 Size distribution of *Ceratonereis erythraeensis* at 0–50 and 50–300 mm depths at Site C from December 1987 to April 1989.

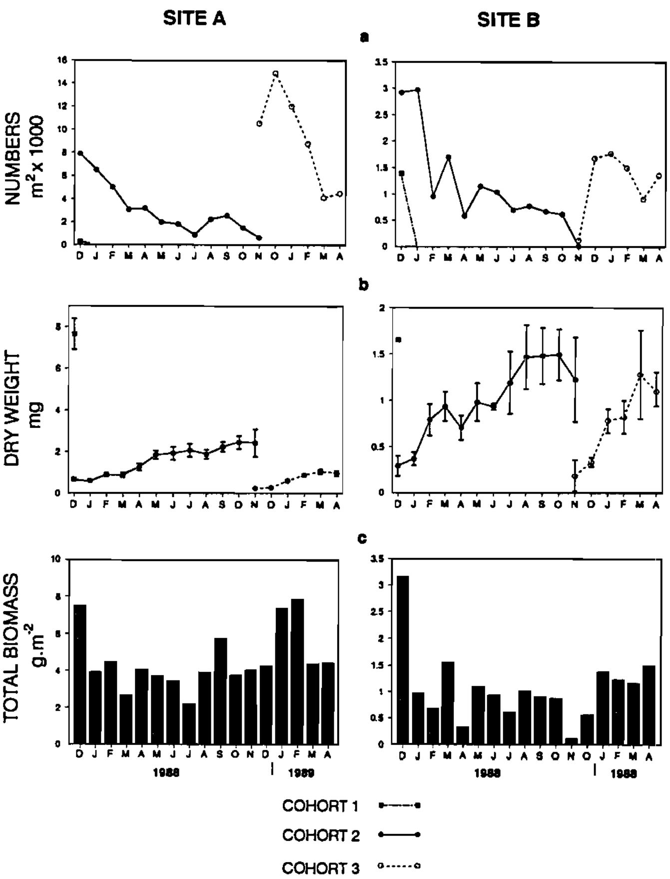

Figure 6 *Ceratonereis keiskama* at Sites A and B; a — numbers (per m^2) of individuals in the three cohorts; b — mean dry weight (mg) of three cohorts (± 95% confidence limits); c — biomass (g m^{-2}) of the total population; d — production (g m^{-2} $month^{-1}$) of the total population.

tion remained stable throughout the winter and spring, but had fallen by 87% by February of the following year. At Site A, Cohort 2 was never as abundant as at Site C, but seasonal patterns of density at the two sites were similar. Owing to earlier recruitment, Cohort 3 was more abundant at Site A than at Site C at the end of the study period.

Biomass

The biomass of *C. keiskama* peaked in summer owing to rapid settlement and growth of recruits (Figures 6a, b & c). The fall in total biomass at Site A in winter was due to mortality of the dominant cohort (2). Lowest biomass at Site B occurred in spring (November). This can be attributed to the disappearance of old individuals of Cohort 2 and the low biomass of recruits of Cohort 3 entering the population (Figure 6b). Mean annual biomass of *C. keiskama* for the two sites was 4,11 g m^{-2}.

Ceratonereis erythraeensis showed different patterns of biomass fluctuation to *C. keiskama*. The lowest biomass was reached in late summer (January–February) owing to the disappearance of the overwintering Cohort 1 and to low numbers and biomass of recruits (Figures 7a, b & c). The high biomass during winter and spring at both sites was maintained by the growth and high abundance of Cohort 2. Despite the drop in numbers of Cohort 2 in summer 1989 at Site A, total biomass continued to rise, mainly owing to the rapid increase in abundance of Cohort 3. Mean annual biomass of *C. erythraeensis* for the whole estuary was 7,59 g m^{-2}.

Biomass stratification

A greater proportion of the biomass of *C. erythraeensis* occurred in the 50–300-mm layer than in the 0–50-mm layer of the substratum (Figure 8). This pattern was reversed only in autumn 1989 at Sites A and D. At the former site, where the pattern was most pronounced, this was due to recruitment of small individuals close to the surface. An increase in biomass in the deeper layer of the substratum during the winter months is probably due to growth and downward movement of older individuals.

On average, 26% (2,26 g m^{-2}) of the total biomass of *C. erythraeensis* was present in the upper layer of the substratum (Table 1). By contrast, the biomass of *C. keiskama* in the upper layer of the substratum was greater than in the deeper layer (Figure 9). On average, 69% (2,06 g m^{-2}) of the total biomass of this species was in the upper layer: this is close to the average biomass of *C. erythraeensis* at the same depth. A marked increase in the biomass of *C. keiskama* in the upper layer at Site A during the spring and summer of 1989 was due to recruitment occurring in this layer. This recruitment occurred slightly later at Site B than at Site A (Figures 2, 3 & 9).

Production

Table 2 shows the computation used to calculate the annual

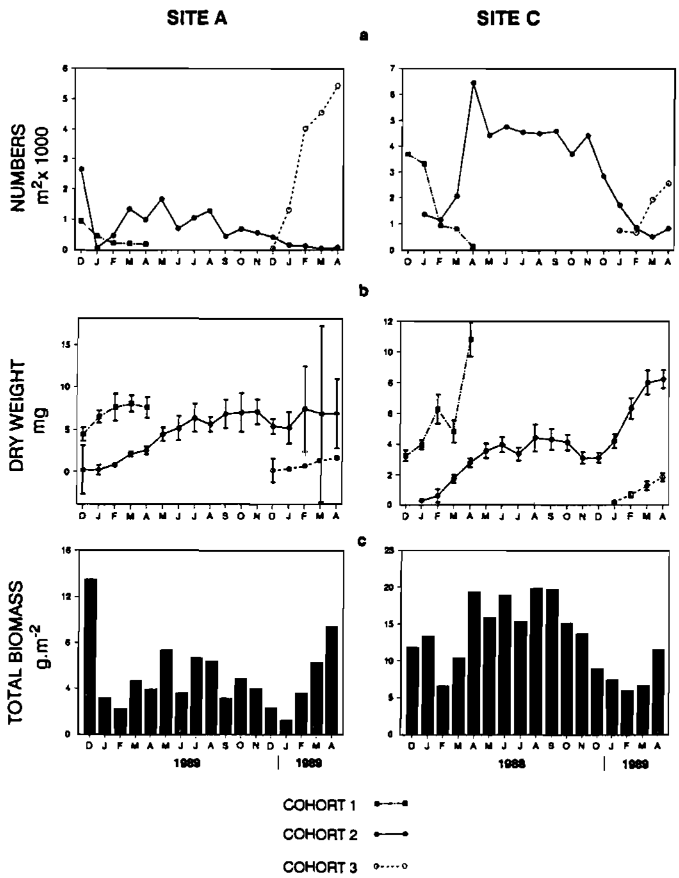

Figure 7 *Ceratonereis erythraeensis* at Sites A and C; a — numbers (per m^2) of individuals in the three cohorts; b — mean dry weight (mg) of three cohorts (± 95% confidence limits); c — biomass (g m^{-2}) of the total population; d — production (g m^{-2} $month^{-1}$) of the total population.

Table 1 Average biomass (g m^{-2}) and percentage of the total biomass of *Ceratonereis erythraeensis* and *C. keiskama* at 0–50 and 50–300 mm depths at each study site from December 1987 to April 1989

	A	B	C	D	Mean	*SD*
Ceratonereis erythraeensis						
Depth 0–50						
Biomass	1,396	2,167	2,243	3,231	2,259	0,752
(%)	(27,6)	(23,5)	(17,5)	(35,7)	(26,1)	(7,6)
Depth 50–300						
Biomass	3,658	7,041	10,658	5,824	6,795	2,931
(%)	(72,4)	(76,5)	(83,1)	(64,3)	(74,1)	(7,9)
Ceratonereis keiskama						
Depth 0–50						
Biomass	3,347	0,768			2,058	1,824
(%)	(66,7)	(71,8)			(69,3)	(3,6)
Depth 50–300						
Biomass	1,673	0,301			0,987	0,969
(%)	(33,3)	(28,2)			(30,8)	(3,6)

production of *C. keiskama* as exemplified by Site B. In cases where a sudden drop in numbers or mean weight of individuals in a cohort occurred in only one month, data were interpolated using values for the preceding and following months. Total annual production of *C. keiskama* for the two sites (A and B) was 7,58 g m^{-2} y^{-1}, mean annual biomass was 4,11 g m^{-2} and the P/B ratio was 1,84 (Table 3).

The production of *C. erythraeensis* was calculated at only two sites (Table 3). Small and scattered mudflats between Sites A and B (5,5 ha = 3,82% of the total area) where not sampled for nereids. Therefore, the estimate of total biomass and production of nereids for the estuary as a whole excludes these mudflats. An annual production of this species for the entire estuary was established as follows. The measured production of *C. erythraeensis* at Sites A and C contributed 9,04 g m^{-2} y^{-1} to the total production of the estuary (Table 3). The mean annual biomass for these areas was 4,76 g m^{-2} and the P/B ratio calculated from these values was 1,90. Using this ratio and annual mean biomass for the whole estuary (7,59 g m^{-2} — Table 3) the total annual production was calculated as 14,42 g m^{-2} y^{-1} (Table 3).

Most of the annual production of *C. keiskama* occurred during January–March (57% at Site A and 86% at Site B) whereas that of *C. erythraeensis* peaked between February and May (73% at Site A and 94% at Site B) (Figure 10A & B). There was little or no production during the winter and spring months by either species.

Discussion

The P/B ratios of both *Ceratonereis* species are within the range of those recorded for other nereid species. The P/B ratio of *Nereis diversicolor* ranges from 1,8 at the Ythan estuary, Scotland, to 9,0 at the Guteborg, Sweden (Moller 1985; Gillet 1990; Chambers & Milne 1975; Heip & Herman 1979). Kay & Bradfield (1973) reported a P/B ratio of 1,6 for *Nereis virens*. The biomass, annual production and P/B ratio of *C. erythraeensis* at the Berg River were lower than at Werribee, Australia (B = 31,0 g m^{-2}; P = 92,0 g m^{-2} y^{-1}; P/B = 2,9 — J.H. Dorsey 1981).

The reproductive cycle of *C. erythraeensis* at the Berg River varied in different parts of the estuary. Similar local variability in the population structure of *C. erythraeensis* was reported from Australia by J.H. Dorsey (1981). Populations with distinctive cohorts also reproduced during summer (January and February). Similarly, the life cycle of *Nereis diversicolor*, a common nereid worm in European estuaries, differs widely between sites (Heip & Herman 1978; Chambers & Milne 1975).

The differences in the population structure of *C. erythraeensis* at the Berg River estuary may be influenced by differential predation pressure between the sites. Predation by birds in particular may be responsible for size-related vertical stratification of worms in the substratum. The relatively high proportion of the biomass of *C. erythraeensis* in the upper layer of the substratum at Site D (Table 1) may be due to the relatively low avian predation pressure at this site. It is difficult to estimate how much of the annual production of nereids is utilized by predators, since an unknown proportion is released in the form of spawned gametes. About 40% of the total production of *Nereis diversicolor* (Chambers & Milne 1975) and almost half of that of *Scobicularia plana* (Hughes 1970) is estimated to be in the form of gametes. The large worms, which make up a high proportion of the worms in the deeper layer of the substratum, are

Table 2 Summary of data used to calculate total annual production (g m^{-2} y^{-1}) and P/B ratio of *Ceratonereis keiskama* at Site B

Date	Age class	Numbers n (m^{-2})	Mean weight $\bar{w}$ (mg)	Mean numbers $\bar{n}$ (m^{-2})	Weight increment Δw (mg)	Production increment $\bar{n} \times \Delta w$ (mg m^{-2})	Total biomass (mg m^{-2})	Month	Mean monthly production (mg m^{-2} month^{-1})	Mean monthly biomass (mg m^{-2})
Dec 1987	1	1390,7	1,678	–	–	–	2333,6			
Dec	2	2915,2	0,293	–	–	–	854,2	D	130,8	1877,0
Jan	2	2968,7	0,369	2942,0	0,076	223,6	1095,5	J	497,3	1238,9
Feb	2	2340,2*	0,793	2654,5	0,424	1125,5	1855,8	F	596,2	1545,0
Mar	2	1711,7	0,938	2026,0	0,145	293,8	1605,6	M	423,7	1386,6
Apr	2	1430,9*	0,961*	1571,3	0,023	36,1	1375,1	A	–85,4	1439,1
May	2	1150,0	0,983	1290,5	0,022	28,4	1130,5	M	28,4	1130,5
Jun	2	1043,1	0,937	1096,6	–0,046	–50,4	977,4	J	–50,4	977,3
Jul	2	695,4	1,194	869,3	0,257	223,4	830,3	J	223,4	830,3
Aug	2	775,5	1,473	735,5	0,279	205,2	1142,5	A	205,2	1142,5
Sep	2	668,6	1,485	722,1	0,012	8,7	992,9	S	8,7	992,9
Oct	2	615,1	1,497	641,9	0,012	7,7	920,8	O	7,7	920,9
Nov	2	80,2	1,230	347,7	–0,267	–92,8	98,7	N	–92,8	119,0
Nov	3	107,0	0,190	–	–	–	20,3			
Dec 1988	3	1684,9	0,336	896,0	0,146	130,8	566,1			
Jan	3	1765,2	0,783	1725,1	0,447	771,1	1382,2			
Feb	3	1497,7	0,824	1631,5	0,041	66,9	1234,1			
Mar	3	909,3	1,284	1203,5	0,460	553,6	1167,5			
Apr	3	1364,0	1,102	1136,7	–0,182	–206,9	1503,1			

* interpolated data (see text)

Total annual production (P): 1,89 (g m^{-2} y^{-1})

Mean annual biomass (B): 1,13 (g m^{-2})

P/B ratio: 1,67

Table 3 Mean annual biomass (m.a.b.) (g m^{-2}) and total annual production (t.a.p.) (g m^{-2} y^{-1}) of *Ceratonereis erythraeensis* and *C. keiskama* at each study site and over all intertidal areas

Site	% of intertidal area	m.a.b. of the site (g m^{-2})	t.a.p. of the site (g m^{-2} y^{-1})	P/B	Contribution of the m.a.b. of the site to the m.a.b. for all intertidal areas (g m^{-2})	Contribution of the t.a.p. of the site to the t.a.p. for all intertidal areas (g m^{-2} y^{-1})
Ceratonereis erythraeensis						
A	63,05	5,58	12,15	2,17	3,52	7,66
B	12,25	12,41	–	–	1,52	–
C	8,56	14,43	16,09	1,11	1,24	1,38
D	12,32	10,65	–	–	1,31	–
					A + C = 4,76	A + C = 9,04
			For all intertidal areas (see text):		B = 7,59 P/B = 1,90 P = 14,42	
Ceratonereis keiskama						
A	83,70	4,69	8,68	1,85	3,93	7,27
B	16,30	1,13	1,89	1,67	0,18	0,31
			For the intertidal areas where it occurs:		P = 7,58 B = 4,11 P/B = 1,84	

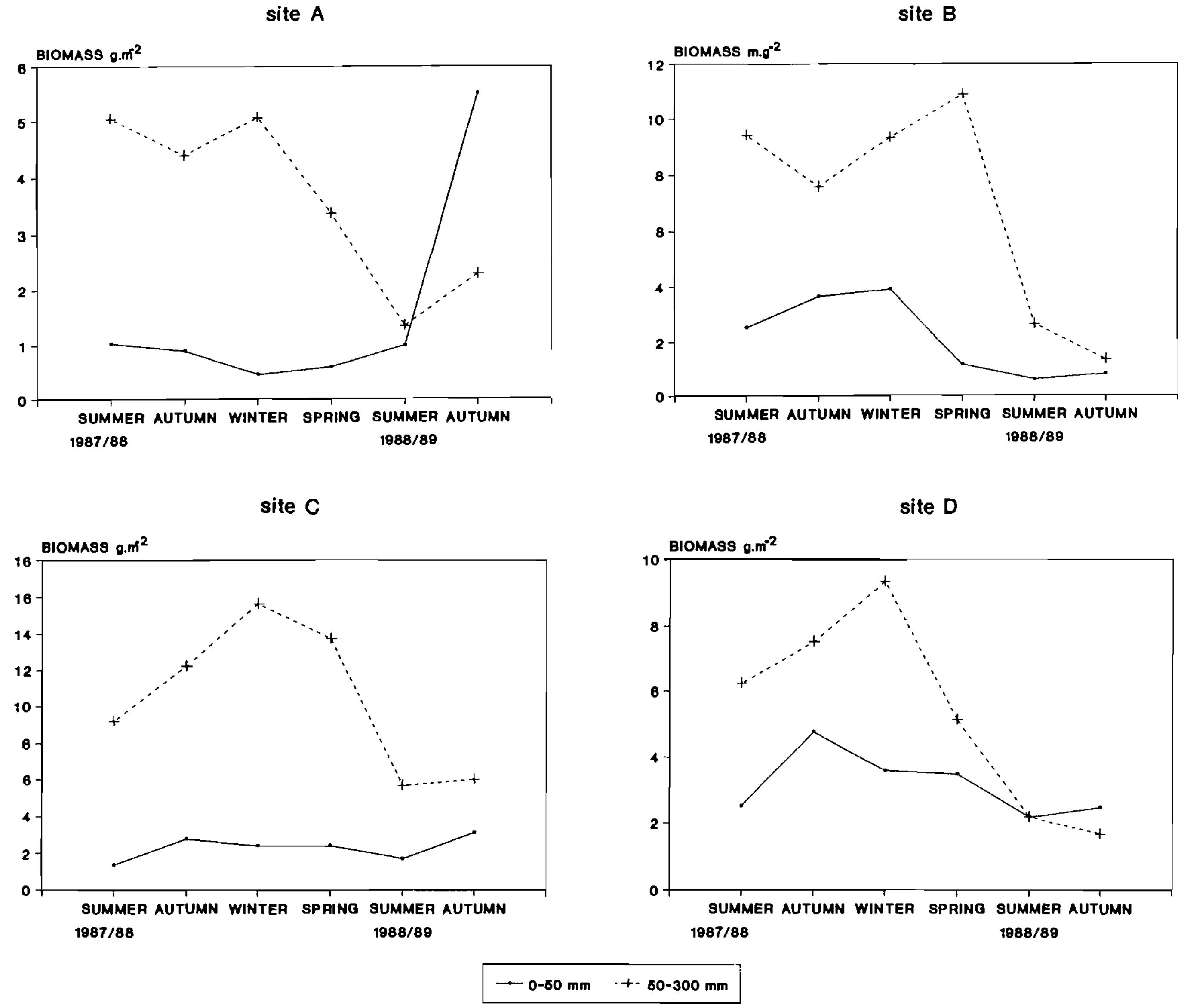

Figure 8 Seasonal variations in the biomass of *Ceratonereis erythraeensis* at 0–50 and 50–300 mm depths at the four study sites.

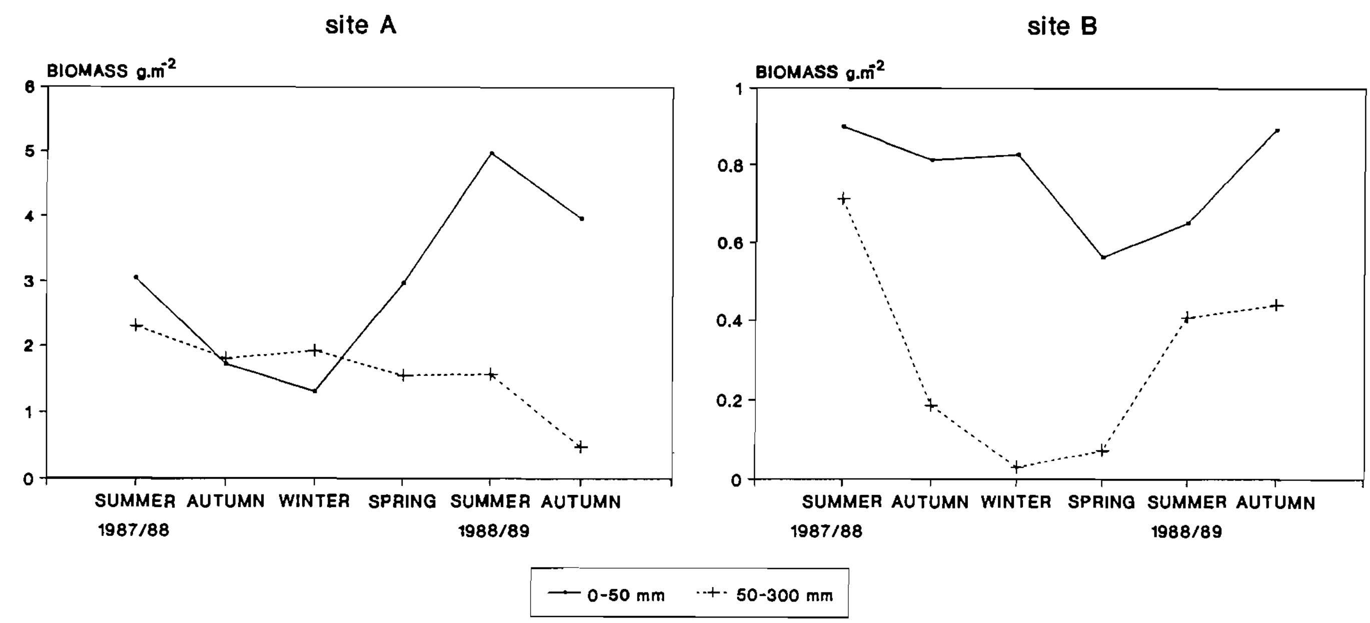

Figure 9 Seasonal variations in the biomass of *Ceratonereis keiskama* at 0–50 and 50–300 mm depths at Sites A and B.

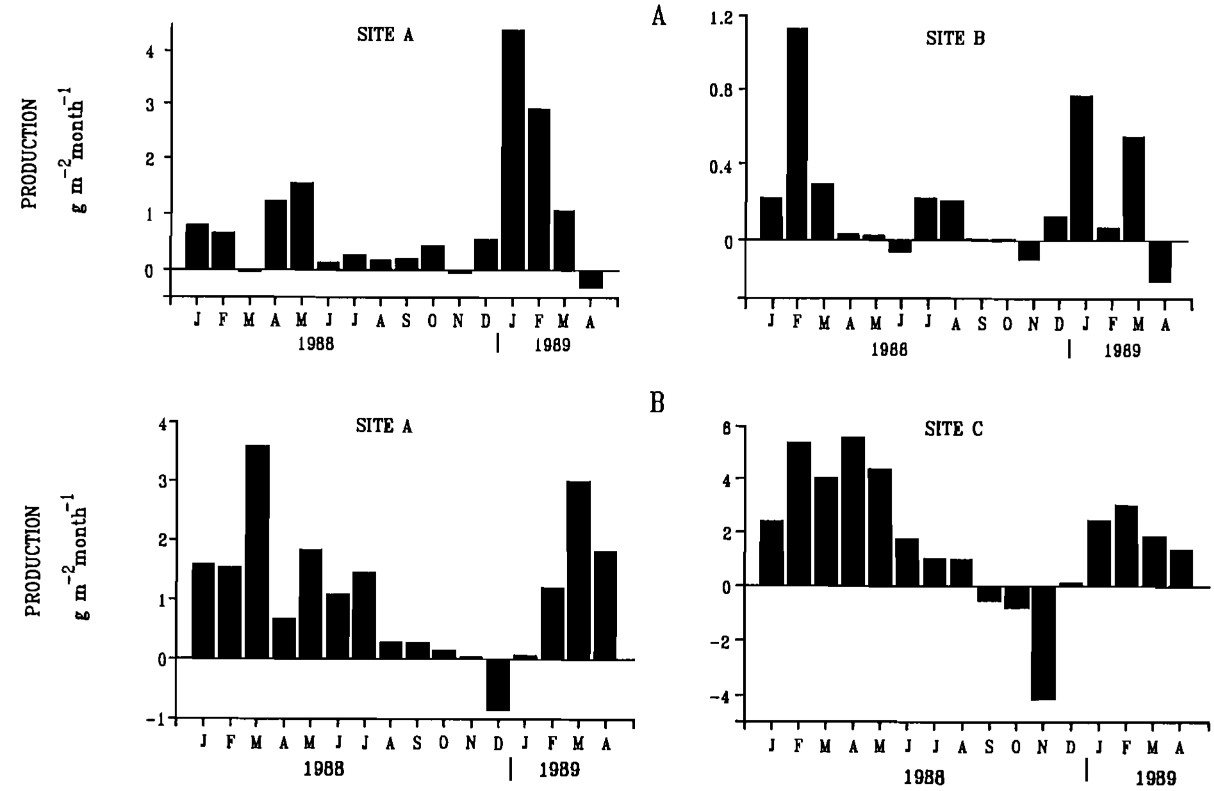

Figure 10 Production (g m^{-2} month^{-1}) of the total population of *Ceratonereis keiskama* (A) and *C. erythraeensis* (B).

unavailable to all but a few avian predators. During winter the proportion of larger individuals of both *Ceratonereis* species increased considerably in the deeper layer of the substratum. Nereid abundance is also lowest at this time of the year. The above factors create poor feeding conditions for invertebrate feeders which, however, are at their lowest density at this time of the year (Velasquez, Kalejta & Hockey 1991). The productivity of estuarine invertebrates peaks at the warmest time of year and is thus asynchronous in the northern and southern hemispheres. The period of maximum predation pressure by shorebirds, however, is synchronous in the two hemispheres, occurring during the boreal winter (austral summer). Thus, in the southern hemisphere, peaks of production and predation coincide, whereas in the north, predation peaks at the time of year when invertebrate productivity is at its lowest. These differences are likely to have profound implications for the carrying capacity of estuaries for shorebird predators.

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References

BAIRD, D. 1988. Synthesis of ecological research in the Swartkops estuary. In: The Swartkops estuary, (eds.) Baird, D., Marais, J.F.K. & Martin, A.P. *S. Afr. Natn. Sci. Prog. Rpt.* 156: 41–56.

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

CHAMBERS, M.R. & MILNE, H. 1975. Life cycle and production of *Nereis diversicolor* O.F. Muller in the Ythan Estuary, Scotland. *Estuar. Coast. Mar. Sci.* 3: 133–144.

CRISP, D.J. 1971. Energy flow measurements. In: Methods for the study of Marine Benthos, (eds.) N.A. Holme, & A.D. McIntyre. Backwell, Oxford, pp. 197–279.

GILLET, P. 1990. Biomass, production and population dynamics of *Nereis diversicolor* (polychaetous annelid) in the Loire estuary (France). *Acta Ocean.* 13: 361–371.

HARDING, J.P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.* 28: 141–153.

HEIP, C. & HERMAN, R. 1979. Production of *Nereis diversicolor* O.F. Muller (Polychaeta) in a shallow brackish-water pond. *Estuar. Coast. Mar. Sci.* 8: 297–305.

HUGHES, R.N. 1970. An energy budget for a tidal population of the bivalve *Scrobicularia plana* (da Costa) *J. Anim. Ecol.* 39: 357–381.

KALEJTA, B. 1992. Aspects of the ecology of migrant shorebirds (Aves: Charadrii) of the Berg River estuary, South Africa. PhD. thesis, University of Cape Town, South Africa.

KALEJTA, B. & HOCKEY, P.A.R. 1991. Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. *Estuar. Coast. Shelf Sci.* 33: 175–191.

KAY, D.G. & BRADFIELD, A.E. 1973. The energy relations of the polychaete *Neanthes* (= *Nereis*) *virens* (Sars). *J. Anim. Ecol.* 42: 673–692.

MOLLER, P. 1985. Production and abundance of juvenile *Nereis diversicolor* and oogenic cycle of adults in shallow waters of Western Sweden. *J. mar. biol. Ass. U.K.* 65: 603–616.

PUTITCK, G.M. 1977. Spatial and temporal variations in intertidal animal distribution at Langebaan Lagoon, South Africa. *Trans. Roy. Soc. S. Afr.* 42: 403–440.

VELASQUEZ, C.R., KALEJTA, B. & HOCKEY, P.A.R. 1991. Seasonal abundance, habitat selection and energy consumption of waterbirds at the Berg River estuary, South Africa. *Ostrich* 62: 109–123.