

Tidal exchange of larvae of *Sesarma catenata* (Decapoda, Brachyura) in the Swartkops estuary, South Africa

R. Pereyra Lago

Department of Zoology, University of Transkei, Private Bag X1 (UNITRA), Umtata, Transkei

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The tidal exchange of larvae of the salt-marsh grapsid crab *Sesarma catenata* was studied in the Swartkops estuary, a tidally driven, shallow estuary in Algoa Bay, South Africa. Plankton samples were collected bimonthly during spring and neap tides from October to March at the tidal inlet. Samples were collected hourly for 25 h in February, and for 13 h in all other months. Hourly estimates of water flux through the tidal inlet of the estuary were calculated using a generalized one-dimensional hydrodynamic model calibrated for the Swartkops estuary. Water flux estimates were used to calculate larval flux through the tidal inlet. Zoea I larvae of *Sesarma catenata* were found in all sampling sessions, with highest abundance during nocturnal ebb tides. Two seasonal peaks of abundance were detected in November and February–March. These coincided with recorded peaks of percentage abundance of gravid females in the adult population. Megalopa larvae were recorded mainly during flood tides from January to March. More than 70 % of all *Sesarma catenata* larvae moving through the tidal inlet of the Swartkops estuary in either direction were exported in any given sampling session. There was net export of zoea I larvae in all cases but one, and net import of megalopa larvae in all cases. The possibility that *Sesarma catenata* larvae may become entrapped in the surf zone circulation system throughout development, as a mechanism to avoid offshore dispersal, is discussed.

Die gety-uitruiling van larwes van die krap wat in brak vleie voorkom, *Sesarma catenata*, is bestudeer in die Swartkops-estuarium, 'n getygedrewe vlak strandmeer aan Algoabaai, Suid-Afrika. Planktonmonsters is twee keer per maand, vanaf Oktober tot Maart, versamel en wel tydens spring- en dooie-gety by die strandmeermund. Monsters is uurliks vir 25 h-tydperke in Februarie en vir 13 h-tydperke in alle ander maande versamel. 'n Eendimensionele hidrodinamiese model wat vir die Swartkops-estuarium gekalibreer is, is gebruik om uurlikse skattings van die watervloed deur die mond te maak. Skattings van hierdie watervloed is gebruik om die larfvloed deur die mond te bereken. Soëa I larwes van *Sesarma catenata* is tydens alle bemonsteringsgeleenthede gevind, met die hoogste voorkoms snags by laagwater. Seisoenale pieke in die voorkoms is in November en in Februarie–Maart waargeneem. Dit het saamgeval met aangetekende pieke in die persentasie-voorkoms van dragtige wyfies in die volwasse bevolking. Megalope larwes is hoofsaaklik tydens vloedgetye van Januarie tot Maart aangetref. Meer as 70% van alle *Sesarma catenata*-larwes wat deur die mond van die Swartkops-estuarium beweeg het, in enige rigting, is tydens bepaalde bemonsteringstydperke uitgevoer. Daar was 'n netto uitvoer van soëa I larwes in alle gevalle behalwe een, en 'n netto invoer van megalope larwes in alle gevalle. Die moontlikheid word bespreek dat *Sesarma catenata*-larwes gedurende hulle hele ontwikkelings tydperk in die sirkulasie van die brandersone gevange mag bly en sodoende aflandige verstrooiing mag vryspring.

The fate of larvae released into the water column by estuarine decapod crustaceans has received considerable attention in the last decade. Two main research approaches have been favoured. Extensive experimental studies on the larval behaviour of vertical migration (reviewed by Sulkin 1984; see also Forward, Cronin & Stearns 1984; Forward 1986) in conjunction with studies on the timing of larval release by gravid females (reviewed by Forward 1987) have lead to the formulation of empirical qualitative models which explain the horizontal larval transport processes in estuaries and over the continental shelf, and predict the temporal distribution of larvae (Kelly, Sulkin & Van Heukelem 1982; Sulkin, Van Heukelem, Kelly & Van Heukelem 1980; Sulkin & Van Heukelem 1982; Sulkin, Van Heukelem & Kelly 1983; Epifanio & Dittel 1982). A second approach involves the direct investigation of the larval distribution in the field (Cronin 1982; Cronin & Forward 1982, 1986; Provenzano, McConaughy, Phillips, Johnson & Clark 1983; Dittel & Epifanio 1982; Epifanio, Valenti & Pembroke 1984). The evidence provided by these two approaches suggests that one of two generic mechanisms of larval dispersal are applicable to the vast majority of the species studied;

one mechanism resulting in retention of larvae throughout development within the parental estuaries, the other resulting in net export of newly hatched zoea larvae from the estuaries to the continental shelf, and subsequent return of megalopa larvae or early juveniles to the estuaries for recruitment (Epifanio 1988).

These studies have generally been qualitative, and many fewer attempts have been made to quantify the net flux of larvae into and out of estuaries. Studies of the flux of decapod larvae in estuaries are restricted to those of Johnson & Gonor (1982) on *Callinassa californiensis*, Emmerson (1983) and Wooldridge (1991) on *Upogebia africana* and *Palaemon pacificus*, Christy & Stancyk (1982) on 14 brachyuran taxa, and Dittel, Epifanio & Lizano (1991) on six brachyuran taxa. In the present study, the net flux of larvae of the saltmarsh grapsid crab *Sesarma catenata* was calculated in the Swartkops estuary, a small tidally driven estuary on the south-east coast of South Africa.

Study area

The Swartkops estuary (33°52'S / 25°38'E) is situated in the south-western corner of Algoa Bay, near Port Elizabeth,

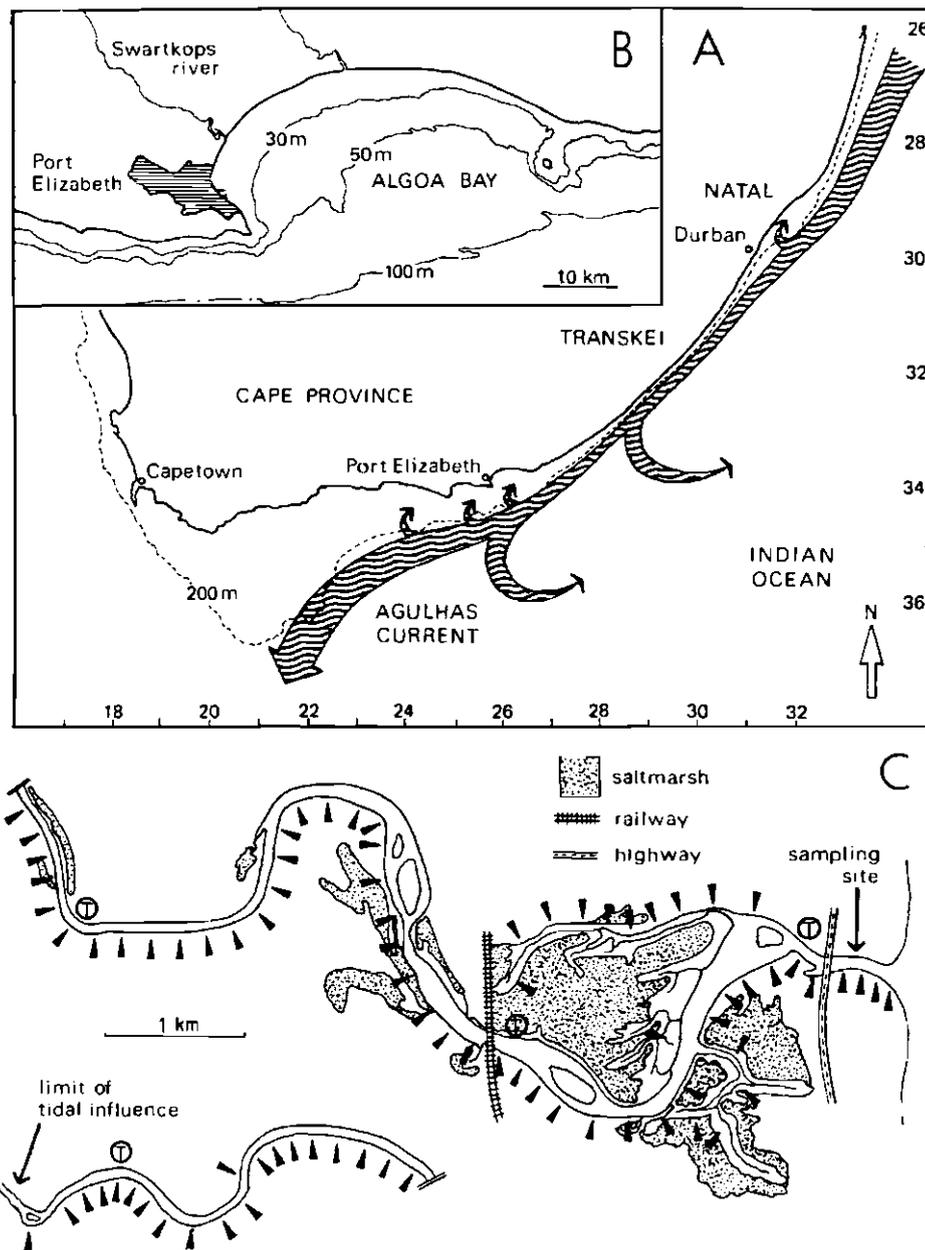


Figure 1 A–B: Area of study; **C:** map of the Swartkops estuary. Solid arrow points indicate where cross-section profiles of the river bed were made. Circled 'T' indicates position of water level recorders.

South Africa (Figure 1A,B). The estuary is 14 km long from its tidal inlet to the limit of the tidal influence, and contains a volume of water of $ca\ 5,1 \times 10^6\ m^3$ at HWST, and $2,6 \times 10^6\ m^3$ at LWST (Winter 1991). Channel depth averages 3 m in relation to MSL and the tidal inlet (Figure 1C) is 4–6 m deep. Tides are semidiurnal and predicted mean tidal amplitudes with respect to MSL are 1,74 m and 0,62 m during spring and neap tides respectively. The average tidal prism of the estuary is $ca\ 2,9 \times 10^6\ m^3$ (Reddering & Esterhuysen 1988).

The hydrology of the estuary is normally dominated by tidal exchanges. The average annual run-off from the catchment area of the Swartkops River ($ca\ 1354\ km^2$) is relatively low; $75 \times 10^6\ m^3$ (Baird, Hanekom & Grindley 1986). The average riverine influx per tidal cycle was estimated by Winter (1991) between April 1983 and June

1984 to be $ca\ 22,3 \times 10^3\ m^3$, with an average inflow rate of $0,5\ m^3\ s^{-1}$. This represents a ratio of 129:1 of tidal prism to freshwater inflow, rendering the latter negligible. Although it is fresh water that maintains the estuarine character of the system, it is the tidal exchange of sea water that prevents the tidal inlet from being clogged by marine sediments and provides the main flushing mechanism for the estuary. Lord & Thompson (1988) calculated the average water replacement time in the Swartkops estuary as $ca\ 25\ h$, or one-half every tidal cycle.

The salinity gradient in the estuary is very low, with salinities at the mouth of 34,5–35,5 ‰ and rarely below 25,0 ‰ at its head. Vertical salinity gradients in the lower estuary (below the railway bridge, Figure 1C) are usually absent and the water column is vertically homogeneous owing to mixing by strong tidal currents.

Extensive intertidal areas (363,27 ha) are situated in the lower estuary (Figure 1C). Of these, ca 182 ha are salt-marshes colonized by *Spartina maritima* and other halophytes (Baird *et al.* 1986). The saltmarshes support a population of *Sesarma catenata* with densities of up to 180 individuals m⁻² (Els 1982).

Material and Methods

Plankton sampling

Plankton samples were collected at the tidal inlet of the estuary (Figure 1C), simultaneously from just below the surface and from approximately 0,5 m above the bottom, from a ski boat. Two WP2 nets fitted with 190 µm pore size mesh and equipped with Kahlisco 005A flowmeters, were towed for 3 min against the general direction of the current at a speed of 3–4 km h⁻¹. Temperature and salinity measurements were taken at the top, mid-depth, and bottom of the water column with a YSI thermosalinometer. Plankton was sampled hourly for a 13-h period during the new moon spring tide and first quarter moon neap tide, every month from mid October 1983 to early April 1984. During spring and neap tides in February 1984, samples were collected hourly for 25 h, spanning two complete tidal cycles and one diel cycle. Samples were preserved in the field in 10% buffered formalin. In the laboratory, samples were diluted to a pre-determined volume according to the amount of material present, and subsampled. Larvae of *Sesarma catenata* were identified, sorted into stages and counted. Instantaneous larval densities (indiv.m⁻³) were estimated for surface and bottom sample series, and considered as average for the sampling time interval.

Calculation of water flux

Water transport through the mouth of the estuary was estimated by applying a generalized one-dimensional hydrodynamic model developed by the National Research Institute for Oceanology, Stellenbosch, South Africa (Huizinga 1985, 1987), and calibrated for the Swartkops estuary by Winter (1991). The model's computation system is based on an explicit finite-difference method used to resolve one-dimensional long wave equations (Huizinga 1985). The computational routines were designed for general applications (e.g. calculating water fluxes, determining maximum flood levels, etc.) and model simulations are obtained after calibration from a set of field data for each case-estuary and particular application subroutine. This model requires three types of external data: (i) variation in water level at the open sea boundary, (ii) riverine water inflow in the upstream boundary, and (iii) wind speed and direction during the simulation period (Huizinga 1985).

The initial calibration data from the Swartkops estuary consisted of 84 cross-section profiles of the estuary bed and flood-plains (spaced every 250 m) from the tidal inlet to the head, including major creeks (see Figure 1C), and time-velocity measurements at various depths at each cross-section. Wind direction and speed were measured hourly at the sampling site, and tidal elevation data was provided by four continuously running tide gauges situated along the length of the estuary (see Figure 1C). Tidal elevation in the sea was obtained from the Port Elizabeth Harbour tidal

records. Subsequent calibration of the model for each sampling session was effected with wind direction and speed and tidal elevation measurements recorded at the sampling site.

Estimates of the volume of water moving through the tidal inlet were obtained at hourly intervals, centred around the actual plankton sampling times. When computing water volumes for a given date, simulation was started at least 24 h prior to the first plankton sampling time to allow for sufficient settling time. The calibration of the model was adjusted by comparing the variations in water level recorded inside the estuary with those simulated by the model. If the simulated and measured water levels were drastically different at any time in any point in the estuary, it could be concluded that the model was not correctly accounting for water movement into and out of the estuary. Results of the simulations for the original model calibration in the Swartkops estuary and the criteria used for considering the model calibrated can be found in Huizinga (1985). The error of the model's simulations in respect of true flux is thought to be less than 15%, and probably less than 5% (Winter 1991).

One-dimensional hydrodynamic models are appropriately used in narrow, shallow estuaries such as the Swartkops, which taper gradually in width from the tidal inlet to the head, i.e. the hydraulic radius does not change rapidly along the length of the estuary. The present model as modified by Winter (1991) was run on a Burroughs B6800 mainframe computer, and had an iteration time step of one second. The reader is referred to Huizinga (1985, 1987, 1988), Baird, Winter & Wendt (1987), and Winter (1991) for more detailed information on the prerequisites, properties, and applicability of the model.

Calculation of larval flux

A paired-sample Wilcoxon ranked test (Zar 1974) was applied to ascertain differences in larval vertical distribution per hourly interval. Subsequently, the series of surface and bottom instantaneous larval concentration data corresponding to each sampling session were time-differenced independently, in order, to eliminate possible time-dependent correlation between two consecutive samples. The relationship between larval concentration in the water column and the tidal phase was studied by applying a cross-correlation analysis (Wilkinson 1989) to the depth-averaged larval density data and tidal elevation data. The instantaneous flux of larvae through the tidal inlet for each hourly interval was calculated as the depth-averaged instantaneous larval concentration, multiplied by the volume of water transported into or out of the estuary. Net larval flux was calculated by adding the total of larvae exported (ebb-negative) to the total of larvae imported (flood-positive) in two consecutive tidal hemicycles (Method I).

Tides in the Swartkops estuary are asymmetrical, ebb tides being longer than flood tides (1–3 h longer depending on meteorological conditions). Since all but February's sampling sessions spanned a fixed 13 h, a number of sessions in this study did not include two complete tidal hemicycles (i.e. from low-to-high-to-low, or from high-to-low-to-high). In some cases (e.g. January 5 and March 8) a

complete ebb or flood tide plus the late and early parts of the preceding and succeeding flood and ebb tides respectively were sampled. While totalling larvae ebb and flood is an accurate reflection of net flux over a time period, successive ebb or flood tides are not strictly comparable in the biological sense, since they may represent independent hatching events in the adult crab population. Net larval flux thus obtained could represent an overestimation of net larval flux per tidal cycle.

To overcome this problem, a second approximation to net flux per tidal cycle was calculated (Method II). Samples from consecutive flood and ebb tidal hemicycles were paired and compared. The order in which these samples were paired was centered on the sample corresponding to the maximum water flux in each consecutive hemicycle, in either direction towards the high and low slack-tide times. Unpaired samples closest to the slack-tide points (representing minimum water flux) were excluded from the calculations. Because of the sample exclusion, this approach represents an underestimation of true absolute flux in both directions. Estimates calculated by these two methods provide a range of values wherein the true net flux per tidal cycle is most likely to occur.

Results

Results of the Wilcoxon test applied to the larval concentration data at the surface and bottom of the water column are summarized in Table 1. Significant differences ($p < 0,10$) were apparent only on November 7 and December 13 sampling sessions. However, as the significance level chosen was relatively low ($p = 0,10$) and the number of non-zero-difference data-points required in the analysis was low in some cases (e.g. November 14, see Table 1), a correlation analysis between the pooled surface and bottom larval density values was performed. This analysis revealed high correlation coefficients (zoea I: $r = 0,79$; $SE = 0,08$; $p < 0,005$; megalopa: $r = 0,61$; $SE = 0,13$; $p < 0,05$) indicating that vertical larval density values co-varied uniformly. This suggests that vertical differences in larval concentration could be considered to be a sampling artefact caused by

different filtration efficiencies in the surface and bottom plankton nets. On this evidence, the mean of the surface and bottom larval density values was considered to be an adequate approximation to larval density integrated over the water column.

Figure 2 shows the depth-averaged larval density per sampling interval during the twelve sampling sessions considered. Zoea I larvae of *Sesarma catenata* were found in the plankton at the mouth of the Swartkops estuary from October 13 1983 to April 4 1984. Megalopa larvae were found only in January, February, and March. Intermediate zoeal stages (zoea II to IV) were found on two occasions, i.e. November 14 and April 4 in low density (Figure 2). In terms of temperature and salinity, the water column at the mouth of the estuary was vertically homogeneous at all times in all sampling dates. No tidal front was detected.

From the evidence in Figure 2, there seems to have been no relationship between larval concentration in the plankton and the lunar phase (spring-neap tides), but a seasonal pattern with larval release peaks in early November and February–March is suggested. This coincides with the pattern of abundance of gravid females in the mud-flats (see Discussion).

Results of the cross-correlation analysis (Wilkinson 1989) applied to the depth-averaged zoea I density values and tidal elevation data are summarized in Table 2. In most cases zoea I density was weakly correlated with tidal amplitude in two ways: (a) negatively with a time lag of +1 to +2 h (i.e. larval peak occurring 1–2 h before low tide), and (b) positively with a time lag of –4 to –5 h (i.e. larval peak occurring 4–5 h after high tide). These two correlations describe the same phenomenon, i.e. a larval density peak coinciding with the mid- and late parts of the ebb tides, usually after the peak in instantaneous water flux (see Figure 2).

Highest zoea I concentrations in the plankton occurred during nocturnal ebb tides, with a difference of 1 to 2 orders of magnitude between consecutive diurnal and nocturnal ebbs (see Figure 2, February) This pattern can also be observed during daytime sampling sessions which included some night-time hours (e.g. November 7 and December 5, Figure 2). Because of their relatively low frequency in the samples, megalopa larvae were not subjected to cross-correlation analysis. With few exceptions, megalopa larvae were always found entering the estuary with flood tides.

The instantaneous larval flux per sampling interval was calculated using the depth-averaged larval density values. Total and net flux estimates of zoea I and megalopa larvae through the tidal inlet of the estuary are summarized in Table 3. Overall, more than 72% of all larvae passing through the tidal inlet in either direction were exported in any given sampling session. Zoea larvae were exported from the estuary in all cases but one (i.e. November 14). Megalopa larvae were imported into the estuary in all cases. As expected, zoea I flux estimates calculated by the second method (paired samples) were generally lower than those calculated by the first method (see Table 3). Both estimates were, however, very close, falling within a 73% to 112% range of one another in almost all cases.

Table 1 Cross-correlation analysis between depth-averaged *Sesarma catenata* zoea I larval density and tidal elevation data. Values of $r < 0,20$ are not included

Date	Correlation (–)		Correlation (+)	
	(r)	Lag (h)	(r)	Lag (h)
Oct. 13	**–0,61	+4	–	–
Nov. 7	–0,21	0	**0,53	–4
Jan. 5	**–0,59	+2	0,33	–4
Jan. 10	–0,41	+1	0,33	–4
Feb. 2–3	**–0,40	+1 – +2	**0,47	–5
Feb. 9–10	*–0,46	+1 – +2	**0,37	–4
Mar. 8	8–0,62	+1	*0,75	–4

* Significant at $p < 0,05$ level

** Significant at $p < 0,10$ level

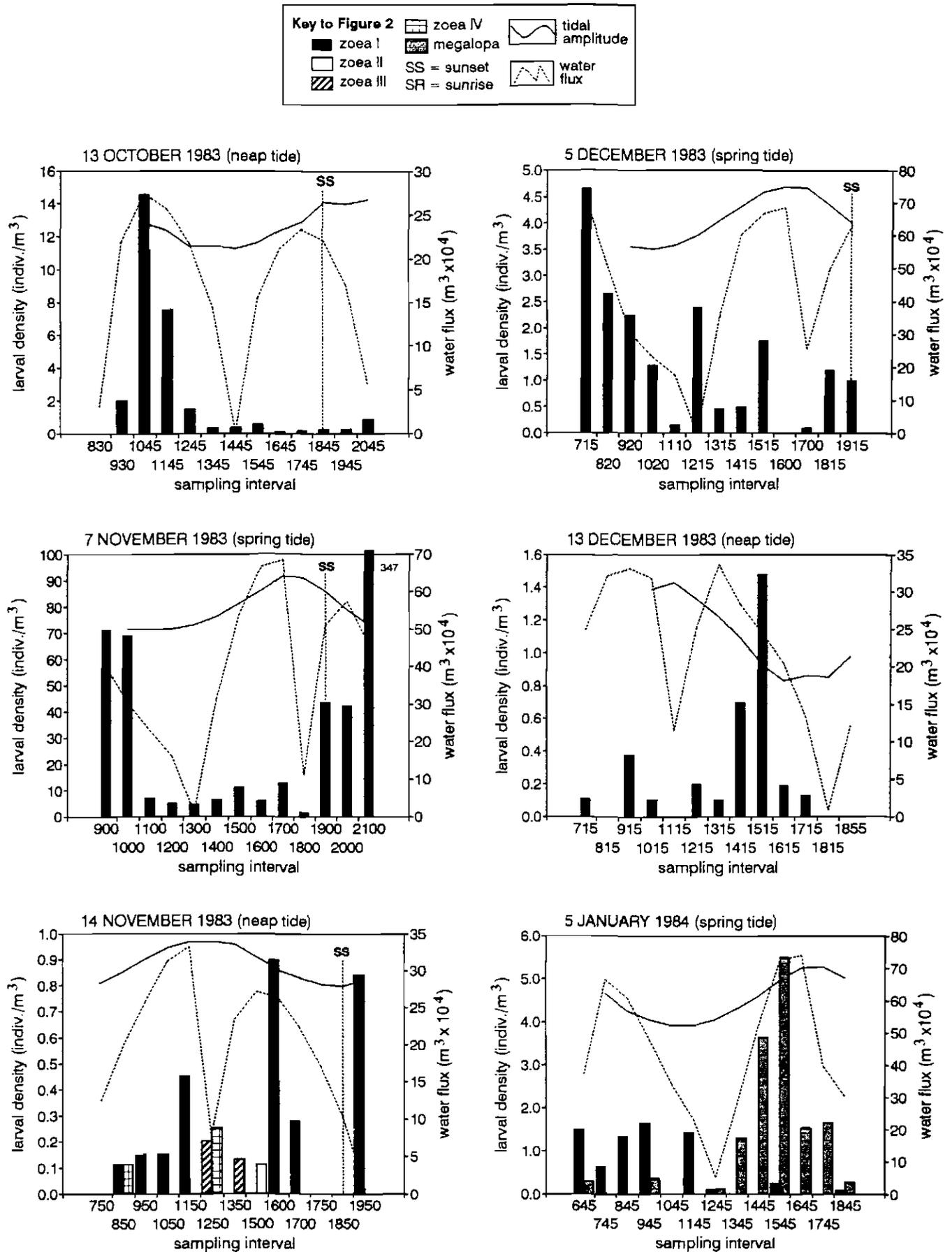


Figure 2 Depth-averaged density of *Sesarma catenata* larval stages at the mouth of the Swartkops estuary for 13 h during spring and neap tides from October to April. Tidal elevation data for March 1 missing.

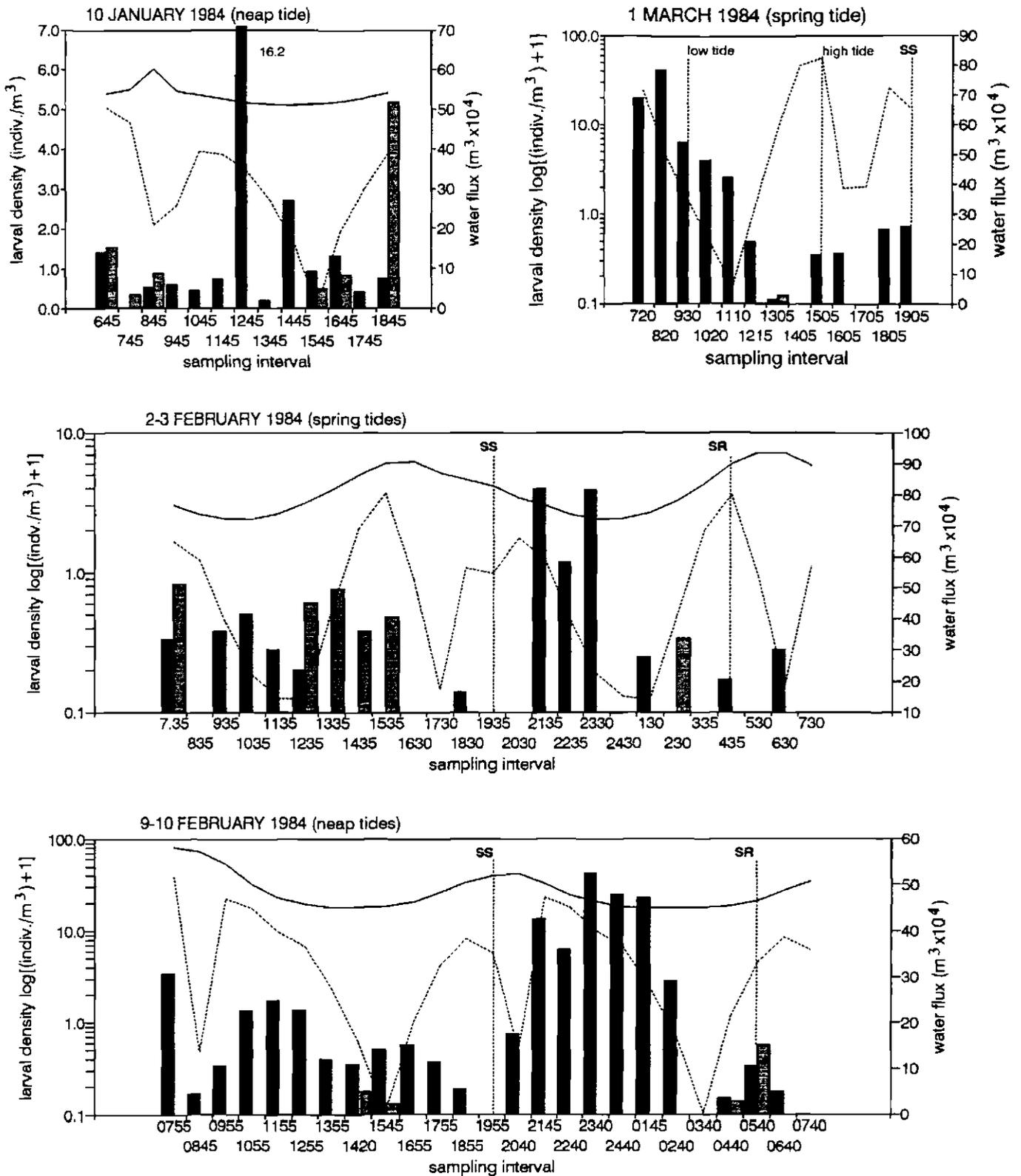


Figure 2 Continued.

Discussion

Highest zoea I density at the mouth of the Swartkops estuary occurred during the late and early morning ebb tides, after the peak in instantaneous water flux (see Figure 2). This suggests that the body of water evacuated from the estuary early in the ebb was that which occupied the main

channel of the estuary at the previous high tide. The water overlaying the mud-flats at high tide, which contained newly hatched zoea larvae, reached the tidal inlet 1 to 2 h thereafter.

Although zoea I net export values (Table 3) during spring tides were higher than their corresponding neap tide values in three months out of five (see Table 3), these differences

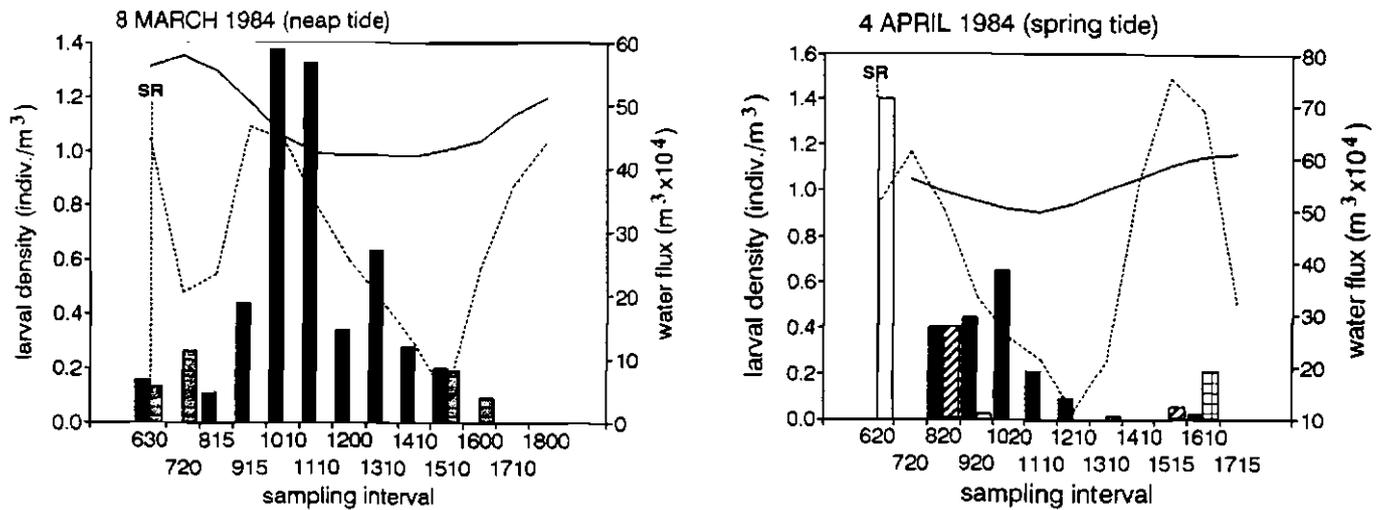


Figure 2 Continued.

Table 2 Paired-sample Wilcoxon ranked test (two-tailed) applied to *Sesarma catenata* zoea I density values at the surface and bottom of the water column per sampling interval. T: 'T' statistic. N: Number of non-zero-difference data-points used in the calculation of T. See text for details

Sampling date	T	p	N
November 7	8	$0,010 > p > 0,005$	13
November 14	6,1	$p > 0,20$	6
December 5	12,7	$0,20 > p > 0,10$	10
December 13	7,3	$0,10 > p > 0,05$	9
January 5	6,9	$0,20 > p > 0,10$	8
February 2-3	13,6	$0,20 > p > 0,10$	10
February 9-10	99,1	$0,20 > p > 0,10$	23
March 1	14,1	$p > 0,20$	10
March 8	10	$p = 0,20$	9

were not statistically significant (two-tailed Wilcoxon test with ln-transformed data, $p > 0,10$). The evidence in Figure 2 does not suggest a clear relationship between timing of larval release in *Sesarma catenata* and the spring-neap tide cycle.

Endogenous larval release rhythms synchronized with the lunar and/or spring-neap tide cycles (usually spring high tides) are a common feature in estuarine and intertidal marine brachyurans (Bergin 1981; Christy 1982, 1986; Saigusa 1980, 1982). This behaviour has been suggested as increasing the survival of newly hatched larva exposed to predation and environmental stress (De Coursey 1979; Christy 1986), and as enhancing the likelihood of larval retention or export from estuaries (Forward, Lohmann & Cronin 1982; Cronin & Forward 1982; Forward, Douglass & Kenny 1986; de Vries & Forward 1989).

As the sampling protocol in the present study was not designed to specifically investigate this feature, the evidence in Figure 2 may be misleading. On the one hand, all sampling sessions in this study except February's were performed

mainly during daytime hours. Thus, the absolute magnitude of nocturnal larval release (i.e. main larval release period within the diel cycle; see above) in these dates was only partially measured, or not at all. On the other hand, the physical window available for larval hatching in the Swartkops estuary is relatively narrow. The bulk of *Sesarma catenata* population (i.e. densities above 50 indiv. m^{-2}) in the saltmarshes is found at elevations between 0,65 m and 0,95 m above MSL (Els 1982). The predicted mean high water levels during the study period were 0,23 m above MSL in neap tides and 0,81 m above MSL in spring tides (South African Tide Tables, SA Navy, 1983, 1984). Since ovigerous females release their larvae inside or at the opening of their burrows (Pereyra Lago 1986), only spring high tides allow the possibility of larval hatching for most of the population. This factor alone may account for the higher net zoea I fluxes measured during spring tides (see Table 3).

The net larval flux of *Sesarma catenata* through the tidal inlet of the Swartkops estuary is that of net export of zoea I and net import of megalopa (Table 3). The consistent absence of zoea II to IV from the estuary indicates that most of the larval development takes place at sea. The same strategy has been observed in *Paratyloidiplax algoense* and *P. edwardsii* in the Swartkops estuary (unpubl. pers. obs.), and *Upogebia africana* in the Swartkops and Swartvlei estuaries (Emmerson 1983; Wooldridge 1991).

Els (1982) reported the presence of gravid females of *Sesarma catenata* in the Swartkops estuary saltmarshes from September to March. The population showed two peaks of reproductive activity (percentage of gravid females): a smaller peak in October, and a main peak in January. Els (1982) also suggested that *S. catenata* females produce only one brood per reproductive season. The average egg incubation period of females kept in the laboratory at a constant temperature of 20°C is 32 days (Pereyra Lago 1986). Assuming an incubation period in the field of 25-40 days, the peaks of reproductive activity in October and January could be responsible for the observed peaks in zoea I abundance in the plankton on November 7 and February 9/10-March 1 (see Figure 2 and Table 3).

Zoeal development in the laboratory at 20°C lasts an

Table 3 Total and net flux of *Sesarma catenata* zoea I and megalopa larvae through the mouth of the Swartkops estuary in all sampling sessions except April 4. Net flux was calculated by Method I (over 13/25 h) and Method II (paired samples). February's larval flux was calculated separately for diurnal and nocturnal tides. Positive values = influx; negative values = eflux. See text for details

Date	Tide	*Flux zoeal		*Flux megalopa		*Net flux (over 13/25 h)		*Net flux (paired samples)	
		ebb	flood	ebb	flood	zoeal	megalopa	zoeal	megalopa
Oct. 13	neap	-6,72	0,20	0,00	0,00	-6,51	0,00	-6,51	0,00
Nov. 7	spring	-20,60	5,94	0,00	0,01	-31,34	0,00	-30,90	0,01
Nov. 14	neap	-0,29	0,59	0,00	0,00	0,30	0,00	0,00	0,00
Dec. 5	spring	-5,63	2,86	0,00	0,00	-2,77	0,00	-3,10	0,00
Dec. 13	neap	-0,70	0,18	0,00	0,00	-0,51	0,00	-0,49	0,00
Jan. 5	spring	-2,90	0,18	-0,37	6,23	-2,72	5,88	-2,38	5,96
Jan. 10	neap	-5,35	1,47	0,00	3,27	-3,88	3,27	-0,36	3,27
Feb. 2/3	spring	-4,33	0,20	-0,55	1,20	-4,13	0,65	-0,48 (dt)	0,51 (dt)
Feb. 2/3	spring							-3,60 (nt)	0,14 (nt)
Feb. 9/10	neap	-37,35	0,75	** -0,67	0,28	-36,60	0,28	-0,01 (dt)	0,02 (dt)
Feb. 9/10	neap							-34,42 (nt)	0,26 (nt)
Mar. 1	spring	-39,27	0,62	0,00	0,04	-38,65	0,04	-37,64	0,04
Mar. 8	neap	-4,49	0,36	0,00	0,13	-4,13	0,13	-3,04	0,10

* Millions; ** thousands; (dt) diurnal tide; (nt) nocturnal tide.

average of 28 days (Percyra Lago 1987). Mean monthly temperatures in the surf-zone of Algoa Bay range from 17°C to 22°C from November to March. Within this range, zoeal stages of *S. catenata* would be expected to remain at sea for 25–30 days before moulting to megalopae and returning to the estuary. However, the recruitment of *S. catenata* megalopae to the estuary showed no synchronicity with the observed peaks of zoea I abundance in the estuary. The first megalopa larvae entering the estuary were found on January 5, two months after the first large hatching event in early November. The expected increase in frequency and numbers of megalopae entering the estuary in late March–early April, following February's main hatching event in the adult population was not observed (see Figure 2).

Larval dispersal patterns which involve export of early zoea larvae and recruitment by megalopae and/or early juveniles have been studied in a few species, most notably *Uca* spp. (Lambert & Epifanio 1982), and *Callinectes sapidus* (Sulkin & Van Heukelem 1982; Epifanio & Dittel 1982). Most of these studies have been carried out in large estuarine embayments on the east coast of North America (e.g. Chesapeake Bay, Delaware Bay), which are vertically stratified systems with net onshore water transport in the bottom layer. The offshore circulation pattern in that region also provides larvae initially dispersed over the continental shelf for hundreds of kilometres, with regular, predictable transport vehicles (e.g. onshore bottom drift, see Scheltema 1975; wind stress currents, see Johnson 1985; Johnson & Hester 1989) to return for recruitment to their point of origin, or similar suitable adult habitat (Epifanio 1988).

The scenario along the south-east coast of South Africa is radically different. The majority of estuaries are small, shallow, and have high tidal exchange ratios. This makes them available for colonization from the sea only during flood tides. The continental shelf is very narrow along the

Natal and Transkei coasts (only 10–12 km wide along the Transkei coast, see Figure 1A), becoming wider only west of Algoa Bay. This results in different current regimes in different sections of the coast. Offshore circulation is dominated by the tropical Agulhas current (see Figure 1A), flowing south-easterly along the shelf break. Shelf circulation is determined by sheer-edge processes on the landward fringe of the Agulhas current, local topographic features on the bottom, and short term wind and wave climate (Harris 1978; Schumann 1987; Shannon 1989). Under these conditions and in the absence of regular, predictable cross-shelf currents, larvae of estuarine invertebrates dispersed offshore and advected into the Agulhas current would have little or no chance of returning to their parental estuaries.

This points in the direction of larval retention within the nearshore area as the most likely alternative to ensure recruitment. Wooldridge (1991) postulated nearshore retention throughout development in larvae of *Upogebia africana* exported from the Swartvlei Lake system. Zoea I of *U. africana* were effectively exported from the estuary, and returned only as post-larval recruits. The distribution of larvae offshore from the tidal inlet was, however, restricted to the 25 m isobath, with highest abundance of zoeal stages in water 10–12 m deep, and of post-larvae within the inner surfzone.

One possible mechanism that larvae of *Sesarma catenata* may utilize to similarly avoid offshore dispersal, is to become entrapped in the surfzone circulation cells. In Algoa Bay (see Figure 1B), McLachlan (1980) and McLachlan *et al.* (1981) showed the surf zone to be a semi-closed system with a clearly identifiable seaward boundary at the outer edge of the rip-head zone (approx. 10 m depth), with a water residence time of ca 10 days (McLachlan 1987). Cellular rip currents produce a wave-induced net onshore water transport in the surface layer of the water column. The

water transported onto the beach by waves is evacuated beyond the breaker line by subsurface rip currents (see McLachlan & Erasmus 1983 for review). By selectively maintaining a high position in the water column, *S. catenata* larvae could utilize this current pattern to remain within the shallow littoral area of Algoa Bay.

Preliminary evidence supports this proposition. The behaviour pattern of the first zoea of *S. catenata* studied in the laboratory shows negative geotaxis, high barokinesis, and positive phototaxis in a natural light field to low and moderate light intensities (Pereyra Lago 1986, 1988). This behaviour would promote upward migration and aggregation of larvae high in the water column in most circumstances likely to occur in nature. No information is available on larval behaviour of *Upogebia africana*. However, considering the overall similarity of the littoral environment in the vicinity of the Swartvlei and Swartkops estuaries (i.e. exposed sand beaches with high energy wave and wind regimes, and wide surf zone), it is likely that the same basic larval retention mechanism may be utilized by both species.

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References

- BAIRD, D., HANEKOM, W.M. & GRINDLEY, J.R. 1986. Swartkops (CSE3). In: Estuaries of the Cape. Part II. Synopses of available information on individual systems. (Eds) A.E.F. Heydorn and J.R. Grindley. Report No. 23. CSIR Research Report No. 422, pages 1–82.
- BAIRD, D., WINTER, P.E.D. & WENDT, G. 1987. The flux of particulate material through a well-mixed estuary. *Continental Shelf Research* 7: 1399–1403.
- BERGIN, M.E. 1981. Hatching rhythms in *Uca pugilator* (Decapoda Brachyura). *Mar. Biol.* 63: 151–158.
- CHRISTY, J.H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (genus *Uca*): test of an hypothesis. *Biol. Bull.* 163: 251–263.
- CHRISTY, J.H. 1986. Timing of larval release by intertidal crabs on an exposed shore. *Bull. Mar. Sci.* 39: 176–191.
- CHRISTY, J.H. & STANCYK, S.E. 1982. Movement of larvae from North Inlet estuary, S.C., with special reference to crab zoeae. In: Estuarine Comparisons, (ed.) V. Kennedy. Academic Press, New York. pages 489–503.
- CRONIN, T.W. 1982. Estuarine retention of larvae of the crab *Rhithropanopeus harrisi*. *Estuar. Coast. Shelf Sci.* 15: 207–221.
- CRONIN, T.W. & FORWARD, R.B. 1982. Tidally timed behaviour: Their effects on larval distributions in estuaries. In: Estuarine Comparisons, (ed.) V. Kennedy. Academic Press, New York. pages 505–520.
- CRONIN, T.W. & FORWARD, R.B. 1986. Vertical migration cycles of crab larvae and their role in larval dispersal. *Bull. Mar. Sci.* 39: 192–201.
- DE COURSEY, P.J. 1979. Egg-hatching rhythms in three species of fiddler crabs. In: Cyclic phenomena in marine plants and animals. (Eds) E. Naylor and R.G. Hatnoll. Pergamon Press, New York. pages 399–406.
- DE VRIES, M. & FORWARD, R.B. 1989. Rhythms of larval release of the sublittoral crab *Neopanope sayi* and the supralittoral crab *Sesarma cinereum* (Decapoda: Brachyura). *Mar. Biol.* 100: 241–248.
- DITTEL, A.I. & EPIFANIO, C.E. 1982. Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. *Estuaries* 5: 197–202.
- DITTEL, A.I., EPIFANIO, C.E. & LIZANO, O. 1991. Flux of larvae in a mangrove creek in the Gulf of Nicoya, Costa Rica. *Estuar. Coast. Shelf Sci.* 32: 129–140.
- ELS, S. 1982. Distribution and abundance of two crab species on the Swartkops estuary saltmarshes, and the energetics of *Sesarma catenata*. M.Sc. thesis, University of Port Elizabeth, Port Elizabeth. 179 pp.
- EMMERSON, W.D. 1983. Tidal exchange of two decapod larvae, *Palaemon pacificus* (Caridea) and *Upogebia africana* (Thalassinidae) between the Swartkops River estuary and adjacent coastal waters. *S. Afr. J. Zool.* 18: 326–330.
- EPIFANIO, C.E. 1988. Transport of crab larvae between estuaries and the continental shelf. In: Lecture notes on coastal and estuarine studies, (ed.) B.-O. Jansson. Springer-Verlag, Berlin, Heidelberg. pages 291–305.
- EPIFANIO, C.E. & DITTEL, A.I. 1982. Comparison of dispersal of crab larvae in Delaware Bay, USA and the Gulf of Nicoya, Central America. In: Estuarine comparisons, (ed.) V. Kennedy. Academic Press, New York.
- EPIFANIO, C.E., VALENTI, C.C. & PEMBROKE, A.E. 1984. Dispersal and recruitment of blue crab larvae in Delaware Bay, USA. *Estuar. Coast. Shelf Sci.* 18: 1–12.
- FORWARD, R.B. 1985. Behavioural responses of larvae of the crab *Rhithropanopeus harrisi* (Brachyura: Xanthidae) during diel vertical migration. *Mar. Biol.* 90: 9–18.
- FORWARD, R.B. 1986. A reconsideration of the shadow response of a larval crustacean. *Mar. Behav. Physiol.* 12: 99–113.
- FORWARD, R.B. 1987. Larval release rhythms of decapod crustaceans. *Bull. Mar. Sci.* 41: 165–176.
- FORWARD, R.B., CRONIN, T.W. & STEARNS, D.E. 1984. Control of vertical migration: Photoresponses of a larval crustacean. *Limnol. Oceanogr.* 29: 146–154.
- FORWARD, R.B., DOUGLASS, J.K. & KENNEY, B.E. 1986. Entrainment of the larval release rhythm of the crab *Rhithropanopeus harrisi* by cycles in salinity change. *Mar. Biol.* 90: 537–554.
- FORWARD, R.B., LOHMANN, K. & CRONIN, T.W. 1982. Rhythms in larval release by an estuarine crab, (*Rhithropanopeus harrisi*). *Biol. Bull.* 163: 287–300.
- HARRIS, T.F.W. 1978. Review of coastal currents in Southern African waters. South African National Science Programmes, CSIR Research Report No. 30, Pretoria, South Africa.
- HUIZINGA, P. 1985. A dynamic one-dimensional water quality model. CSIR Research Report No. 561, Pretoria, South Africa.
- HUIZINGA, P. 1987. Computational aspects of the NRIO one-dimensional estuaries model. CSIR Memorandum No. 8703, Pretoria, South Africa.
- HUIZINGA, P. 1988. A mathematical model of the Swartkops River and estuary to study river floods. In: The Swartkops

- Estuary. (Eds) D. Baird, J.F.K. Marais and P. Martin. South African National Scientific Programmes. CSIR Report No. 156, pages 69–75.
- JOHNSON, D.F. 1985. The distribution of brachyuran crustacean megalopae in the waters of the York River, lower Chesapeake Bay, and adjacent shelf: Implications for recruitment. *Estuar. Coast. Shelf Sci.* 20: 693–708.
- JOHNSON, D.F. & HESTER, B.S. 1989. Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. *Estuar. Coast. Shelf Sci.* 28: 459–472.
- JOHNSON, G.E. & GONOR, J.J. 1982. Tidal exchange of *Callinassa californiensis* (Crustacea, Decapoda) larvae between the ocean and the Salmon River estuary, Oregon. *Estuar. Coast. Shelf Sci.* 14: 501–516.
- KELLY, P., SULKIN, S.D. & VAN HEUKELEM, W.F. 1982. A dispersal model for larvae of the deep sea red crab *Geryon quinquedens* based upon behavioural regulation of vertical migration in the hatching stage. *Mar. Biol.* 72: 35–43.
- LAMBERT, R. & EPIFANIO, C.E. 1982. A comparison of dispersal strategies in two genera of brachyuran crabs in a secondary estuary. *Estuaries* 5: 182–188.
- LORD, D.A. & THOMPSON, G.A. 1988. The Swartkops estuary: Pollution status. In: The Swartkops Estuary. (Eds) D. Baird, J.F.K. Marais, & P. Martin. South African National Scientific Programmes. CSIR Research Report No. 156, pages 16–24.
- McLACHLAN, A. 1980. Exposed sandy beaches as semi-closed ecosystems. *Mar. Environm. Res.* 4: 59–63.
- McLACHLAN, A. 1987. Sandy beach research at the University of Port Elizabeth: 1976–1986. Institute for Coastal Research, University of Port Elizabeth, Research Report No. 14, 113 p.
- McLACHLAN, A. & ERASMUS, T. (eds.) 1983. Sandy Beaches as Ecosystems, W. Junk, The Hague, 757 pp.
- McLACHLAN, A., ERASMUS, T., DYE, A.H., WOOLDRIDGE, T., VAN DER HORST, G., LASIAK, T.A., & McGWYNNNE, L. 1981. Sandy beach energetics: An ecosystem approach towards a high energy interface. *Estuar. Coast. Shelf Sci.* 13: 11–25.
- PEREYRA LAGO, R. 1986. Larval development of *Searma catenata* Ortmann (Brachyura, Grapsidae) and behavioural responses of larvae to environmental stimuli in the Swartkops estuary. M.Sc. thesis, University of Port Elizabeth, 292 pp.
- PEREYRA LAGO, R. 1987. Larval development of *Sesarma catenata* Ortmann (Brachyura, Grapsidae, Sesarminae) reared in the laboratory. *S. Afr. J. Zool.* 22: 200–212.
- PEREYRA LAGO, R. 1988. Phototactic behaviour and the nature of the shadow response in larvae of the estuarine crab *Sesarma catenata*. *S. Afr. J. Zool.* 23: 150–154.
- PROVENZANO, A.J., McCONAUGHA, J.R., PHILLIPS, K.B., JOHNSON, D.F. & CLARK, J. 1983. Vertical distribution of first stage larvae of the blue crab *Callinectes sapidus* at the mouth of Chesapeake Bay. *Estuar. Coast. Shelf Sci.* 16: 489–499.
- REDDERING, J.S.V. & ESTERHUYSEN, K. 1988. The Swartkops estuary: Physical description and history. In: (Eds.) The Swartkops Estuary. (Eds) D. Baird, J.F.K. Marais, & P. Martin. South African National Scientific Programmes, CSIR Report No. 156, pages 7–15.
- SAIGUSA, M. 1980. Entrainment of a semilunar rhythm by a simulated moon light cycle in the terrestrial crab *Sesarma haematocheir*. *Oceologia* 46: 38–44.
- SAIGUSA, M. 1982. Larval release rhythm coinciding with solar day and tidal cycles in the terrestrial crab *Sesarma*. Harmony with the semilunar timing and its adaptive significance. *Biol. Bull.* 162: 371–386.
- SCHELTEMA, R.S. 1975. Relationship of larval dispersal, gene flow and natural selection to geographic variation of benthic invertebrates in estuaries and along coastal regions. In: Estuarine Research, (ed) L.E. Cronin, Academic Press, New York, pages 372–391.
- SCHUMANN, E.H. 1987. Aspects of shelf circulation off the east and south coasts of South Africa. In: Proceedings of the 6th National Oceanographic Symposium, 6–10 July, 1987. SANCOR-NRIO-University of Stellenbosch, paper No. 614.
- SHANNON, L.V. 1989. The physical environment. In: Ocean of Life off Southern Africa. (Eds) A. Payne & R. Crawford. Vlaeberg Publishers, Cape Town, pages 12–27.
- SULKIN, S. 1984. Behavioural basis of depth regulation in the larvae of brachyuran crabs. *Mar. Ecol. Progr. Ser.* 15: 181–205.
- SULKIN, S. & VAN HEUKELEM, W. 1982. Larval recruitment in the crab *Callinectes sapidus* Rathbun: an amendment to the concept of larval retention in estuaries. In: Estuarine Comparisons, (ed.) V. Kennedy. Academic Press, New York, pages 459–475.
- SULKIN, S.D., VAN HEUKELEM, W. & KELLY, P. 1983. Behavioural basis of depth regulation in hatching and postlarval stages of the mud crab *Eurypanopeus depressus*. *Mar. Ecol. Progr. Ser.* 11: 157–264.
- SULKIN, S.D., VAN HEUKELEM, W., KELLY, P. & VAN HEUKELEM, L. 1980. The behavioural basis of larval recruitment in the crab *Callinectes sapidus* Rathbun: A laboratory investigation of ontogenetic changes in geotaxis and barokinesis. *Biol. Bull.* 159: 402–417.
- WILKINSON, L. 1989. SYSTAT: The System for Statistics. Evanston, Illinois, U.S.A.: Second Edition, SYSTAT Inc.
- WINTER, P.E.D. 1991. The estuarine-marine exchange of dissolved and particulate material at the Swartkops River estuary, Algoa Bay, South Africa. Ph.D. Diss., University of Port Elizabeth, 115 pp.
- WOOLDRIDGE, T.H. 1991. Exchange of two species of decapod larvae across an estuarine mouth inlet and implications of anthropogenic changes in the frequency and duration of mouth closure. *S. Afr. J. Sci.* 87: 519–525.
- ZAR, J.H. 1974. Biostatistical Analysis. Prentice Hall, New Jersey.