Reproduction and larval distribution of the penaeid prawn *Macropetasma africanus* (Balss) in Algoa Bay

A.C.Cockcroft* and T.Wooldridge
Zoology Department, University of Port Elizabeth, P.O.Box 1600, Port Elizabeth, 6000 Republic of South Africa

Received 10 November 1986; accepted 20 March 1987

Breeding adults and larvae of *Macropetasma africanus* were sampled over a two-year period in Algoa Bay, South Africa. Gonadal macro- and microscopic examination enabled classification of breeding females into four stages of development. Breeding females were present throughout the study with a summer peak of late maturing and mature females. Larvae were present in the plankton throughout the study with peak abundance in summer. Protozoea, mysis and post-larval stages were recorded with the mysis stage most abundant. Significantly higher numbers of the mysis and post-larval stages were taken at shallow stations (5 m) off sandy beaches than at the deeper stations (18 m). The presence of breeding females in the mature stage of ovarian development and the increase in larval abundance in summer indicates spawning throughout the year with peak intensity in summer.

Monsters van broeiende volwassenes en larwes van *Macropetasma africanus* is oor 'n tydperk van twee jaar in Algoa Baai, Suid-Afrika versamel. Met behulp van makro- en mikroskopiese ondersoek van gonades van broeiende wyfies kon hulle in vier ontwikkelingstadia verdeel word. Broeiende wyfies was teenwoordig reg deur die studietydperk met 'n piek van volwasse wordende en volwasse wyfies gedurende die somer. Larwes was reg deur die studietydperk in die plankton teenwoordig, met die hoogste getalle in die somer. Protozoea, mysis en post-larwale stadia is aangeteken. Hiervan was die mysis-stadium die volopste. Die mysis- en post-larwale stadia was aansienlik hoër by die vlak stasies (5 m) van sandstrande as by die dieper stasies (18 m). Die teenwoordigheid van broeiende wyfies in 'n volwasse stadium van ovariumontwikkeling en die toename in larwale getalle in die somer dui op gameetvrystelling reg deur die jaar met 'n piekintensiteit in die somer.

*To whom correspondence should be addressed

The penaeid *Macropetasma africanus* is endemic to marine waters of southern Africa. Juveniles utilize surf zones as nursery and maturation areas before migrating further offshore to spawn (Cockcroft & McLachlan 1986). *M. africanus* is dioecious with males and females maturing at a total length of 33 mm (Barnard 1950; De Freitas 1980). It is a significant component of the nearshore food web and forms part of the diet of at least 21 fish species (Lasiak 1982). Its high biomass, presence throughout the year and importance as a food source for higher trophic levels make it an important faunal component of sandy beach surf zones (Cockcroft 1982). Previous work on this species includes the description of larval stages (Cockcroft 1985), the effect of temperature on larval growth, development and survival (Cockcroft & Emmerson 1984), distribution (Cockcroft & McLachlan 1986), and food and feeding behaviour (Cockcroft & McLachlan 1986a).

Surf zone benthic invertebrates breed in Algoa Bay throughout the year with two spawning peaks e.g. *Donax serra* (McLachlan & Hanekom 1979), or are exclusive summer breeders e.g. *Bullia rhodostoma* (McLachlan & van der Horst 1979). The caridean shrimp *Palaemon pacificus* breeds through the year with peak activity in summer. Egg-bearing females move from tidal pools to the nearshore region of Algoa Bay just prior to larval release (Emmerson 1985).

Various methods have been used to determine decapod crustacean reproductive cycles. These include the gonad index method (Pillay & Nair 1971), the use of visual or histological means to determine the gonadal developmental stage of gravid females (Cummings 1961; Rao 1968), the number of eggs and/or larvae present in the plankton (Temple & Fisher 1968; Munro, Jones & Dimitriou 1968; Subrahmanyam 1971; Price 1979) and the time of appearance of juveniles in nursery areas (Baxter & Renfro 1967; Williams 1969).

By sampling the breeding and larval components of the population, this study aimed at the determinination of the reproductive cycle and larval distribution of *M. africanus* in Algoa Bay.

Field methods

Nearshore sampling for adult prawns

Nearshore samples were collected during four cruises undertaken by the research vessel *T.B.Davie* during 1980 in the area shown in Figure 1. Sample depth ranged from 9 to 18 m. Detailed location of stations sampled and fishing gear used is given in Wallace Kok, Buxton & Bennett (1984). In April and July 1980 and February, May, July, September and December 1981 samples were collected off the Swartkops River mouth (Figure 1) using a beam trawl net (12 mm stretch mesh) attached to a 3 m × 1,5 m frame to which a 6 m rigging bridle and a large marker buoy were attached. The unit was towed for approximately 30 min per haul behind a boat powered by an outboard motor. The frame trawl net proved effective in sampling the epibenthic *M. africanus*. Disturbance caused the prawns to move backwards and into the water column (personal observation) where they were caught in the net. Samples were preserved in formalin and analysed in the laboratory.

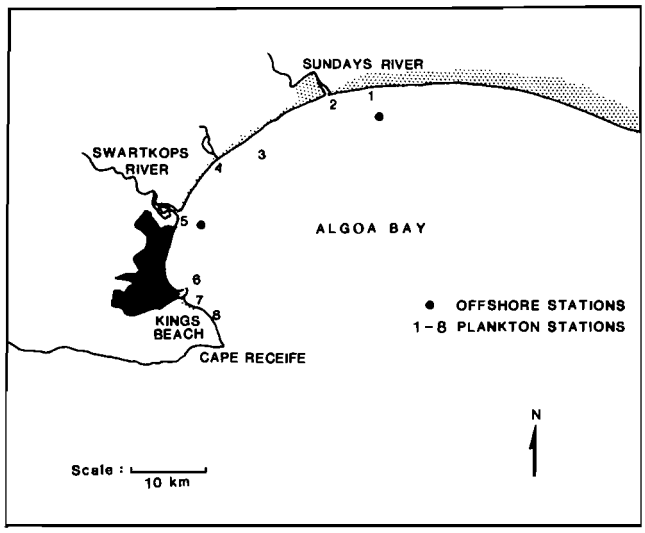

Figure 1 Algoa Bay showing location of plankton and nearshore sampling sites.

Plankton sampling

A large conical plankton net (1,5 m diameter and fitted with 500 μm mesh) was used to sample eight stations in Algoa Bay (Figure 1). Sampling was done at night and a single oblique hawl was performed at each station. At the six stations located behind the breaker line the hauls were oblique from 5 m to surface while at the two deeper stations (18 m) the hauls were from 15 m to surface. The volume of water filtered in each tow was determined using a KAHLSICO 005 WA 130 flowmeter. Samples were preserved in 10% buffered formalin for later analysis.

Laboratory methods

Adult prawns

A random subsample of 200 individuals (or total sample if $N < 200$) from each monthly sample were sexed and the total length of each prawn measured. Females were classified into one of four gonadal development stages using ovary width and colour as criteria. These stages were: I Immature, II Early maturing, III Late maturing and IV Mature. No attempt was made to define a spent or recently spent stage. The histological examination of gonads allowed their gross morphology to be related to developmental stages of the oocytes. Ovaries representing stages II to IV were each divided into anterior, middle and posterior regions. These were fixed for at least two weeks in Bouin's solution. The tissues were then routinely dehydrated, embedded in Histosec and 8–10 μm sections cut from each region. These were mounted, stained with Harris' haematoxylin, counterstained with Eosin Y and examined microscopically.

Larvae

Plankton samples were examined microscopically and all penaeid larvae were removed. When plankton volumes were too large, four sub-samples were used. Larval stages were identified (Cockcroft 1985) and the counts obtained were used to calculate abundance per standard tow (500 m^3 of water).

Table 1 Relationship between gross morphology and histological appearance of breeding female gonads

Stage	Gross morphology	Histological appearance
I	Immature: No visible sign of gonadal development. Ovary thin, transparent, unpigmented and confined to abdomen.	
II	Early Maturing: Anterior lobes of ovary developing. The light green ovary visible for the first time through the exoskeleton on the dorsal side. Scattered melanophores appear over the dorsal surface of the gonad.	Oocytes and small ova stain blue with hematoxylin.
III	Late Maturing: The anterior and middle lobes of green ovary fully developed, increased number of melanophores scattered on dorsal surface.	Large irregular shaped eggs stain red with eosin.
IV	Mature: Ovary dark green, fully distended and conspicuous through the exoskeleton.	Eggs stain red with eosin. Eggs have peripheral bodies in radial patterns.

Results

Gonad development stages

The relationship between gross external morphology and development of gonadal oocytes is shown in Table 1. Development was always uniform throughout the gonad.

Seasonal breeding cycle

The temporal distribution of sex classes (Figure 2a) indicates a peak in the percentage frequency of breeding females in summer. Owing to the sampling interval (two to three months), observed peaks were abrupt (November 1980 and December 1981). The percentage frequency of adult males in offshore samples remained fairly constant with slightly elevated proportions during the colder months in both years of study. The percentage frequency of non-breeding females was greatest in August 1980 and February 1981 and lowest in the summer months of November 1980 and December 1981.

Figure 2b illustrates each gonadal development stage as a percentage of the total monthly sample. The percentage of Stage II females was greatest in February and November 1980 and in February and May 1981. Stage III females showed relatively high profiles in samples taken in November 1980 and December 1981 and very clear peaks of Stage IV females were evident for both these summer months. The presence of Stage III and IV females throughout the study with peaks in summer indi-

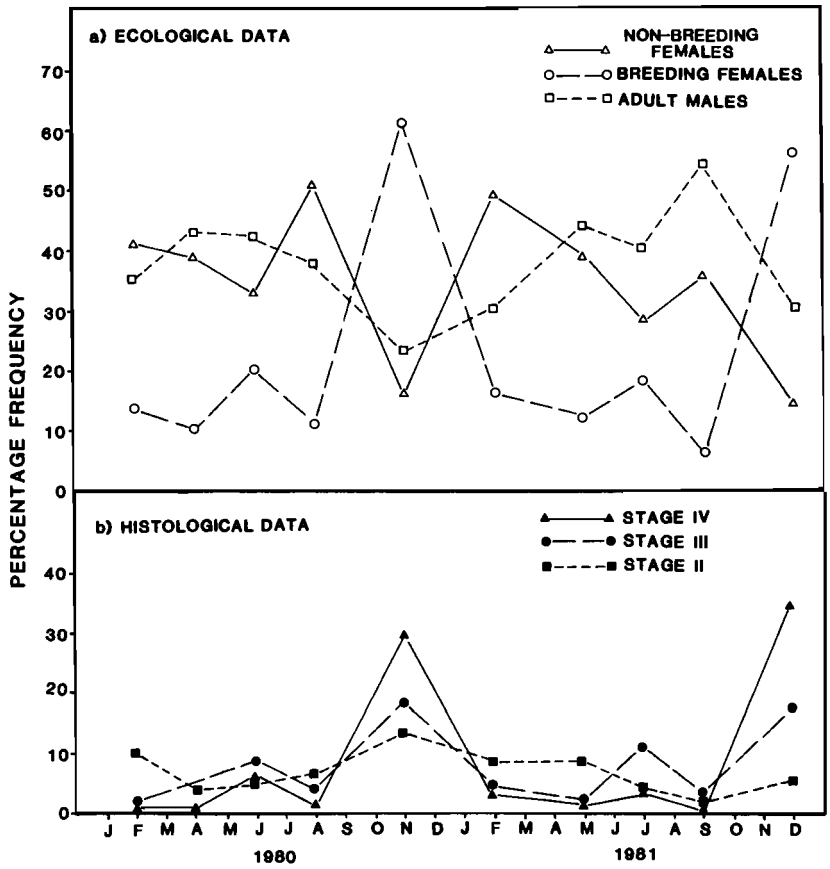

Figure 2 Temporal distribution of sex classes (a) and gonadal development stages (b) during 1980 and 1981.

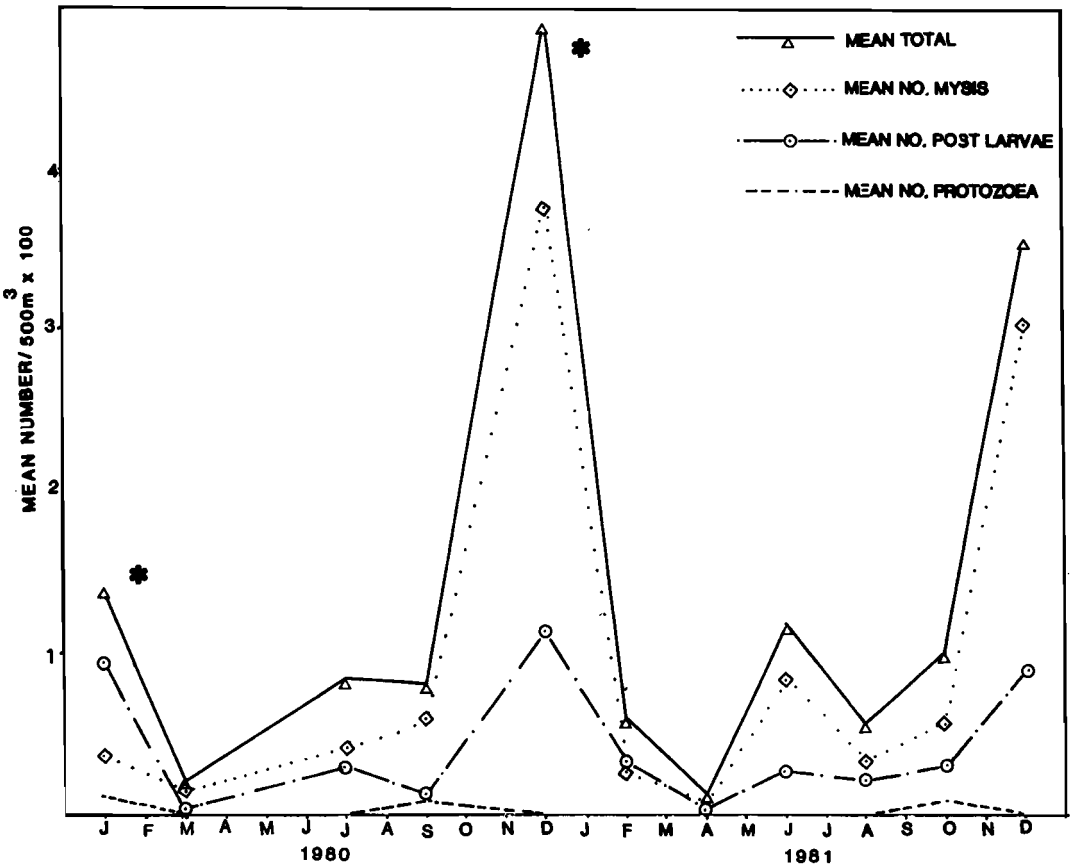

Figure 3 Mean monthly numbers of larvae and post larvae taken at all stations during the study period. * = Only Stations 1–4 sampled.

Table 2 Numbers of (a) protozoea, (b) mysis and (c) post-larvae of *M. africanus* / 500 m^3 taken at all stations on each occasion during the study; (-) indicates not present in samples; mean number per month (x_1) and per station (x_2) indicated; * no data

Station	Jan	May	July	Sep	Dec	Feb	Apr	Jun	Aug	Oct	Dec	x_2
(a) Protozoea												
1	6	–	–	6	–	–	–	–	–	14	–	2,4
2	5	–	–	10	–	–	–	–	–	10	–	2,3
3	21	–	–	12	–	–	–	–	–	22	–	5,0
4	11	–	–	13	–	–	–	–	–	11	–	3,2
5	*	–	–	9	*	–	–	–	–	19	–	3,1
6	*	–	–	21	*	–	–	–	–	26	–	5,2
7	*	–	–	4	*	–	–	–	–	–	–	0,4
8	*	–	–	–	*	–	–	–	–	–	–	–
x_1	10,8	–	–	9,4	–	–	–	–	–	12,8	–	
(b) Mysis												
1	24	9	27	93	121	20	12	47	34	61	71	46,3
2	47	10	40	25	68	31	2	52	13	32	31	31,0
3	35	9	7	16	6	9	4	14	7	4	12	11,2
4	35	23	52	55	1319	14	11	125	94	155	812	245,0
5	*	17	6	23	*	34	7	70	44	66	172	48,7
6	*	6	2	37	*	15	18	237	8	26	142	54,5
7	*	47	10	15	*	75	29	107	47	84	294	78,6
8	*	20	129	233	*	33	1	40	40	8	215	79,8
x_1	32,8	17,6	34,1	62,1	378,5	28,8	10,5	86,5	35,8	54,5	218,6	
(c) Post-larvae												
1	125	1	5	10	116	49	2	16	22	48	71	42,7
2	100	6	7	7	136	25	1	18	62	50	74	44,2
3	22	–	7	13	5	–	6	3	–	–	–	5,1
4	124	9	79	14	191	47	9	42	21	78	318	84,7
5	*	6	57	17	*	68	7	26	21	14	18	26,0
6	*	2	4	6	*	15	5	71	16	2	82	22,0
7	*	20	4	5	*	26	25	40	14	25	126	31,6
8	*	6	46	1	*	37	1	9	16	56	48	24,4
x_1	92,8	6,3	26,1	9,1	112,0	33,0	6,8	28,1	21,5	34,1	92,0	

cates spawning throughout the year with greatest intensity in summer.

Female size at spawning

Stage II to IV females ranged from 42–70 mm total length. The size at sexual maturity (size at which 50% of the females showed visible gonadal development) could only be determined in November 1980 (48,5 mm) and December 1981 (46,5 mm). The mean size of Stage IV females in these summer months was 59,6 ± 4,2 mm and 56,2 ± 3,7 mm respectively. The mean size of the relatively few Stage IV females sampled in the other months of the study remained fairly constant at *ca.* 57 mm with exceptions in April (49,4 ± 2,7 mm) and August 1980 (51,5 ± 2,4 mm).

Offshore plankton

Plankton data are tabulated in Table 2 and illustrated in Figure 3. *M. africanus* larvae and post-larvae were always present with a peak in larval abundance in December 1980 and 1981. Mean numbers for all stations sampled on these occasions were 490 (range 11–1510) and 310 (range 12–1130) per standard trawl, or 0,98 and 0,69 larvae/m^3, respectively. Lowest mean monthly numbers per standard trawl were recorded in May 1980 (23,9; range 8–67) and April 1981 (17,3; range 2–54).

Protozoea were taken in relatively low numbers on three occasions (Table 2). Protozoea III predominated with Stages I and II present in October 1981 and September 1980, respectively. Statistical analysis (ANOVA) showed significantly higher numbers of protozoea at deeper stations (Stations 3 and 6, 18 m) than at inshore stations (depth 5–8 m)($P < 0,05$).

Mysis were abundant in most samples with Stages II and III predominant. Highest mean numbers of mysis were recorded in December 1980 and December 1981 (378 and 218 per standard tow or 0,76/m^3 and 0,44/m^3, respectively). The highest number of mysis recorded was 1319/500 m^3 (2,64/m^3) in December 1980 at Station 4.

Significantly higher (ANOVA, $P < 0,05$) numbers of the mysis stages were recorded at inshore stations off sandy beaches (Stations 1, 4 and 7) compared to deeper stations (Stations 3 and 6) and stations adjacent to estuary mouths (Stations 2 and 5).

Post-larvae were also present on all sampling occasions. Highest mean numbers of post-larvae were recorded in January and December 1980, and December 1981 when 92,8; 112 and 92 larvae per standard tow, respectively, were recorded. Both early and advanced post-larvae were taken during the study with the former predominating in September 1980 and October 1981. In January and December 1981 both early and advanced post-larvae were present in similar proportions. Significantly higher (ANOVA, $P < 0,05$) numbers of post-larvae were taken off sandy beaches (Stations 1, 4 and 7) compared to deeper stations (Stations 3 and 5).

Discussion

Environmental factors such as light, temperature, food and salinity are known to influence reproductive cycles in marine animals (Giese 1959). In the present study the breeding cycle of *M. africanus* appears closely linked to seasonal temperature (Figure 4). Cockcroft & McLachlan (1986) proposed that offshore movement of adult non-breeding females in August/September from the Sundays River and Kings Beach surf zone was linked to the rise in mean monthly water temperature. The increase in percentage frequency of *M. africanus* breeding females and females in the mature stage of ovarian development indicates a summer spawning peak with less intense breeding occuring throughout the remainder of the year. As breeding females were not an important component of the surf zone population (Cockcroft & McLachlan 1986) it is apparent that gonad maturation occurs after females enter deeper water. Caillouet (1972) found that oogenesis in *Penaeus duorarum* started during the estuarine phase of the life cycle but maturation of the ova was incomplete until the prawns migrated offshore. The numbers of gonadal development stages described for *M. africanus* are similar to those recorded for various penaeid species (Hudinaga 1942; King 1948; Cummings 1961; Rao 1968; Santiago 1977). Histolgical examination showed no sequential variation of egg development stage in different parts of the ovary. A quantitative assessment of gonad maturation in *P. duorarum* (Caillouet 1972) also showed no significant difference between regions.

Copulation in some penaeid species results in the deposition or insertion of paired spermatophores onto or into the female theylcum (King 1948). In penaeids with open thelycae (e.g. *M. africanus*) it has been suggested that copulation occurs in the post-moult phase when the exoskeleton has already hardened (Perez-Farfante 1969). In penaeids with complicated or closed thelycae mating occurs between hard-shelled males and recently moulted females. In contrast to fertilization in carideans which takes place within 24 h of copulation, many penaeids are capable of retaining viable sperm for several weeks (Wickens 1976). Cockcroft & Emmerson (1984) noted the spawning of viable eggs in *M. africanus* under

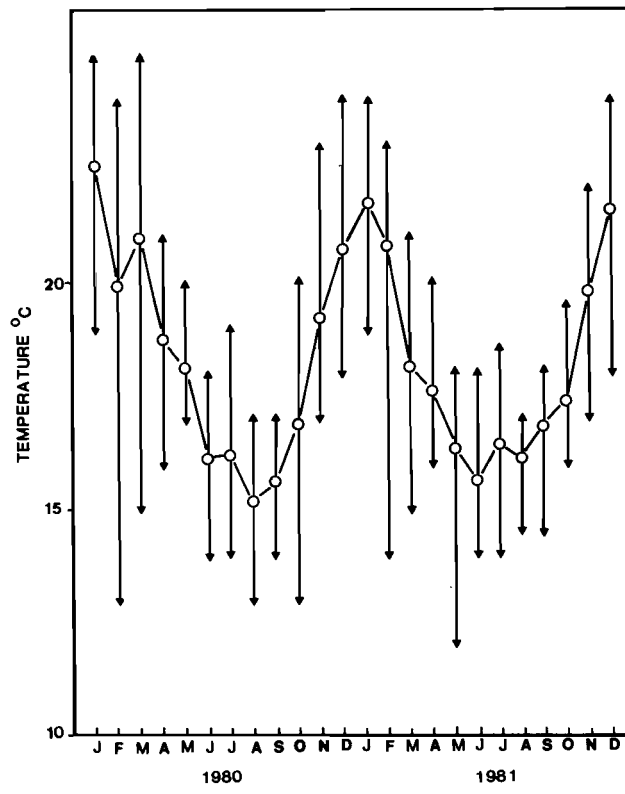

Figure 4 Mean monthly surf zone temperatures for 1980–1981 (from Humewood Beach Office Records).

laboratory conditions despite the absence of a conspicuous spermatophore.

The size of females at sexual maturity for the summer months of November 1980 and December 1981 was 48,5 and 46,5 mm, respectively, while the mean size of Stage IV females in these months was 59,6 ± 4,2 mm and 56,2 ± 3,7 mm, respectively. The number of *M. africanus* eggs spawned (E), as a function of female total length (L), obtained from laboratory spawnings, is given by the expression $E = 18,59\ L^{2,11}$ (Cockcroft & Emmerson 1984). Using this expression it is estimated that the number of eggs spawned per female in summer ranged from $9,146 \times 10^4 - 1,035 \times 10^5$ per spawning. The frequency of spawning is not known in *M. africanus*, although in other penaeids individuals may spawn repeatedly in a single season (Lindner & Anderson 1956; Emmerson 1980). A temperature increase rather than absolute temperature is considered to induce spawning in some penaeids (Eldred, Williams, Martin & Joyce 1965; Jones, Dimitriou, Edwald & Tweedy 1970; Subrahmanyam 1971).

Larval development in *M. africanus* takes 16–26 days (Cockcroft & Emmerson 1984), so that the presence of larvae in plankton is indicative of recent spawning. Larvae were present in the plankton throughout the year with a marked summer peak. The distribution of larval stages was not random in the area sampled. Significantly higher numbers of protozoea were taken at the deeper stations than at the inshore stations while the reverse was the case for both mysis and post-larval stages. Jones *et al.* (1970) found post-larval *P. duorarum* restricted to in-

shore waters while earlier stages were more widely distributed. The concentration of post-larvae *M. africanus* off sandy beaches in summer corresponds to peaks in juvenile recruitment to adjacent surf zone nursery areas (Cockcroft & McLachlan 1986). Correlation between spawning peaks and the number of post-larvae in or near nursery areas has been observed by Baxter &nd Renfro (1967); Christmas, Gunter & Musgrave (1966); Gunter (1961) and Williams (1969).

The presence of *M. africanus* breeding females and larvae in relatively low numbers throughout the year with summer peaks in abundance, indicates a summer spawning peak, with background spawning throughout the year. Emmerson (1985) reported a similar breeding cycle for the shrimp *P. pacificus*; egg-bearing females moved from tidal pools just prior to larval release and were recorded in the nearshore region of Algoa Bay from August to November. Post-larval recruitment indicated year-round spawning activity with a major peak in November.

The reproductive cycles of these related crustacean species appear closely linked to the annual water temperature cycle in Algoa Bay. The relatively small annual temperature range (compared to Northern Hemisphere) enables some continuous spawning throughout the year with peak reproductive activity in the warmer summer months when larval growth, survival and development are enhanced (Cockcroft & Emmerson 1984).

Acknowledgements

The authors wish to thank Mrs J.Harris for typing the text, Miss M.Maree for preparing the figures and Miss L.McGwynne for appraising the typescript. Miss L.E.Beckley, Dr J.H.Wallace and the crew of the *T.B.Davie* are thanked for the offshore samples. The first author gratefully acknowledges a post-graduate bursary from the Council for Scientific and Industrial Research.

References

BARNARD, K.H. 1950. Descriptive catalogue of South African decapod crustacea. *Ann. S. Afr. Mus.* 38: 1–837.

BAXTER, K.N. & RENFRO, W.C. 1967. Seasonal occurrences and size distribution of post-larval brown and white shrimp near Galveston, Texas, with notes on species identification. *Fishery Bulletin*, 66(1): 149–158.

CAILLOUET, C.W. Jr. 1972. Ovarian maturation induced by eye-stalk ablation in pink shrimp, *Penaeus duorarum* Burkenroad. In: Proceedings of the Third Annual Meeting World Mariculture Society, Louisiana State University, Baton Rouge, (ed.) Avault, J.W. pp. 205–225.

CHRISTMAS, J.Y., GUNTER, G. & MUSGRAVE, P. 1966. Studies on annual abundance of post-larval penaeid shrimp in the estuarine waters of the Mississippi, as related to subsequent commercial catches. *Gulf Res. Rep.*, 2: 177–212.

COCKCROFT, A.C. 1982. Aspects of the biology of the swimming prawn *Macropetasma africanus* (Balss). MSc thesis, University of Port Elizabeth, South Africa.

COCKCROFT, A.C. 1985. The larval development of *Macropetasma africanum* (Balss, 1913) (Decapoda, Penaeoidea) reared in the laboratory. *Crustaceana* 49(1): 52–74.

COCKCROFT, A.C. & EMMERSON, W.D. 1984. The effect of temperature on the growth, development and survival of *Macropetasma africanus* (Balss) (Penaeoidea:Penaeidae) larvae reared in the laboratory. *J. Exp. Mar. Biol. Ecol.* 84: 203–210.

COCKCROFT, A.C. & McLACHLAN, A. 1986. Distribution of juvenile and adult penaeid prawns *Macropetasma africanus* (Balss) in Algoa Bay. *S. Afr. J. Mar. Sci.* 4: 245–255.

COCKCROFT,A.C.& McLACHLAN,A. 1986a. Food and feeding habits of the surf zone penaeid prawn *Macropetasma africanus* (Balss). P.S.Z.N.I: Marine Ecology 7(4): 345–357.

CUMMINGS, W.C. 1961. Maturation and spawning of the pink shrimp, *Penaeus duorarum* Burkenroad. *Trans. Am. Fish Soc.*, 90(4): 462–468.

DE FREITAS, A.J. 1980. The Penaeoidea of South Eastern Africa. Ph.D. thesis, University of the Witwatersrand, South Africa.

ELDRED, B., WILLIAMS, J., MARTIN, G.T. & JOYCE, E.A. 1965. Seasonal distribution of penaeid larvae and post-larvae of the Tampa Bay area, Florida. *Tech. Serv. Fla. St. Bd. Conserv.* 44: 1–47.

EMMERSON, W.D. 1980. Induced maturation of prawn *Penaeus indicus*. *Mar. Ecol. Prog. Ser.* 2(2): 121–131.

EMMERSON, W.D. 1985. Seasonal abundance, growth and production of *Palaemon pacificus* (Stimpson) in eastern Cape tidal pools. *S. Afr. J. Zool.* 20(4): 221–231.

GIESE, A.C. 1959. Comparative Physiology: Annual reproductive cycles of marine vertebrates. *Ann. Rev. Physiol.* 21: 547–576.

GUNTER, G. 1961. Habitat of juvenile shrimp (Fam. Penaeidae). *Ecology* 42: 588–589.

HUDINAGA, M. 1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. *Jap. J. Zool.* 10: 305–393.

JONES, A.C., DIMITRIOU, D.E., EDWALD, J.J. & TWEEDY, J.J. 1970. Distribution of early developmental stages of pink shrimp, *Penaeus duorarum*, in Florida waters. *Bull. Mar. Sci.* 20(3): 634–661.

KING, J.E. 1948. A study on the reproductive organs of the common marine shrimp, *Penaeus setiferus* (Linnaeus). *Biol. Bull. Mar. Biol. Lab.* Woods Hole 94(3): 244–262.

LASIAK, T.A. 1982. Structural and functional aspects of the surf zone fish community in the Eastern Cape. Ph.D. thesis, University of Port Elizabeth, South Africa.

LINDNER, M.J. & ANDERSON, W.W. 1956. Growth migrations, spawning and size distribution of shrimp *Penaeus setiferus*. *Bull. U.S. Bur. Fish.* 56(106): 555–645.

McLACHLAN, A. & HANEKOM, N. 1979. Aspects of the biology, ecology and seasonal fluctuations in biochemical composition of *Donax serra* in the East Cape. *S. Afr. J. Zool.* 14: 183–193.

McLACHLAN, A. & VAN DER HORST, G. 1979. Growth and reproduction of two molluscs from an exposed sandy beach. *S. Afr. J. Zool.* 14: 194–201.

MUNRO, J.L., JONES, A.C. & DIMITRIOU, D. 1968. Abundance and distribution of the larvae of the pink shrimp (*Penaeus duorarum*) on the Tortugas Shelf of Florida, August 1962 – October 1964. *Fishery Bull. Fish Wildl. Serv. U.S.* 67(1): 165–181.

PéREZ-FARFANTE, I. 1969. Western Atlantic shrimps of the genus *Penaeus*. *Fishery Bull. Fish. Wildl. Serv. U.S.* 67(3): 461–591.

PILLAY, K.K. & NAIR, N.B. 1971. The annual reproductive cycles of *Uca annulipes, Portunus pelagicus* and *Metapenaeus affinis* (Decapoda: Crustacea) from the south-west coast of India. *Mar. Biol.* 11: 152–166.

PRICE, A.R.G. 1979. Temporal variations in abundance of penaeid shrimp larvae and oceanographic conditions off Ras Tanura, Western Arabian Gulf. *Estuar. Cstl. Mar. Sci.* 9: 451–465.

RAO, P.V. 1968. Maturation and spawning of the penaeid prawns of the south-west coast of India. *F.A.O. Fish. Rep.* 57: 285–302.

SANTIAGO, A.C. 1977. Successful spawning of cultured *Penaeus monodon* Fabricius after eyestalk ablution. *Aquaculture* 11(3): 185–196.

SUBRAHMANYAM, C.B. 1971. The relative abundance and distribution of penaeid shrimp larvae off the Mississippi coast. *Gulf Res. Rep.* 3(2): 291–345.

TEMPLE, R.F. & FISHER, C.C. 1968. Seasonal distribution and relative abundance of planktonic-stage shrimp (*Penaeus* spp.) in the north-western Gulf of Mexico, 1961. *Fishery Bull. U.S. Fish Wildl. Serv.* 66(2): 323–334.

WILLIAMS, A.B. 1969. A ten year study of mesoplankton in North Carabina estuaries. Cycles of abundance among penaeidaen shrimps. *Chesapeake Sci.* 10: 36–47.

WALLACE, J.H., KOK, H.M., BUXTON, C.D. & BENNETT, B. 1984. Inshore small-mesh trawling survey of the Cape south coast. 1. Introduction, methods, stations and catches. *S. Afr. J. Zool.* 19(3): 134–164.

WICKENS, J.F. 1976. Prawn biology and culture. *Oceanogr. Mar. Biol. Ann. Rev.* 14: 435–507.