Seasonal abundance, growth and production of *Palaemon pacificus* (Stimpson) in eastern Cape tidal pools

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The shrimp *Palaemon pacificus* was sampled monthly from six tidal pools for two years. The shrimp populations varied seasonally with peak numbers and biomass found in summer (December to March) following a major influx of juveniles in November. These recruits were composed of discrete modal groups (bimodal) which spread and became less obvious by April (polymodal). Females had a greater mean size range than males. The sex ratio varied temporally and overall male:female ratios varied from 1:1,66 to 1:2,96. Average shrimp total length was significantly correlated to the average and maximum pool depth and to log pool volume while the average number of cohorts per year was found to be negatively correlated to these parameters. In smaller pools the shrimp disappeared above 20 – 30 mm but remained up to reproductive age in the deeper pools. Average residence time was positively correlated to pool depth, but not to log volume. Mean summer growth rates were almost double those in winter and were combined in the von Bertalanffy growth equation $L_t = 64{,}51\ (1 - e^{-0{,}08902(t - 0{,}1001)})$. *P. pacificus* reaches first maturity from egg at six months for males and 12 months for females. Mean annual production varied between pools from 0,22 to 2,0 g m^{-2} and biomass from 0,06 to 0,5 g m^{-2}. The highest P/B ratio of 4,24 was obtained from the smallest pool which had a low biomass but high productivity and shrimp turnover.

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Monsters van die gamaal *Palaemon pacificus* is maandeliks vir twee jare vanuit ses getypoele geneem. Die gamaalbevolkings het met die seisoene gevarieer en die getalle en biomassa het in die somer (Desember tot Maart) 'n piek bereik na 'n groot invloei van jeugdiges in November. Hierdie nuwe aankomelinge was saamgestel uit diskrete modale groepe (bimodaal) wat gesprei het en minder sigbaar geword het in April (polimodaal). Wyfies het 'n groter bestek van gemiddelde grootte as mannetjies gehad. Die geslagsverhouding het by tye verskil en algehele mannetjie: wyfie verhoudings het gewissel van 1:1,66 tot 1:2,96. Daar was 'n betekenisvolle korrelasie tussen die gamale se gemiddelde totale lengte en die gemiddelde en maksimum poeldiepte asook die logpoelvolume, terwyl die gemiddelde aantal kohortgroepe per jaar negatief gekorreleer was tot hierdie parameters. In kleiner poele het die gamale verdwyn bo 20 – 30 mm, maar in die dieper poele gebly tot op die reproduktiewe ouderdom. Gemiddelde verblyftyd was positief gekorreleer tot poeldiepte, maar nie tot logvolume nie. Gemiddelde somergroeitempo's was amper dubbel die tempo in die winter en is saamgevoeg in die von Bertalanffy-groeivergelyking $L_t = 64{,}51\ (1 - e^{-0{,}08902(t - 0{,}1001)})$. *P. pacificus* bereik eerste volwassenheid vanaf eierstadium na ses maande vir mannetjies en na 12 maande vir wyfies. Gemiddelde jaarlikse produksie het verskil tussen poele en wel van 0,22 tot 2,0 g m^{-2} en biomassa van 0,06 tot 0,5 g m^{-2}. Die hoogste P/B verhouding van 4,24 is verkry vanaf die kleinste poele wat 'n lae biomassa gehad het, maar 'n hoë produktiwiteit en gamaalomset.

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The caridean shrimp *Palaemon pacificus* (Stimpson) is widely distributed in the Indo-Pacific from the Red Sea to Japan and in southern Africa from Walvis Bay on the west coast (Barnard 1950; Day 1980) to Kosi Bay on the east coast (Broekhuysen & Taylor 1959). It is found in rock pools, estuaries and in near-shore waters to a depth of 45 m, (Barnard 1950) yet despite its ubiquity, very little research has been undertaken on this species. By contrast the palaemonid shrimps in the northern hemisphere have received considerable attention both from the ecological (Rodriguez & Naylor 1972; Morgan 1980; Berglund 1982; Alon & Stancyk 1982) and the aquacultural aspect (Wickins 1972; Schulte 1976).

A programme was initiated to investigate the life history, abundance, growth and production of *P. pacificus* in tidal pools, estuaries and in near-shore waters of the eastern Cape coast of South Africa in order to better understand the autecology of this adaptable species living under heterogeneous regimens. One part of the programme dealt with the tidal pool environment and is reported here. The shrimp populations from six different tidal pools are compared with reference to seasonal abundance, sex ratio, size distribution, growth and production.

Methods

Study area

Port Elizabeth (34°00′S/25°30′E) is situated in Algoa Bay on the south-eastern coast of South Africa (Figure 1). The sheltered bay is formed behind a rocky headland of Table Mountain Group sandstone (Stephenson, Stephenson & Bright 1938; South African Committee for Stratigraphy 1980). To the west of Cape Recife the coast is exposed and rugged with folded and jointed quartzitic sandstone (Stephenson *et al.* 1938) which has been weathered to form innumerable tidal rock pools and gullies. Six sites were selected, two inside the bay (McArthur and Pollock) and four on the exposed side (Noordhoek, Willows, Minhetti and Beachview; Figure 1). Two of the sites, namely McArthur and Willows are artificially constructed bathing pools while the other four are natural tidal pools. All the pools were situated between the mean spring high water and the mean neap high water zones.

Sampling techniques

Pool volume was estimated by three methods, namely measuring the pool dimensions, dye dilution and pumping. With the first method pool depths, widths and lengths were measured on a grid system and averaged. Evans blue was used for the dye technique where concentrate was poured into the pool, mixed, and a diluted sample taken to be read on a Pye

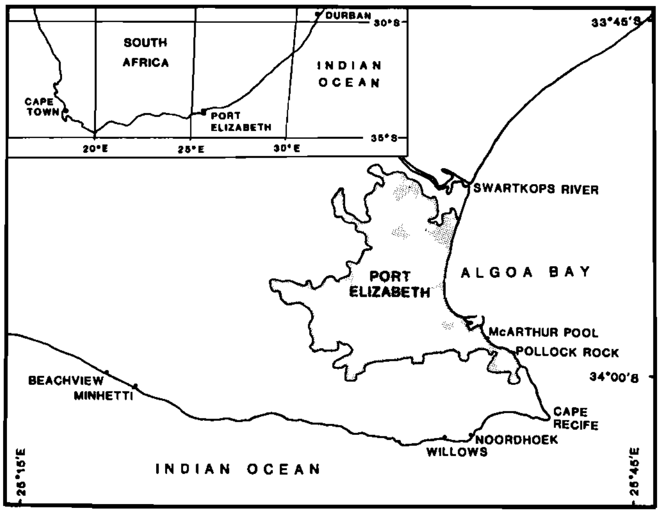

Figure 1 Map of the study area showing the location of the six tidal pools sampled.

Unicam spectrophotometer at 458 nm. A dilution series was made for each batch of concentrate used. A domestic water meter was coupled to the outlet of a portable pump in the third method and the pool was pumped dry during spring low tide. The last two methods, however, could only effectively be used in pools of < 15 000 ℓ. Pools were sampled for shrimps monthly during spring low tide for two years between May 1980 and July 1982. Salinity (optical refractometer) and temperature (thermometer) readings were also taken, and in the four natural pools a hand net with 1 mm mesh was used to remove all the shrimps. A 50 × 50 cm (0,25 m^2) box net with a clear plexiglass rim attached to a 3 m pole was used to sample the sides of the larger artificial pools. Samples were frozen until analysed. The following parameters were investigated: sex (> 18 mm TL; presence or absence of a genital papilla at the base of the 5th pereiopoda, and appendix masculina), total length (TL mm; from rostrum tip to telson tip) and dry mass (cleared dry mass for natural pools and per m^2 for artificial pools; 80 °C for 24 h). Harding (1949) and Cassie's (1954) graphical method using probability paper was applied in the analysis of cohorts to demonstrate recruitment and growth. The general von Bertalanffy (1938) equation was fitted to the growth data. A Walford plot of $L_t + 1$ versus L_t (length at age t in months) was used to calculate the constants $L\infty$ and K (Walford 1946). Production was determined by the growth method of Crisp (1971) using the formula $P_g = \Sigma_t \Delta W_t \bar{N}_t$, where P_g is the production by growth, ΔW_t is the increase in shrimp mean mass over time interval t (months) and $\bar{N}_t$ is the mean number of individuals over time interval t. These P values were divided by the mean annual standing biomass of the populations for each site to give the Production/Biomass (P/B) ratio. The modal means of the various cohorts were converted to dry mass values for productivity estimates using the combined male/female, length/dry mass relationship $M = 0{,}00069\,L^{3{,}3676}$; $r = 0{,}993$; $n = 86$, where M is the dry mass and L the total length (Emmerson, unpublished data).

Results

Physical conditions

Water temperature curves were very similar for the six sites with winter minima of around 13 °C and summer temperatures of 24 – 30 °C. Small pools such as Minhetti exhibited greater variation than large pools such as Willows or McArthur (Figures 2a – f).

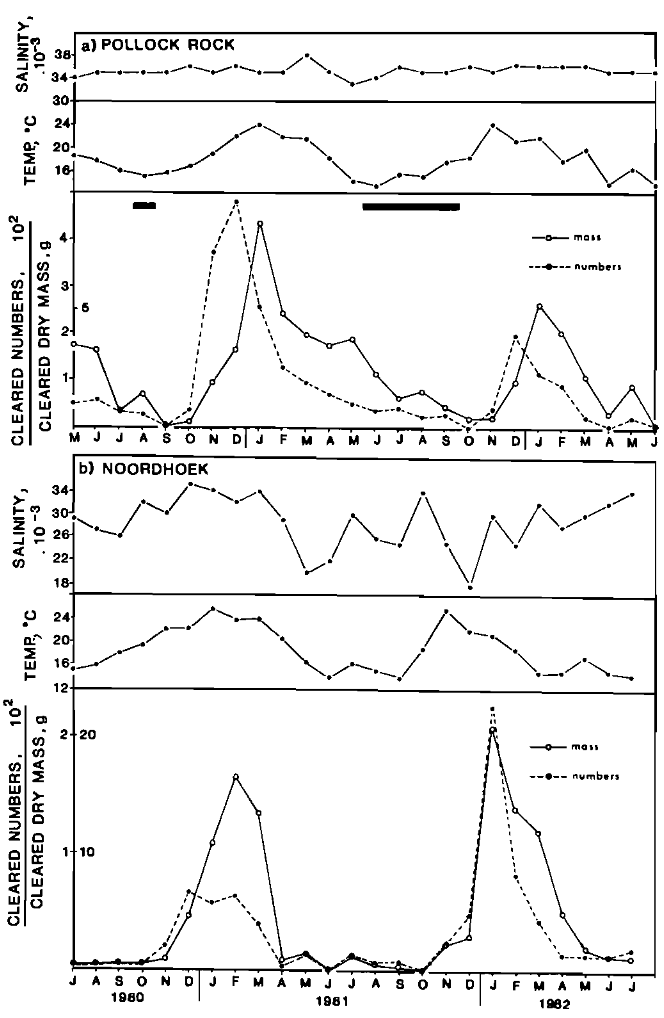

Figure 2a & b Seasonal variation in *Palaemon pacificus* numbers and dry mass at (a) Pollock and (b) Noordhoek. Salinity and temperature values for each pool are given.

The eastern Cape coast experiences two rainfall maxima per annum, one in April, the other in September (Reddering & Esterhuysen 1981) and pool salinities varied accordingly, with the larger pools having less variation than the smaller ones. Noordhoek and Beachview had additional fresh-water sources in the form of seepage so they exhibited greater salinity fluctuations (Figures 2b & d).

The pool volumes are given in Table 1. The two artificial pools were too large to be measured by pumping or using dye, while Noordhoek was also too large to be effectively pumped dry between tides. Pumping appeared to be the most accurate method of estimating pool volume. Inaccuracies occurred with direct measurement owing to pool topography and 'squaring-off' of measurements. The dye had to be very concentrated using the dye-dilution method to obviate inaccuracies associated with over-dilution. Maximum pool depth varied from 2,6 m in McArthur to 0,3 m in Minhetti. *Enteromorpha* sp., *Ulva rigida, Arthrocardia* sp. and *Sargassum heterophylla* formed the major algal species in the pools.

Population structure

A total of 2 177 shrimp were sexed and measured for population analysis from McArthur pool, 2 285 from Pollock, 7 920 from Noordhoek, 2 064 from Willows, 3 307 from Minhetti and 17 403 from Beachview.

In all six pools the shrimp were greatly affected by season,

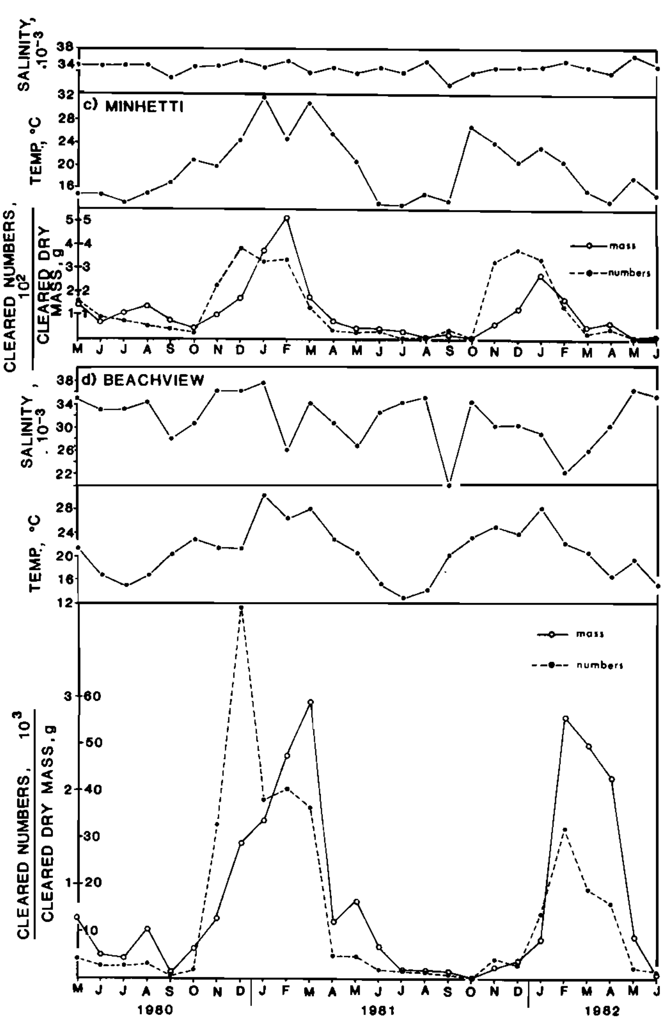

Figure 2c & d Seasonal variation in *Palaemon pacificus* numbers and dry mass at (c) Minhetti and (d) Beachview. Salinity and temperature values for each pool are given.

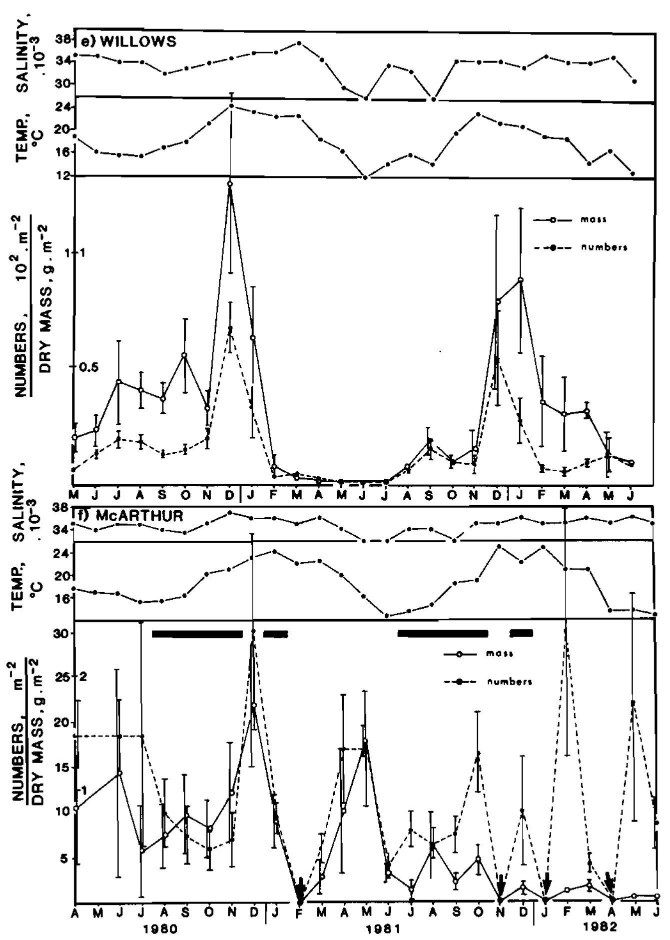

Figure 2e & f Seasonal variation in *Palaemon pacificus* numbers and dry mass at (e) Willows and (f) McArthur. Salinity and temperature values for each pool are given. Horizontal bars represent periods of females carrying eggs, vertical lines represent one S.E. and arrows indicate when the pool was drained.

with peak numbers found in summer between December and February. Peak cleared dry mass generally followed a month later from December to March (Figures 2a – f). Males, females and juveniles (< 18 mm TL) were combined for size-frequency analysis as low shrimp numbers, especially between June and October did not allow separate analysis. Size-frequency distributions followed a pattern of bimodality in summer (November to March) and became polymodal with fresh recruitment and growth spread. Examples of a small (Minhetti), medium (Beachview) and large (McArthur) pool are shown in Figures 3a, b and c. Bimodality appeared to be delayed until February – March in McArthur pool (Figure 3c). The shrimp grew into winter at which stage the populations were polymodal. The shrimp then moved out of the pools leaving low numbers to overwinter until the main early summer invasion of juveniles during November. In McArthur the overwintering population persisted through to January (Figure 3c). Recruitment of juveniles into the pools, especially the smaller ones was continuous (Figure 3a) with the major influx during November and another less defined minor peak in winter (July).

A feature of the summer recruitment was the fast growth of the new generation and the progressive disappearance of the larger individuals. The new recruits were composed of discrete modal groups from November to December (over 90% of the population) which spread and became less obvious by April (approximately 33% of the population). The overwintering populations consisted of early summer, summer, autumn and early winter recruited shrimp in the larger pools

Table 1 Tidal pool volume, depth, cover and shrimp size for six sites in the Port Elizabeth area

	Pool volume (ℓ)			Pool depth (m)		Shrimp TL (mm)		Cover	
Site	Measure	Dye	Pumping	Mean	Max.	Mean	Max.	Algal	Substrate
McArthur	4 600 000	–		1,59	2,6	24,13	52	*Enteromorpha*	sand/concrete/rock
Willows	1 027 300	–		0,85	1,85	19,38	48	*Ulva/Arthrocardia*	sand/concrete/rock
Noordhoek	25 000	23 077		0,456	1,08	15,06	38	*Arthrocardia*	sand/rock
Beachview	11 704	12 800	14 457	0,422	1,1	20,94	48	*Enteromorpha*	sand/rock
Pollock	5 774	6 000	4 575	0,71	1,15	16,29	60	*Sargassum*	sand/rock
Minhetti	320	300	300	0,10	0,30	12,80	36	*Arthrocardia*	rock

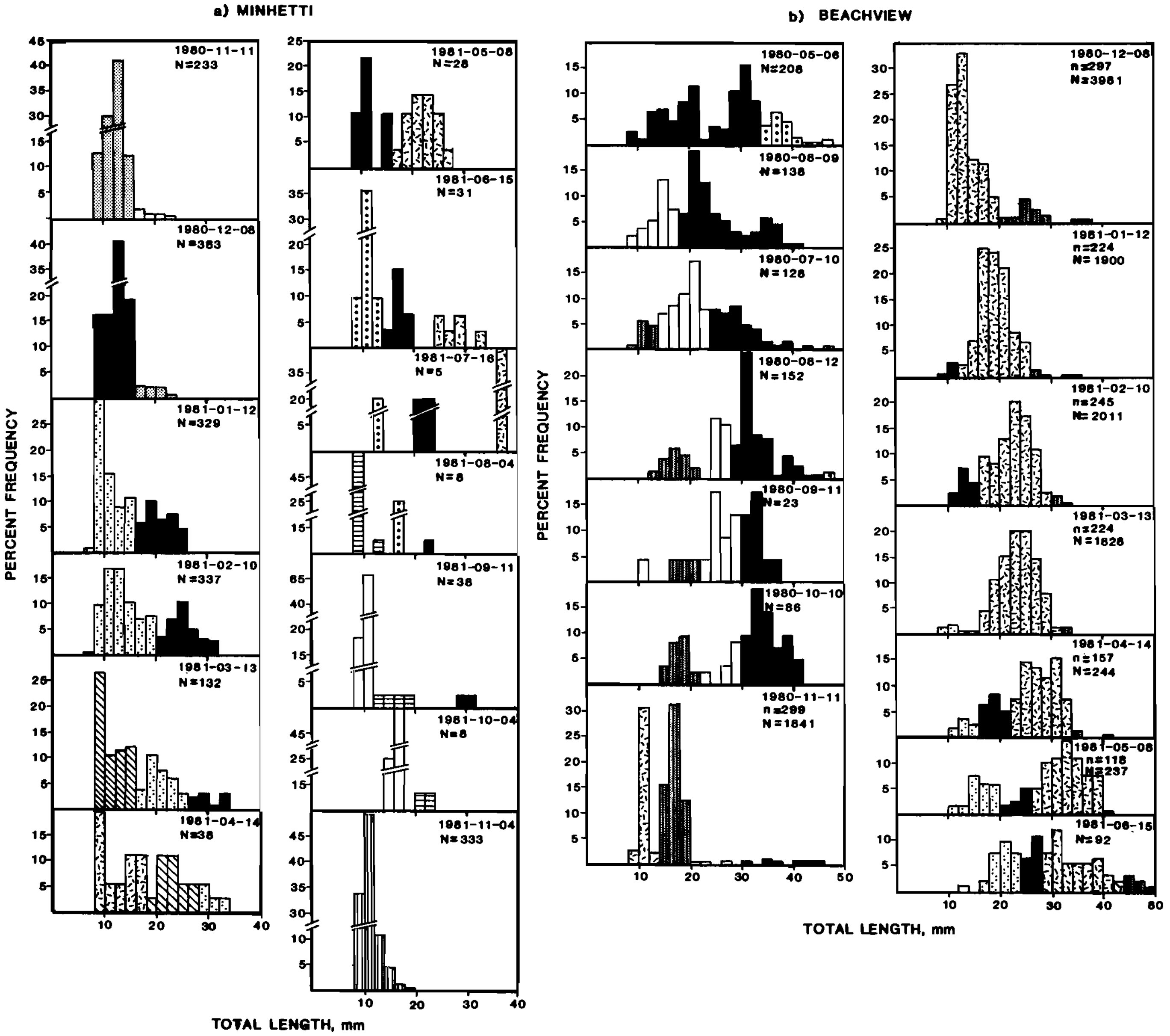

Figure 3a & b Representative size frequency distributions (as % of sample size *n*) of (a) Minhetti and (b) Beachview tidal pools.

such as McArthur and Beachview, but in the small pools such as Minhetti the population was composed of only autumn and early winter recruits. Egg-bearing females were found only in McArthur and Pollock (Figures 2a and f) as part of the overwintering population which extended through to January in McArthur. Mean sizes of juveniles (< 18 mm), males and females were plotted to show changes in population structure with season. Examples of a small, medium and a large pool are shown in Figures 4a, b and c.

The following trends were observed in all the pools. The lowest average total length for males and females occurred between November and January owing to the postlarval shrimp invasion of the pools. Females had a greater average size range than males. The average male and female size range especially for females increased from November through to June/July, after which the average size and range decreased as the larger shrimp left their nursery pools. In Noordhoek the peak was earlier (March) while in Beachview the peak was only reached during November in 1980 (Figure 4b). Within pools there was little difference between average male and female total length despite a considerably larger female size range. Mean juvenile TL declined with fresh postlarval recruitment during June/July and November/December in Noordhoek and Beachview (medium pools) but was almost continuous in Minhetti and Pollock (smaller pools) with a consistently lower mean juvenile TL.

The mean total length of *P. pacificus* was significantly correlated to the average and maximum pool depth and to log volume (Table 2; Figure 5). Maximum total length was not, however, correlated to maximum and average depth nor to log volume ($p > 0,05$). Pool size, therefore, is clearly an important factor influencing average shrimp size.

Sex ratio

The tidal pool *P. pacificus* populations showed a temporal variation in sex ratio with the lowest percentage of males present around November and the highest percentage between May and July (Figures 6a, b and c). The overall ratios of males:females were 1:1,66 in McArthur, 1:1,8 in Willows, 1:1,79 in Noordhoek, 1:1,88 in Beachview, 1:2,59 in Minhetti and 1:2,96 in Pollock. There was a tendency towards a higher male:female ratio in the smaller pools, but the best correlation ($r = 0{,}745$; $t = 2{,}23$) showed no significance from zero ($p = 0{,}09$). Generally there were more females present than

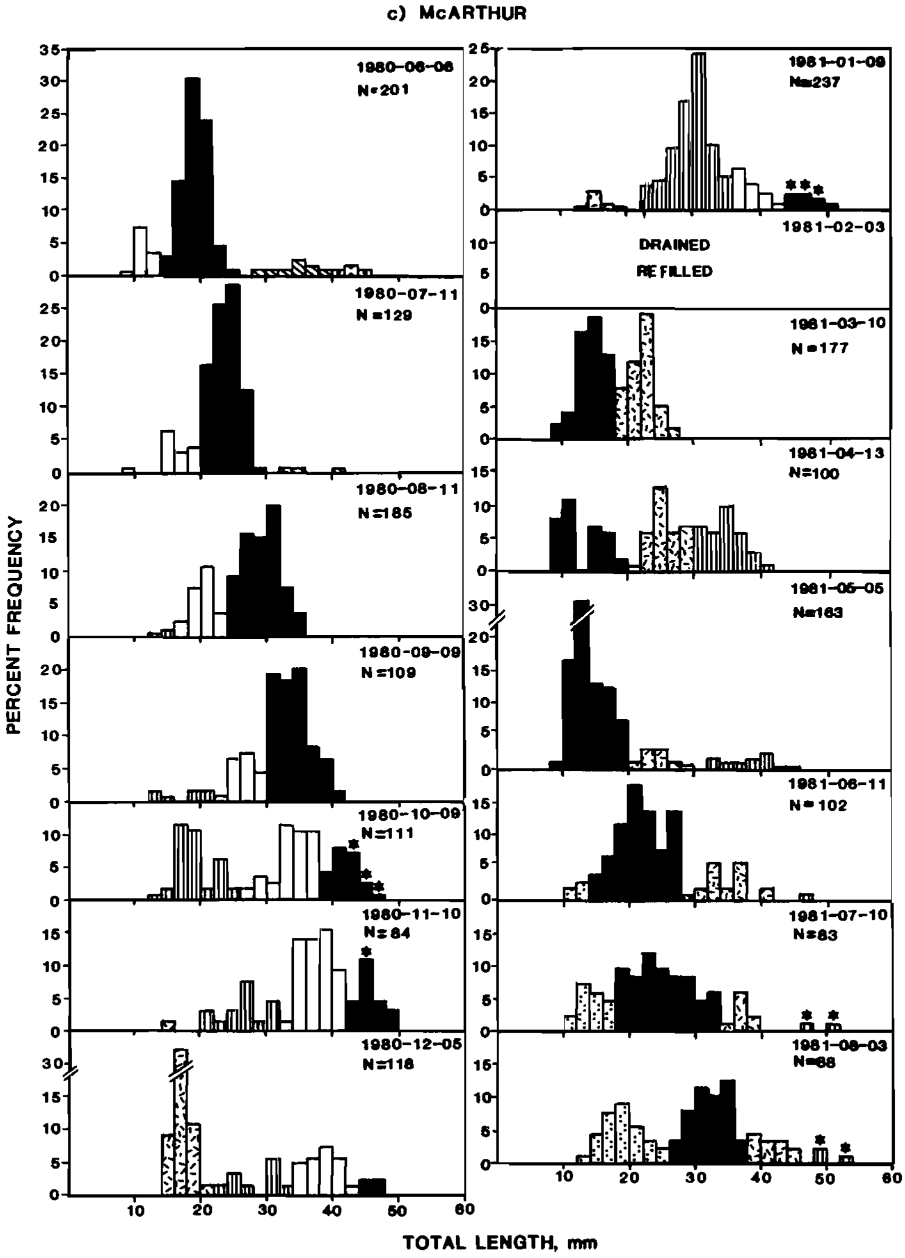

Figure 3c Representative size frequency distributions (as % of sample size *n*) of McArthur tidal pool; ★ represents size class females carrying eggs.

Table 2 The relationship of pool depth and volume on shrimp size. S, significant at 95%; NS, not significant

Comparisons	Best fit	*r*	*n*	*t*	Significance
av. TL *vs.* max. depth	linear	0,869	6	3,512	S
av. TL *vs.* av. depth	power	0,815	6	2,811	S
max. TL *vs.* max. depth	power	0,651	6	1,715	NS
max. TL *vs.* av. depth	power	0,735	6	2,167	NS
max. TL *vs.* log volume	power	0,463	6	1,046	NS
av. TL *vs.* log volume	power	0,822	6	2,881	S

males, especially in Pollock where the ratio was nearly 1:3.

Size at maturity

The smallest males which produced spermatophores from their gonopores were 25 mm in total length, while the smallest female bearing eggs was 41 mm TL (from Pollock).

Growth and residence time

The growth of the various tidal pool populations of *P. pacificus* was obtained from the analysis of cohorts, mainly by following the progression of the summer (November to January) cohorts through winter to spring, as given in Figures 3a, b and c. Examples of recruitment and growth in a small pool (Minhetti), medium pool (Beachview) and a large pool (McArthur) are shown in Figures 7a, b and c. The average number of cohorts per year was found to be negatively correlated to average and maximum pool depth as well as to log volume (Table 3; Figure 8). In the smaller pools such as Minhetti there was continual recruitment of the 8 – 10 mm size class yielding an average of 8,5 cohorts per annum, whereas in large pools such as McArthur, the average cohort recruitment was 4,5 per annum. Pool size was thus an important factor influencing juvenile recruitment. In smaller pool populations a truncation of cohorts was found to exist with the shrimp disappearing above 20 – 30 mm TL, indicating a rapid turnover. As shrimp size was shown to increase concomitantly with pool size (Table 2; Figure 5) so the shrimp

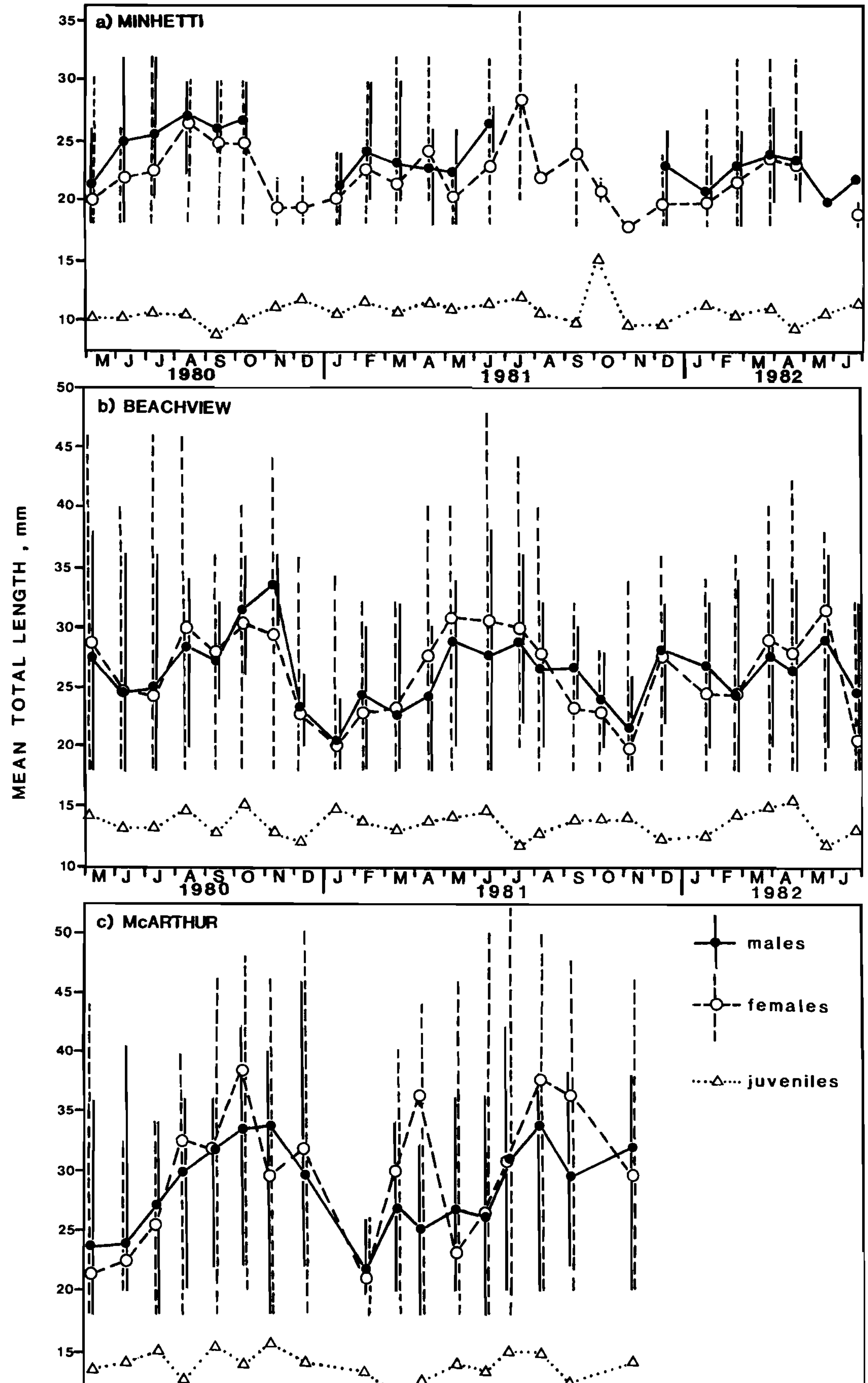

Figure 4 Mean total lengths of juvenile, male and female *Palaemon pacificus* from (a) Minhetti (b) Beachview and (c) McArthur tidal pools. Ranges are given.

residence time increased, even up to reproductive age in some of the deeper pools, namely McArthur and Pollock. Average residence time was found to be positively correlated to pool depth (average and maximum depth), but not to log volume

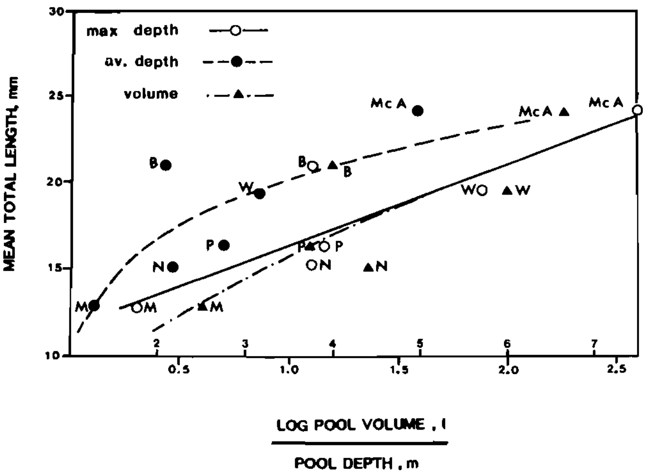

Figure 5 The relationship between pool size and the mean annual total length of *Palaemon pacificus*. B = Beachview, M = Minhetti, McA = McArthur, N = Noordhoek, P = Pollock, W = Willows.

(Table 4; Figure 9).

Mean summer growth rates were almost double those in winter with mean annual growth rates varying from 0,099 mm per day at Willows to 0,167 mm per day in Minhetti (Table 5). When monthly cohort growth for the pools was combined (Figure 10) for all seasons the calculated von Bertalanffy growth equation was found to be:

$$L_t = 64,51\ (1 - e^{-0,08902(t\ -\ 0,1001)})$$

where $L_\infty = 64,51$; $K = -0,08902$ and $t_0 = 0,1001$.

Production

Production appeared to be independent of pool size and varied from 0,22 (Noordhoek) to 2,0 (Beachview) g per m^2 per annum (Table 6). Mean annual standing biomass also varied from the relatively sparsely populated Noordhoek (0,06 g m^{-2}) to the well-populated Beachview (0,5 g m^{-2}).

Discussion

Life history

Egg-bearing females were found in Pollock and McArthur from June to October and July to December respectively while embryo-bearing females were found from August to October (Pollock) and during January (McArthur). Nearshore trawling in Algoa Bay during 1981 (Emmerson, unpublished data) showed embryo-bearing females to be present from August to November. Two batches of *P. pacificus* larvae were reared in the laboratory at 20 °C and took 25 – 27 days from zoea 1 to postlarva (Emmerson, in press). Thus if 3 – 4 weeks is added for larval development, then postlarvae and juveniles can be expected to appear on the shore from September to November/December and through to February. These times coincide closely with the observed main influx of postlarvae during November/December. Monthly plankton tows in McArthur pool for over a year from June 1980 to October 1981 revealed no *P. pacificus* larval stages (as described by Han & Hong 1978), yet all the larval stages have been collected inshore (unpublished data). It would therefore appear that the egg-bearing females moved from the tidal pools to the nearshore region just prior to larval release. Höglund (1943) similarly showed that there is an offshore winter migration of *Leander* (= *Palaemon*) *squilla* in Swedish waters. Egg-bearing females were only found in Pollock and McArthur, probably as the other four pools were too shallow or too exposed. Both *Polaemon serratus* and *P. squilla* also spawn in spring with the main postlarval influx occurring in summer (July to August) respectively (Forster 1951a,b). Recruitment of *Palaemonetes pugio* in South Carolina estuaries also occurs mainly in summer (July) (Alon & Stancyk 1982). As there is postlarval recruitment into the smaller pools e.g. Minhetti all year, it would indicate that there is spawning activity all year with the main peak in November. The growth rates calculated in Table 5 were generally higher than the published values for *P. pugio* of 0,085 to 0,09 mm day^{-1} (Sikora 1977; Alon & Stancyk 1982). Growth, especially in summer was rapid in Minhetti as this shallow pool heated up rapidly during the day, while there was adequate algal cover. Although Beachview was the warmest pool on average, growth was not high possibly due to its consistently high shrimp biomass (Table 6) and competition for food, with only little *Enteromorpha* sp. as cover. Berglund (1980) found that *Enteromorpha intestinalis* L. was the food item eaten most by the shrimp *Palaemon squilla*. Willows displayed the poorest growth (Table 5), probably as a function of very sparse cover. Salinities were never low enough to substantially affect growth, especially as the pools were flushed with fresh sea water during high tide.

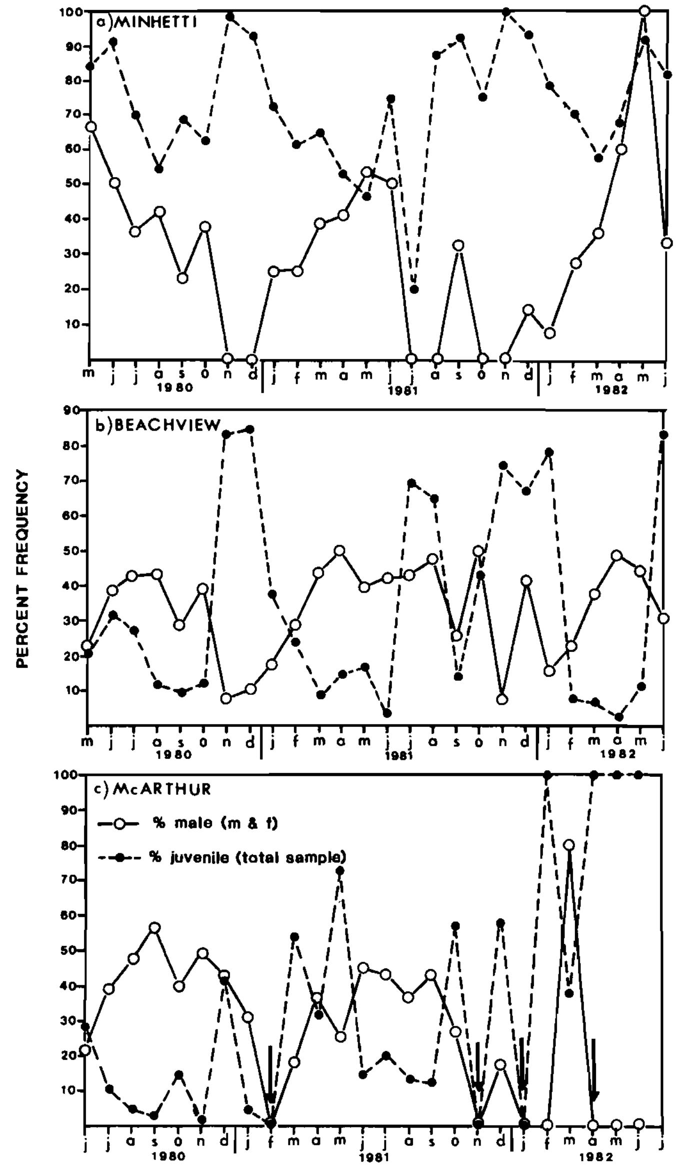

Figure 6 Seasonal variation in the sex composition of *Palaemon pacificus* from (a) Minhetti (b) Beachview and (c) McArthur tidal pools.

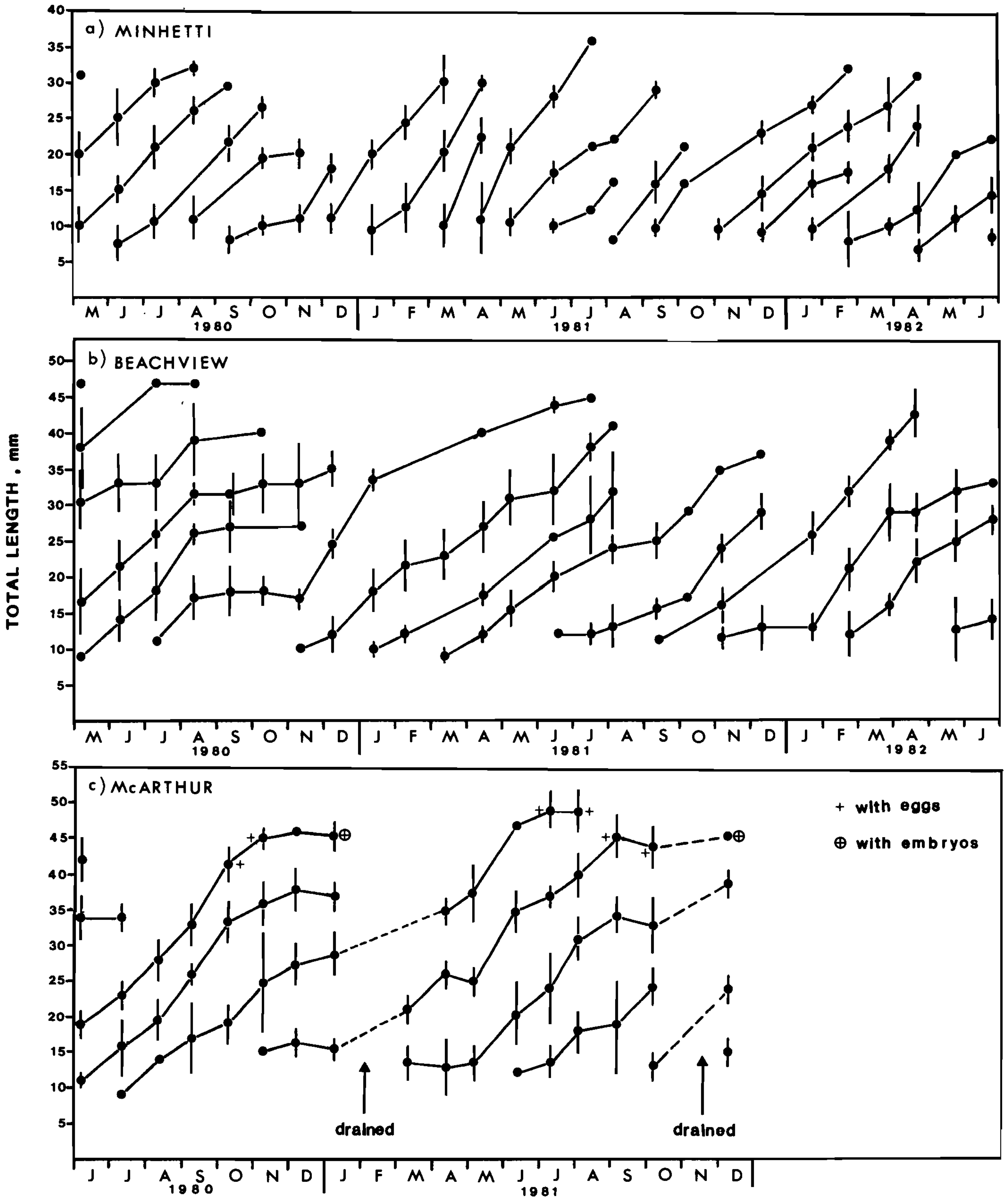

Figure 7 Progressive growth of *Palaemon pacificus* cohorts recruited into (a) Minhetti (b) Beachview and (c) McArthur tidal pools. 2 *S.D.*s are given.

Average shrimp TL was significantly correlated to pool depth and volume (Figure 5) showing that deeper water allowed the shrimp to grow bigger. Forster (1951a) also noted that larger *P. serratus* were found in deeper water than small shrimp. As *P. pacificus* were recruited as small postlarvae, they therefore initially preferred shallow pools, hence the negative correlation that was obtained between mean cohort number per year and pool size (Figure 8). These shrimp grew rapidly in the small pools so living space, cover and food became limiting and they would have to move out, hence the positive correlation between mean residence time and pool size (Figure 9). In larger pools there was stratification, with young shrimp in the shallows and moving progressively deeper with progressive growth and age. The shrimp were largest in winter, prior to moving out of the pools. It is uncertain why breeding females remained in McArthur for so long, but it could be that the sheer size of the system delayed the seaward movement of shrimp. Once *P. pacificus* move out of the tidal

Table 3 The relationship of pool size on shrimp recruitment. S, significant at 95%; S*, significant at 98%

Comparisons	Best fit	*r*	*n*	*t*	S
n cohorts *vs.* max. depth	log	0,9694	6	7,898	S*
n cohorts *vs.* av. depth	log	0,9125	6	4,461	S
n cohorts *vs.* log volume	power	0,9648	6	7,337	S*

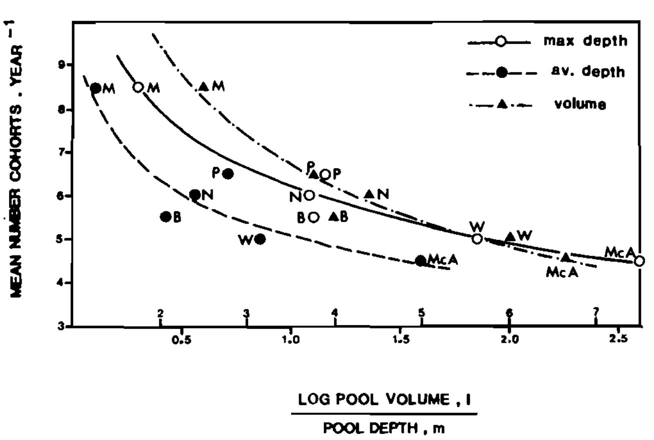

Figure 8 The relationship between pool size and the mean number of *Palaemon pacificus* cohorts recruited per annum. B = Beachview, M = Minhetti, McA = McArthur, N = Noordhoek, P = Pollock, W = Willows.

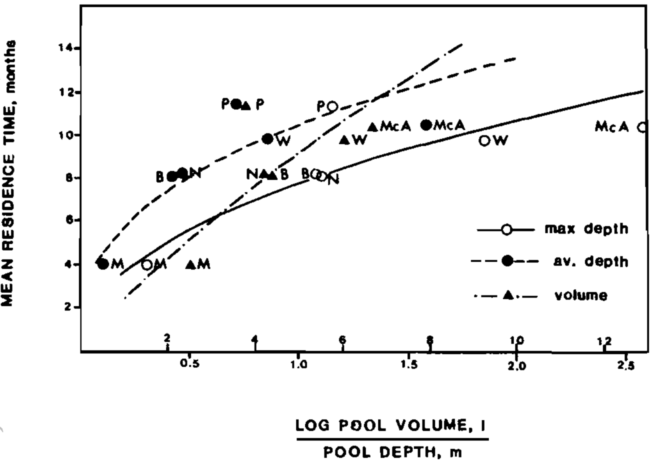

Figure 9 The relationship between pool size and the mean residence time of recruited *Palaemon pacificus*. B = Beachview, M = Minhetti, McA = McArthur, N = Noordhoek, P = Pollock, W = Willows.

Table 4 The relationship of pool depth and volume on shrimp residence time. S*, significant at 98%; S, significant at 95%; NS not significant

Comparisons	Best fit	*r*	*n*	*t*	S
av. residence time *vs.* max. depth	power	0,8983	6	4,089	S
av. residence time *vs.* av. depth	power	0,9322	6	5,151	S*
av. residence time *vs.* log volume	power	0,7661	6	2,384	NS

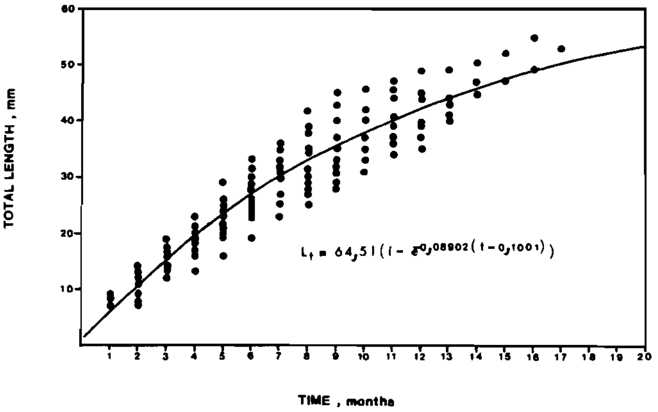

Figure 10 Combined summer and winter growth curve for tidal pool *Palaemon pacificus*. The von Bertalanffy equation is given.

Table 5 Summer, winter and mean annual growth rates of *P. pacificus* in six tidal pools

Site	Mean annual growth rate mm day⁻¹ Summer	Winter	Annual	Mean annual temp. °C
McArthur	0,146	0,100	0,122	18,50
Willows	0,140	0,081	0,099	18,78
Noordhoek	0,135	0,093	0,113	18,92
Beachview	0,150	0,085	0,119	20,24
Pollock	0,200	0,097	0,150	18,15
Minhetti	0,226	0,112	0,167	19,57
$\bar{x}$			0,128	19,03

Table 6 Mean annual somatic production, P, mean annual standing biomass (dry), B and P/B ratios of *P. pacificus* for six tidal pools. Surface areas were taken as the 'wetted' area calculated from the mean pool volumes given in Table 1

	Approx. pool substrate surface area, m²	Mean annual somatic production g pool⁻¹	g m⁻²	Mean annual standing biomass, B g pool⁻¹	g m⁻²	P/B ratio
McArthur	3 962,35	23,263	1,163	–	0,4934	2,357
Willows	1 168,05	11,750	0,587	–	0,2992	1,964
Noordhoek	72,58	16,257	0,224	4,528	0,0624	3,592
Beachview	33,13	67,328	2,032	16,673	0,5033	4,037
Pollock	20,46	8,615	0,421	2,387	0,1167	3,608
Minhetti	4,18	4,801	1,149	1,133	0,2711	4,238

pools into the open sea, they are more vulnerable to predation. Specimens have been identified from the guts of the linefish *Argyrosomus hololepidotus, Cheimerius nufar, Pomatomus saltatrix* and *Epinephalus gauza* (M. Smale, pers. comm.). Similarly *Crangon septemspinosa* forms an important dietary component for many fish species in Canadian waters (Corey 1981).

Hanekom (1982) resolved only 2 – 3 cohorts per annum in the Kromme estuary. This appears to be low, but if the curves in Figure 8 are extrapolated for 2 – 3 cohorts per annum in a large (depth and volume) section of the estuary, then it appears correct, indicating that the same constraints that affect shrimp cohort number in tidal pools probably apply to shrimp in other regimes such as estuaries.

Productive dynamics

Temporal changes in the sex ratio have been observed in other species of palaemonid shrimp such as *Palaemon squilla* (Forster 1951b) and *Palaemonetes pugio* (Sikora 1977; Alon & Stancyk 1982). Forster (1951a) also observed a 1:2 sex ratio for *Palaemon serratus*. Wildish (1977) noted that a female-biased sex ratio increases the reproductive potential of a species. Little difference was noted between average *P. pacificus* male and female total length. This contrasts with *Palaemonetes pugio* where Alon & Stancyk (1982) found a considerable difference in average size between males and females. The size of first maturity for *Palaemon pacificus*, 25 mm TL and 41 mm TL for males and females respectively, is about double that of *Palaemonetes pugio* which is 15 mm TL for males and 18 – 21 mm TL for females (Alon & Stancyk 1982).

From Figure 10, first maturity of *P. pacificus* from egg is reached after 6,2 and 12 months respectively for males and females (3,5 weeks for egg carriage, 3,5 weeks for larval development plus 4,5 and 10,3 months postlarval development). Breeding females were found after a year in McArthur (Figure 7c) and Pollock. *Palaemonetes pugio*, by contrast, reached maturity much earlier in 3,5 – 4,8 months (Alon & Stancyk 1982). *Palaemon serratus* males in British waters reached maturity at 42 mm TL (6 – 7 months) and females around 50 mm TL (Forster 1951a), but this appeared to be age from recruitment.

Size at first maturity is obviously dependent on maximum size (L_∞), ambient conditions and growth rates, and will thus be shorter for a small shrimp like *Palaemonetes pugio* and larger for a larger shrimp such as *Palaemon serratus* which reaches 100 mm TL (Forster 1951a). The calculated L_∞ of 64,51 mm TL is very close to the observed largest *P. pacificus* caught which measured 66,0 mm TL (Barnard 1950). From the growth equation (Figure 10) this is equivalent to a 3,3-year-old animal. The chances of surviving for this length of time are probably quite small, so the main contribution to breeding would come from the one-year-old overwintering population of breeding females that have moved into the nearshore region from tidal pools and estuaries (Emmerson 1983). Hanekom (1982) working on a population of *P. pacificus* from the Kromme estuary obtained the following growth equation:

$$L_t = 37{,}6954\ (1 - e^{-0{,}1011\ (t\ -\ 1{,}1389)}).$$

His L_∞ was low, probably as the largest shrimp encountered in the estuary was only 36 mm TL.

Production

Beachview had the highest somatic production, due probably to the high standing biomass (Table 6) of medium-sized animals (Table 1) contributing to growth. Minhetti, by contrast, had only half the standing biomass of Beachview (Table 6) yielding just over half the somatic production of Beachview due to a much smaller average shrimp size (Table 1), yet nevertheless displayed the highest P/B ratio of 4,2. Noordhoek displayed the lowest production of only 2,2 g m^{-2} year^{-1} reflecting the pool's general paucity in food, with only patches of *Arthrocardia* sp. as cover (Table 1).

The P/B ratios of the two artificial pools, McArthur and Willows, were low as a result of the relatively high mean annual standing biomass. These values should have been lower yielding higher P/B ratios as the method of sampling had an effect. Most shrimp were found on the sides of the pool, which were sampled and not the bottom, whereas the calculations took the entire 'wetted' pool surface area into consideration.

Hanekom (1982) obtained a somatic production value of 8,48 g m^{-2} year^{-1}, a mean annual standing biomass of 2,76 g m^{-2} and a P/B ratio of 3,07 for *P. pacificus* in the Kromme estuary, while Emmerson (unpublished data) measured a mean annual production value of 12,2 g m^{-2}, a mean standing biomass of 2,16 g m^{-2} and a mean P/B of 5,6 for *P. pacificus* in the Swartkops estuary. The high P values obtained in estuaries were due to sampling in rich *Zostera capensis* weed beds which differ markedly in structure to the comparatively bare rock pools. The calculated P/B ratios were nevertheless similar to the tidal pool values calculated in Table 6.

Redant (1980) and Kuipers & Dapper (1981) also obtained high P/B values for *Crangon crangon* (6,0 and 7,7 to 9,3 respectively) obtained from open tidal flat systems (Belgian coast and Dutch Wadden Sea respectively).

P. pacificus occupies the same niches as *P. squilla* in Sweden i.e. *Zostera* and rock pools. Berglund (1980) classified *P. squilla* as an r-strategist and it would appear that *P. pacificus* is the same owing to its ability to survive in many different habitats, its high dispersal ability, mobility and its small size. Thomson & Lehner (1976) similarly found that rocky intertidal fish are also dominated by r-selected fish species. To conclude, it may be stated that *P. pacificus* is both an abundant and an important macrofaunal component in temperate Cape waters, particularly in sheltered estuaries and tidal pools. If it is considered that the Cape coastline encompasses 167 river mouths and estuaries, and is 2 200 km long (Heydorn & Tinley 1980) of which a considerable portion is rocky shore, then the biomass and production of *P. pacificus* may be seen in perspective.

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