

Tidal exchange of two decapod larvae *Palaemon pacificus* (Caridea) and *Upogebia africana* (Thalassinidae) between the Swartkops River estuary and adjacent coastal waters

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Two 24-h plankton and seine-netting studies were carried out in the Swartkops estuary mouth, one during a spring-tide, the other on a neap-tide in order to determine larval movements of the prawns *Palaemon pacificus* and *Upogebia africana* in and out of the estuary. Two size classes of the former were caught, namely zoea 6 and adults. No zoeae 1, 2, 3, 4 or 5, post-larvae or juveniles were caught. Zoea 1 of *U. africana* are flushed out of the estuary into Algoa Bay on the nocturnal ebb-tide with very few returning on the subsequent flood-tide. Net fluxes were 97,1% and 99,9%. Larval life is then spent at sea after which the pre-postlarvae invade the estuary to reach the estuarine nursery areas. For *P. pacificus* this was during zoea 6, mainly on the nocturnal flood-tides. Net fluxes of *P. pacificus* zoea 6 were 95,8% and 100%. Most larval movement occurred at peak velocities as they utilize the tidal currents in dispersion and recruitment. Some *P. pacificus* zoea 6 are washed out again on ebb-tides, but lateral movement to the banks during slack-tide appears to be a mechanism to prevent this occurring. *P. pacificus* adult movement in the mouth region was better correlated with nocturnal activity than with tidal movements. *S. Afr. J. Zool.* 1983, 18: 326 – 330

Twee 24-h plankton- en treknetopnames is gemaak in die Swartkops getyrviermond waarvan een gedurende 'n springgety en 'n tweede gedurende 'n dooiegety uitgevoer is om die larwale bewegings van die garnale, *Palaemon pacificus* en *Upogebia africana* in en uit die getyrvier vas te stel. Twee klasgroottes van *P. pacificus* is gevang, naamlik zoea 6 en volwassenes. Geen zoeae 1, 2, 3, 4 of 5, post-larwale of onvolwassenes is gevang nie. Zoea 1 van *U. africana* word uitgespoel uit die getyrvier in Algoabaai gedurende die nagtelike dooiegety. Baie min keer terug met die daaropvolgende vloedgety. Totale uitspoelings was 97,1% en 99,9% vir die twee opnames. Larwale stadia vind in die see plaas waarna die vroeë post-larwale stadium die getyrvier binnedring om die voorkeurvoedingsgebied in die getyrvier te bereik. In die geval van *P. pacificus* was dit tydens die zoea 6-stadium, hoofsaaklik gedurende die nagtelike vloedgetye. Totale invloei van *P. pacificus* zoea 6 was 95,8% en 100% vir die twee opnames. Die grootste larwale beweging het in hoogste snelhede voorgekom wanneer getystrome benut is vir verspreiding en vestiging. Sommige zoea 6 van *P. pacificus* is weer gedurende dooiegetye uitgespoel, maar dit blyk dat laterale beweging na die oewers gedurende laaggety dit teëwerk. Volwasse *P. pacificus* beweging in die mondgebied was beter gekorreleer met nagtelike aktiwiteit as met getybeweging. *S.-Afr. Tydskr. Dierk.* 1983, 18: 326 – 330

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The caridean shrimp *Palaemon pacificus* (Stimpson) is extremely abundant in temperate East Cape waters, especially during summer when numbers can reach over 1 000 m⁻² both in tidal pools and in estuarine *Zostera capensis* beds, (Hanekom 1982; pers. obs.). Post-larvae appear in the *Zostera* beds and tidal pools mainly between November and January where they grow utilizing these sheltered nursery areas. Despite extensive sampling over two years in three East Cape estuaries, namely the Sundays, Swartkops and Krom, no gravid females were found in the estuarine *Zostera* beds, yet the research vessel 'T.B. Davie' cruises yielded large gravid females offshore (pers. obs.). These findings suggest that *P. pacificus* spawns and undergoes larval development offshore before the post-larvae immigrate back into estuaries and tidal pools. By contrast, the mudprawn *Upogebia africana* (Ortmann), which is extremely abundant in Cape estuaries (Hill 1967; Hanekom 1980), has a main breeding peak in spring. Little is known of its larvae and their fate, while the larval stages themselves have yet to be described.

Hughes (1972), Sandifer (1975), Cronin & Forward (1979), Staples (1980a & b) and Johnson & Gonor (1982) have all shown that there is a considerable onshore/offshore movement of both adult and larval Decapoda in relation to spawning and juvenile recruitment. Most of these studies have been confined to daylight hours (Sandifer 1975; Johnson & Gonor 1982). Two 24-h sampling studies in the mouth of the Swartkops River estuary were thus planned over a spring and a neap-tide with opposite tidal regimes to observe whether there was any exchange of larval *P. pacificus* or *U. africana* between the estuary and the sea and if so, to quantify this in terms of the net flux of prawns.

The first sampling period was from 12h00 on 28 October 1980 through to 12h00 on the following day (Series 1) and the second sampling period was run from 12h00 on 8 October 1981 through to 12h00 on the next day (Series 2). October was chosen as it is the beginning of the breeding season for both *P. pacificus* and *U. africana*.

Materials and Methods

A station was established in mid-channel in the Swartkops mouth by securing a buoy to a heavily weighted anchorage. Surface and bottom temperatures, salinities and current measurements were taken every 1½ h from a boat by means of a thermometer, AO refractometer and calibrated current meter (OGAWA SEIKI model OSK 861) respectively. Bottom water samples were obtained by using a heavily weighted sampler.

Biological samples were also taken every 1½ h. Surface and

bottom plankton samples were obtained using two 57-cm WP2 nets each fitted with 190- μ m mesh netting and a calibrated KAHLSICO model 005-WA 130 flowmeter. One net was used just below the water surface, while the other was fitted with a 3-m pole to allow it to be held just above the bottom of the channel bed. Plankton tows were carried out as described by Melville-Smith & Baird (1980) in midstream against the current flow, and lasted no longer than approximately 1 min under conditions of strong flow, to avoid the accumulation of suspended sand in the bottom net.

Seine-net samples were taken to monitor adult movements using a 2,5 m \times 15 m net with 2,8-mm stretched mesh which was laid by boat from the channel edge and pulled in by hand to sample an area of approximately 80 m² or a volume of approximately 160 m³. One unit of effort was taken to be the number of prawns caught by this 37,5-m² net per haul (CPUE). All samples were preserved in 10% formalin. Prawns were counted and staged in the laboratory according to the larval descriptions given by Han & Hong (1978). Total lengths (TL) of adults were taken from the rostrum tip to the telson tip.

Estimates of flux were made from the plankton data according to the methods of Boon (1978) and Kjerve & McKeller (1980), as modified by Johnson & Gonor (1982).

The cross-sectional areas for each sampling interval were computed from a programme using tidal height data from Port Elizabeth harbour.

As the larval stages of *U. africana* have not been described, it was decided to hatch zoea from berried females for comparative purposes. Ripe females carrying eggs with eye-spots were collected from the Swartkops mud-flats, transported to the laboratory and left overnight in glass aquaria containing aerated seawater at approximately 24 °C. The following morning, hatched zoea 1 were removed with a teat pipette and preserved in 10% formalin.

Results

Hydrography

The tides affecting the Swartkops estuary are semidiurnal with

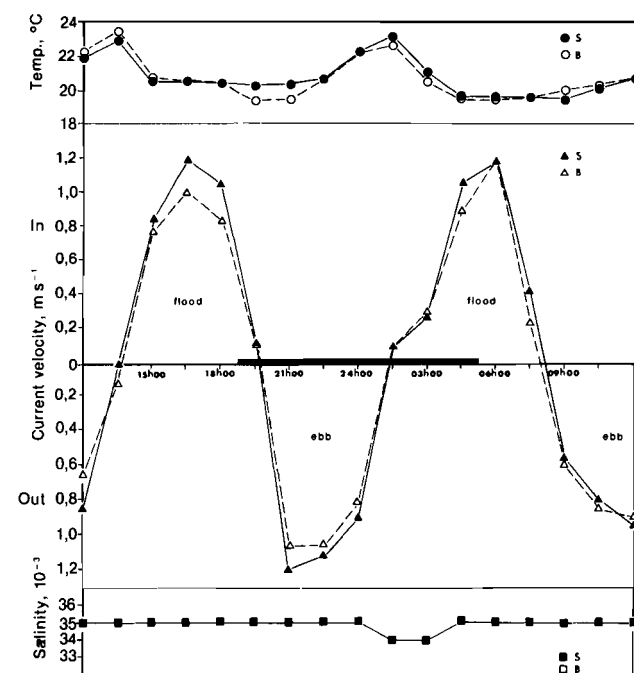


Figure 1 Surface (S) and bottom (B) current velocity, temperature and salinity in the Swartkops mouth during the first 24-h study (spring-tide, Series 1). The black bar represents darkness.

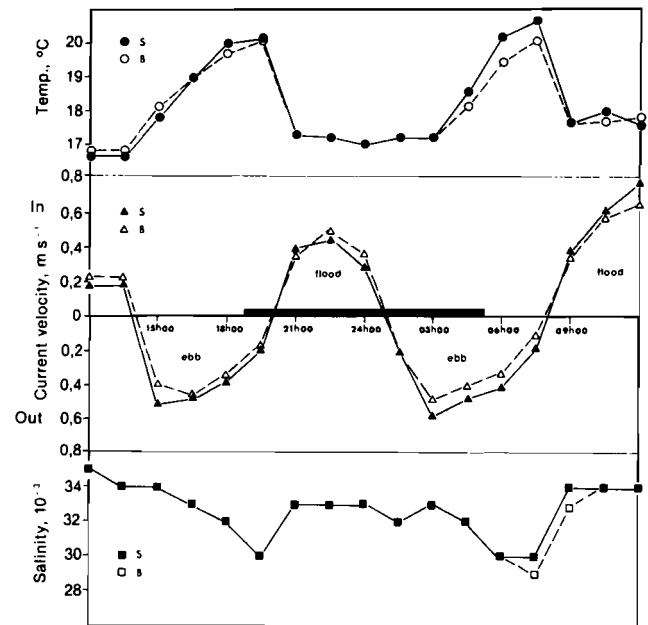


Figure 2 Surface (S) and bottom (B) current velocity, temperature and salinity in the Swartkops mouth during the second 24-h study (neap-tide, Series 2).

two ebb and two flood-tides per day. Figures 1 and 2 show the surface and bottom current velocity, temperature and salinity for the first and second 24-h series respectively. Peak current velocities in the first series (spring-tide; Figure 1) were double those of the second series (neap-tide; Figure 2) as the tidal prism was larger in Series 1. Surface velocities were generally slightly greater than bottom velocities due to bed friction. Estuarine water was 3–4 °C warmer than the sea with the temperature gradually increasing on the ebb-tide and then cooling rapidly as new seawater flowed in with the flood-tide. Little difference was noted between surface and bottom temperature and salinities due to turbulent mixing in the mouth.

Prawn distribution

Upogebia africana zoea 1 hatched in the laboratory were found to be identical to the thalassinid zoea 1 larvae present in the plankton samples. Figure 3 shows the abundance of *U. africana* zoea 1 in the plankton for Series 1 and 2 respectively. In both series there was a pronounced occurrence of zoea 1 during the nocturnal ebb-tide (up to approximately $2 \times 10^3 \text{ m}^{-3}$) with a smaller peak during the daylight ebb in Series 2 (Figure 3). Very few were recorded on the following flood-tides. During Series 1, there tended to be more larvae in bottom waters, but more in surface waters during Series 2 (Figure 3). Late stage thalassinid larvae resembling *U. africana* were collected during the nocturnal flood-tide. No intermediate larval stages between zoea 1 and these late stage larvae were found.

Two distinct groups of *P. pacificus* were caught, namely zoea 6 and adults. No zoeae 1, 2, 3, 4 or 5, post-larvae or juveniles were caught. The adults averaged between 26,6–28,9 mm TL.

Sixth-stage zoeae of *P. pacificus* were observed to move into the estuary with the early to mid-flood tide (Figure 4). In Series 1, more zoea 6 were collected during the nocturnal flood-tide but this was not apparent during Series 2 (Figure 4). Generally more zoea 6 were found in surface waters.

In the plankton samples, adults were only collected during the nocturnal ebb-tide while no adults were caught during the

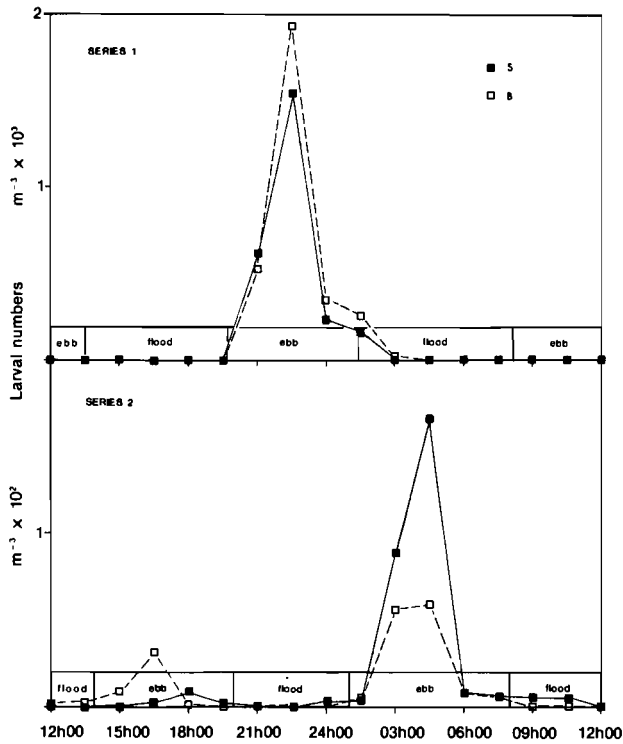


Figure 3 Changes in the numbers of *Upogebia africana* zoea 1 over two 24-h periods (Series 1 and Series 2) in the Swartkops estuary mouth.

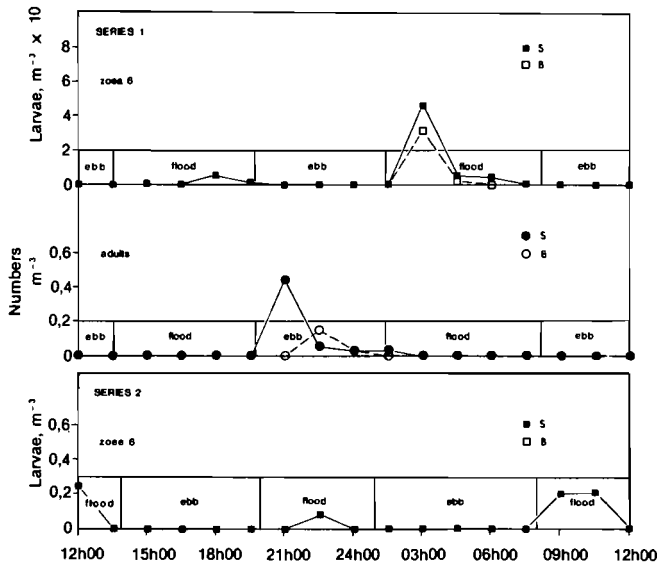


Figure 4 Changes in the numbers of *Palaemon pacificus* zoea 6 and adults in the plankton over two 24-h periods (Series 1 and Series 2) in the Swartkops estuary mouth.

day (Series 1) or at all during Series 2 (Figure 4).

The prawn flux for both species can be seen in Table 1. For both series there was a net efflux of *U. africana* zoea 1 with a net efflux of 500 661 per day during Series 1 and a net efflux of 16 096 per day during Series 2, representing a 99,9% and 97,1% seaward movement respectively. Conversely, the net flux of *P. pacificus* zoea 6 was into the estuary with 4 303 entering during Series 1 and 28 during Series 2 (95,8% and 100% respectively). There was a small efflux of *P. pacificus* adults out of the estuary during Series 1, while no adults were recorded entering the estuary. No adults were sampled in the plankton during Series 2.

Zoae 1 of *U. africana* and zoeae 6 of *P. pacificus* were

Table 1 The flux of larval *U. africana* and *P. pacificus* through the Swartkops estuary mouth during a spring-tide (1st Series) and a neap-tide (2nd Series). Net = net flux per day

		<i>U. africana</i>		<i>P. pacificus</i>			
		<i>Zoea 1</i>		<i>Zoea 6</i>		<i>Adults</i>	
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
1st Series	In	679	0,14	4 499	95,83	0	0
	Out	501 340	99,86	196	4,17	76	100
	Net	500 661		4 303		76	
				(In)		(Out)	
2nd Series	In	499	2,92	28	100	Nil	—
	Out	16 595	97,08	0	0	—	—
	Net	16 096		28		Nil	—
				(In)			

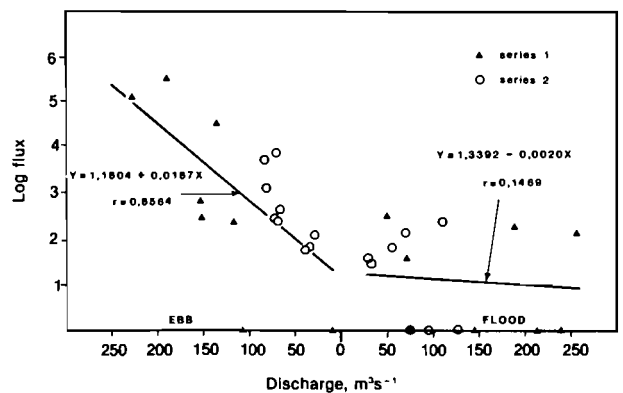


Figure 5 The correlation between log of larval flux for *Upogebia africana* zoea 1 and the average discharge per sample interval at the Swartkops estuary mouth. Data from Series 1 and Series 2 were pooled, while ebb and flood data were regressed separately.

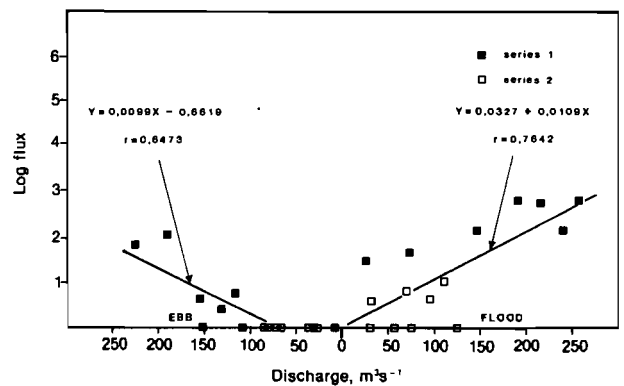


Figure 6 The correlation between log of larval flux for *Palaemon pacificus* zoea 6 and the average discharge per sample interval at the Swartkops estuary mouth. Data from Series 1 and Series 2 were pooled, while ebb and flood data were regressed separately.

both shown to utilize tidal currents to move out of and into the Swartkops estuary respectively. Peak larval movement was closely associated with tidal velocity and discharge (Figures 5 & 6). *U. africana* larvae utilized the ebb discharge (Figure 5; $r = 0,66$; $p < 0,005$) for dispersal, while there was no significant correlation between flux and discharge during flood-tides (Figure 5; $r = 0,15$; $p < 0,1$). *P. pacificus* zoea 6 also exhibited a significant utilization of flood-tides for recruitment

into the estuary (Figure 6; $r = 0,76$; $p < 0,001$), while some larvae were found to be flushed out during ebb-tide (Figure 6; $r = 0,85$; $p < 0,001$).

The seine-net results for the two series can be seen in Figure 7. The mesh was small enough to retain *P. pacificus* zoea 6 and adults. Peak zoea 6 numbers were similarly obtained during the flood-tides especially the nocturnal ones, but in addition, substantial numbers of zoea 6 were also netted during slack-tide (Figure 7). This was not found for the plankton samples which were taken in mid-stream (Figure 4). Peak numbers of adults were also seine-netted during the nocturnal slack-tide (Figure 7) while no adults were caught during the day. Similarly on the neap-tide the few adults which were netted were captured during the night only (Figure 7).

An analysis of the seine-net catches can be seen in Table 2. There was a net inflow of *P. pacificus* zoea 6, especially during spring-tide (80,3%), while with the adults the movement in and out of the estuary was roughly equal and was more closely associated with darkness than with the tides.

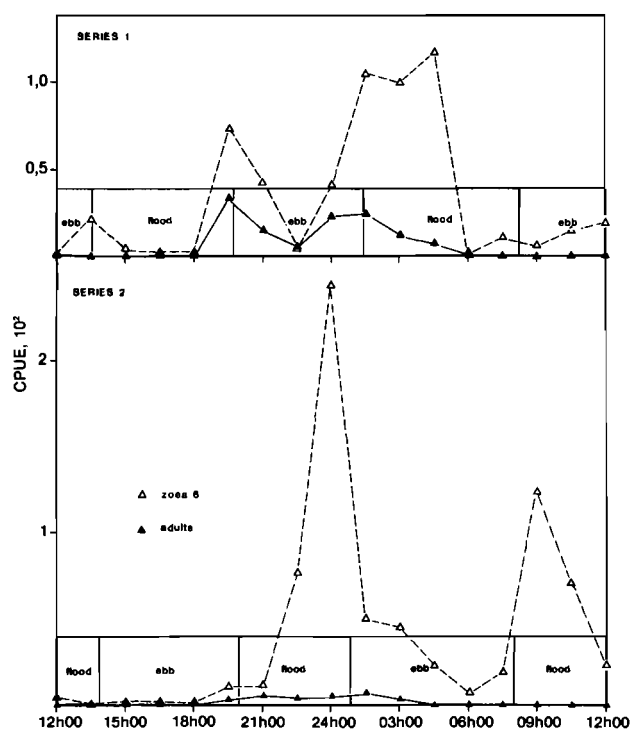


Figure 7 Catch per unit effort of *Palaemon pacificus* zoea 6 and adults by seine-net over two 24-h periods (Series 1 and Series 2) in the Swartkops estuary mouth.

Table 2 An analysis of *P. pacificus* movement through the Swartkops mouth during a spring-tide (1st Series) and a neap-tide (2nd Series) using a seine-net

		Zoea 6		Adults	
		n	%	n	%
1st Series	In	315	67,3	52	54,2
	Out	153	32,7	44	45,8
	Net	162 (In)	—	8 (In)	—
2nd Series	In	549	80,3	12	50
	Out	135	19,7	12	50
	Net	414 (In)	—	0	—

Discussion

Because (i) large breeding *P. pacificus* adults have been trawled in Algoa Bay ('T.B. Davie' cruises), (ii) larval stages are common in inshore plankton samples (Wooldridge & Beckley pers. comm.), and (iii) a continuous size range of this prawn from zoea 6 and post-larvae through to sub-adults can always be found in estuarine *Zostera* beds (pers. obs.), the following life history is proposed. *P. pacificus* spawns offshore where the larvae develop. Post-larvae then move into the estuaries, especially areas of *Zostera* and tidal pools, and later migrate out as pre-adults to develop offshore, spawn and so complete the reproductive cycle. This is the classical life history also displayed by penaeids (Champion 1970; Gopalakrishnan 1976; Kurata 1981). No early zoeal stages of *P. pacificus* were found in any of the plankton samples, while there was adult movement in the mouth region (Tables 1 & 2) and zoeal recruitment into the estuary from the sea. The life history of *P. pacificus* is thus similar to that of penaeids, with the only modification being that the young prawns invade the estuary during zoea 6 and not as post-larvae.

Results from this study showed that a very high percentage (97,1% and 99,9%) of *U. africana* zoea 1 are discharged out of the estuary mainly on the nocturnal ebb-tide with very few found returning on the incoming tide (Tables 1 & 2; Figure 5). Drift card analysis (Baird pers. comm.) has shown the presence of a northward-flowing, inshore current during most months of the year in Algoa Bay so that the larvae emerging from the estuary would be carried away by this longshore current and would not be re-introduced into the estuary on the succeeding flood-tide. An identical occurrence has been reported by Johnson & Gonor (1982) for *Callinassa californiensis* zoeae 1 although these authors may have missed most of the larval flux as they did not sample nocturnally. *U. africana* zoeae 1 are thus dispersed into nearshore marine waters to undergo larval development before invading estuaries on the flood-tides during the late larval stages. Although positive identification of the thalassinid late larval stages in the plankton is required, these larvae are probably *U. africana* as the only other thalassinid in the Swartkops estuary, *Callinassa kraussi*, has a short non-planktonic larval stage (Forbes 1973).

P. pacificus zoeae 6 displayed a tidal periodicity of immigration with larval flux significantly correlated with the flood-tide. Although ebb discharge was also correlated with larval flux, zoea 6 numbers were low, yielding influx retentions of between 95,8 – 100% (Figure 6). Staples (1980a) did several 24-h studies at the mouth of the Norman River in the Gulf of Carpentaria, Australia, and found an identical immigration pattern for the post-larvae of the prawn *Penaeus merguensis*. He found that approximately 96% of these post-larvae were recruited during the flood-tide.

Apart from the nocturnal flood-tide peak in numbers of zoea 6, smaller peaks were found during slack-tide when the seine-net was used near the channel edge (Figure 7). As similar minor peaks were not found in the plankton samples (Figure 4) from mid-channel it is suggested that the zoea 6 move laterally to the edges during slack-tide to avoid being flushed out as the tide ebbs. Wooldridge & Erasmus (1980) showed that a number of species of estuarine zooplankton utilized lateral migration as a means of maintaining position in the Sundays estuary. Staples (1980a) also found that incoming post-larvae settle out in the shallow water along the river banks. *Palaemon pacificus* has also been seen moving into shallow marginal waters in creeks during the slack-tide to invade the exposed *Zostera* beds with the ensuing flood tide (own observations).

With regard to adult emigration, Staples (1980b) has shown that *Penaeus merguensis* emigrates during the wet season and that this is directly related to river flow. If this holds true for *Palaemon pacificus* as well then it would explain the small tidal exchange of adults in the Swartkops mouth during Series 1 and Series 2 (October) when river flow was very low.

It may be concluded that *P. pacificus* and *U. africana* utilize tidal currents for either dispersing early larval stages or recruiting late larval stages respectively. The efficiency with which this is done at the Swartkops mouth is very high with larval fluxes in the plankton varying from 95,8% to 100% for *P. pacificus* and 97,1% and 99,9% for *U. africana*.

Several species of penaeid prawn have also been found to be transported into estuaries on the flood tide (Wickins 1976; Staples 1980a). A number of hypotheses concerning the mechanisms used by immigrating larvae have been forwarded from passive (Racek 1959) and active (Hughes 1969) mechanisms to vertical diurnal larval movement to maintain position offshore (Penn 1975; Sandifer 1975) and to changes in salinity and water-type preference (Hughes 1972; Keiser 1975; Mair 1980; Spaargaren 1980). The small observed changes in salinity and temperature during the tidal cycles (Figures 1 & 2) may thus be significant but experimental confirmation is required.

Barber & Lee (1975) and Staples (1980a) suggest that it is probably a combination of passive and active transport which is responsible for the overall transport of larvae into an estuary. *P. pacificus* zoea 6 could actively congregate at the mouth before the flood tide, be washed in passively utilizing the flood-tide and then actively swim for the edge at slack-tide to ensure a good larval retention.

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