

# Tidal exchange of ichthyoplankton in the Swartkops estuary mouth, South Africa

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Tidal exchange of fish eggs, larvae and juveniles in the mouth of the Swartkops estuary was examined by plankton and seine-netting during two 24-h sampling sessions. Small larvae of resident estuarine species such as *Caffrogobius multifasciatus*, *Psammogobius knysnaensis* and *Omobranchus woodi* appear to be passively swept out of the estuary on the ebb-tide. Early juveniles of marine species which utilize the estuary as a nursery ground, such as *Rhabdosargus holubi*, *Liza richardsoni* and *Heteromycteris capensis*, enter the estuary on the flood-tide. Catches of these species near the bank during ebb-tide suggest that they actively migrate towards the banks to prevent being swept back out to sea.

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Die gety-uitruiling van eiers, larwes en kleinvisies in die Swartkopsriviermonding is deur middel van planktonmonsters en treknetvangste tydens twee 24 h-periodes ondersoek. Dit wil voorkom asof larwes van spesies wat getyrieviere bewoon soos *Caffrogobius multifasciatus*, *Psammogobius knysnaensis* en *Omobranchus woodi* passief uit die riviermonding met die ebgety uitgespoel word. Kleinvisies van mariene spesies wat die getyrievier as 'n grootwordgebied gebruik soos *Rhabdosargus holubi*, *Liza richardsoni* en *Heteromycteris capensis* dring die getyrievier binne tydens die vloedgety. Vangste van hierdie spesies langs die wal gedurende die ebgety impliseer dat die kleinvisies moontlik aktief na die kante toe swem om uitspoeling terug see toe te verminder.

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Most marine fish species spawn at sea but the larvae and early juveniles of some of these species leave the marine environment to enter sheltered, food-rich estuarine nursery areas (Gunter 1967; Clark, Smith, Kendall & Fahay 1969; Wallace 1975; Wallace & van der Elst 1975; Day, Blaber & Wallace 1981). The factors influencing the recruitment of the early life stages of these fishes into estuaries are multiple (Blaber & Blaber 1980; Whitfield 1980, 1983) and the actual process of transport into the estuary may be by active swimming or passive drift with tidal currents (Creutzberg 1958; Gunter 1967; Pacheco & Grant 1973).

To investigate this process of recruitment into estuaries, two 24-h sampling sessions were conducted in the mouth of the Swartkops estuary (33°52'S/25°38'E) in South Africa. This estuary was selected because its ichthyofauna is well known (Winter 1979; Marais & Baird 1980; Melville-Smith & Baird 1980; Beckley 1983a), the ichthyoplankton in the adjacent coastal waters of Algoa Bay has also been studied (Beckley 1983b) and other workers were concurrently investigating crustacean movements into the estuary (Emmerson 1983; Wooldridge 1983). By sampling continuously over 24-h periods, it was possible to monitor the time of day and phase of tide during which fish larvae and early juveniles entered the estuary and hence obtain an indication of the extent of passive drift and active swimming during this process.

## Materials and Methods

Sampling in the mouth of the Swartkops estuary was conducted in early spring when recruitment into the estuary was evident from catches of small juveniles in the macrophyte beds in the estuary (Beckley 1983a). The first sampling session was after spring-tides, from 12h00 on 28 October 1980 through to 12h00 the following day (Session 1) and the second was after neap-tides from 12h00 on 8 October 1981 through to 12h00 the next day (Session 2).

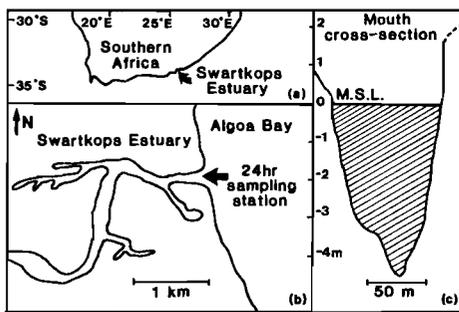
A station was established in mid-channel in the mouth of the Swartkops estuary (Figure 1) by securing a mooring buoy to a heavy anchor. At 90-min intervals, measurements of surface and bottom (1 m above substratum) water temperature, salinity and current velocity were taken from a small boat secured to the mooring. A weighted water-sampling bottle, a thermometer accurate to 0.1°C, an AO refractometer accurate to 1‰ and a calibrated OGAWA SEIKI Model OSK861 current meter were used for these measurements. Data on tidal height were obtained from an Ott gauge installed at the Port Elizabeth harbour located 10 km south of the estuary.

Biological samples were also taken every 90 min. Surface

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**Figure 1** (a) Location of the Swartkops estuary; (b) sampling station locality; (c) cross-section of the mouth region (after Reddering & Esterhuysen 1980).

and bottom plankton samples were collected using two 57 cm diameter WP2 nets, each fitted with a calibrated KAHLSCO Model 005-WA130 flowmeter and 190  $\mu\text{m}$  St Martins nylon mesh netting. The nets were connected to booms installed on either side of the bow of the boat, with one net positioned just below the water surface and the other held about 1 m above the substrate by means of a long steel rod. Plankton tows were carried out in midstream against the current and were restricted to about a minute in duration in order to prevent accumulation of suspended sand in the nets.

Seine-netting was also undertaken at 90-min intervals using a 15 m  $\times$  2,5 m (2 mm stretched mesh) net. The net was laid from the boat parallel to the north bank and then hauled onto the shore. Efficiency of the seine-net was, however, extremely variable because of the strong tidal currents and catch per unit effort (CPUE) cannot be used with any confidence for quantitatively comparing exchange of juvenile fish over the tidal cycle.

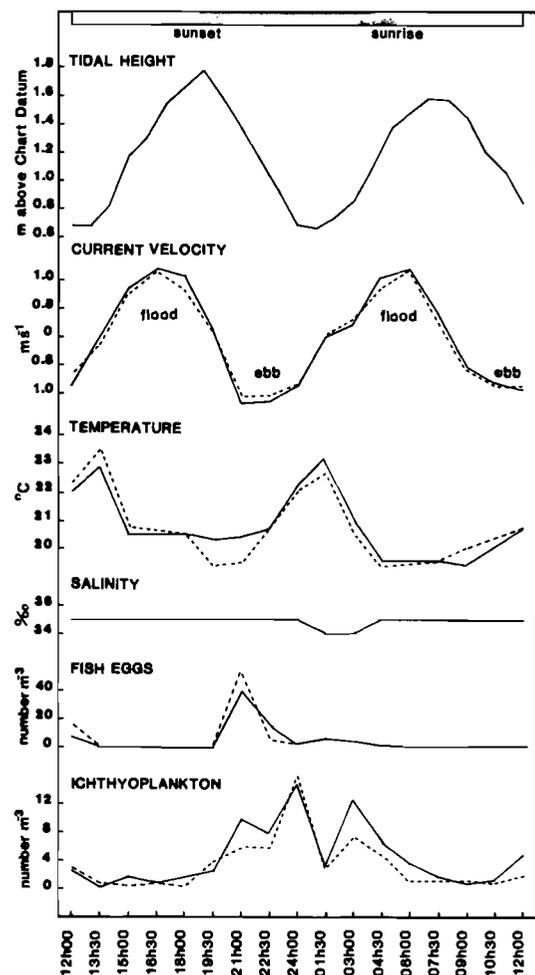
All biological samples were preserved in 10% formalin. In the laboratory, the plankton samples were sorted using a dissecting microscope to separate fish eggs, larvae and juveniles from the rest of the plankton. The larvae and juveniles were identified (using Ranzi 1933; Smith 1965; Haigh 1972; van der Elst & Wallace 1976; Louw & O'Toole 1977; Akatsu, Ogasawara & Yasuda 1977; Melville-Smith 1978; Brownell 1979) and standard lengths measured to the nearest 0,1 mm. Fish in the seine-net catches were also identified and total lengths measured to the nearest 1 mm.

Terminology used follows that of Jones, Martin & Hardy (1978) with a yolk-sac larva being the stage between hatching and absorption of yolk, a larva being the stage between absorption of yolk and acquisition of the minimum adult fin ray complement and a juvenile being the stage between acquisition of the minimum adult fin ray complement and sexual maturity.

## Results

### Session 1

The October 1980 24-h sampling session coincided with post spring-tide conditions (five days after full moon) and darkness lasting about 10 h. During this sampling session, predicted times for low tide in Algoa Bay were 12h17 and 00h45 and high tide 18h39 and 07h07. Tidal height had a range of 1,1 m and tidal current velocity in the estuary mouth reached  $1,2 \text{ m s}^{-1}$  (Figure 2). Surface and bottom current velocities followed the same pattern, as did surface and bottom temperatures and salinities (Figure 2). Water temperature increased on the ebb-tide with the outflow of warm estuarine water and decreased on the flood-tide with the inflow of cooler sea water.

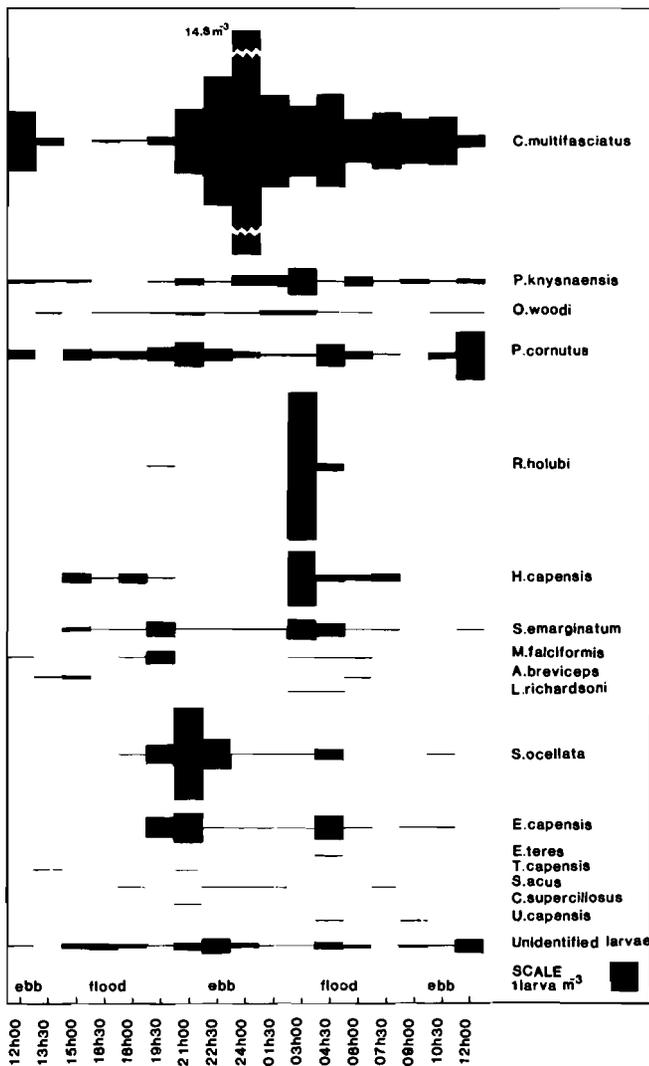


**Figure 2** Physical and biological data from Session 1 (— surface, - - - bottom if it differs from the surface value).

The density of fish eggs in the plankton ranged from 0–53,8 eggs  $\text{m}^{-3}$  with a mean of 4,9 eggs  $\text{m}^{-3}$  (Figure 2). There was a marked efflux of small unidentified eggs (0,7–0,8 mm diameter with a single oil globule) from the estuary on the evening ebb-tide. The density of fish larvae and juveniles in the plankton tows ranged from 0,2–15,9  $\text{m}^{-3}$  with a mean of 3,9  $\text{m}^{-3}$ . Densities of fish larvae and juveniles in the surface and bottom samples followed the same pattern although they were slightly but significantly higher in the surface samples (Wilcoxon paired sample test  $p < 0,05$ ).

The larvae and juveniles captured in the plankton tows comprised 17 species and some unidentified larvae (probably more than one species). *Caffrogobius multifasciatus* was the dominant species of larval fish and occurred in 91% of the samples. *Psammogobius knysnaensis* and *Parablennius cornutus* occurred in 76% and 74% of the samples, respectively. Numerically (based on density values), *Caffrogobius multifasciatus* constituted 53% of all larvae and juveniles captured in the plankton tows, *Parablennius cornutus* 9%, *Rhabdosargus holubi* 8%, *Sardinops ocellata* 8%, *Heteromycteris capensis* 5% and the rest collectively 17%.

Figure 3 gives the density  $\text{m}^{-3}$  of larvae and juveniles (surface and bottom samples averaged) for each species captured in Session 1. *Caffrogobius multifasciatus* larvae were particularly abundant during the evening ebb-tide and 99% of these larvae were 2–3 mm in length. *Rhabdosargus holubi* (10–13 mm), *Heteromycteris capensis* (7–10 mm) and to a lesser extent, *Spondylisoma emarginatum* (8–12 mm) showed an influx on the flood-tides whilst, surprisingly, there



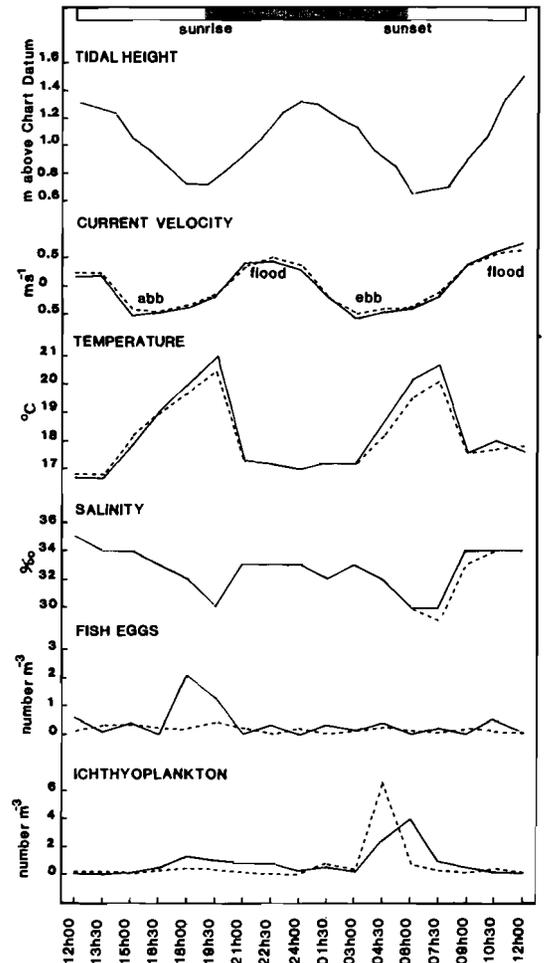
**Figure 3** Density of fish larvae and juveniles in the plankton samples of Session 1 (surface and bottom samples averaged).

was an efflux of the pelagic species *Sardinops ocellata* (11–21 mm) and *Engraulis capensis* (7–21 mm) on the evening ebb-tide. Mean number of species per sample was significantly higher during the night ( $\bar{x} = 8,8$ ) than during the day ( $\bar{x} = 4,9$ ) ( $t$  test for independent sample means  $p < 0,005$ ). Mean density of larvae and juveniles was also significantly higher at night ( $\bar{x} = 7,4 \text{ m}^{-3}$ ) than during the day ( $\bar{x} = 1,5 \text{ m}^{-3}$ ) ( $t$  test for independent sample means  $p < 0,005$ ).

In the seine-net catches of Session 1, a total of 1 775 fish of 23 species was captured (Table 1). Juvenile sparids, specifically *Rhabdosargus holubi*, *Spondyliosoma emarginatum* and *Diplodus sargus*, were captured most frequently and were present in 82%, 94% and 88% of the hauls respectively. Juvenile *Liza richardsoni*, *Sarpa salpa*, *Heteromycteris capensis*, *Parablennius cornutus* and the shoaling pelagic species *Etrumeus teres*, *Sardinops ocellata* and *Engraulis capensis* also occurred.

### Session 2

The October 1981 24-h sampling session coincided with post neap-tide conditions (2 days after first quarter) and darkness lasting about 11 h. During the sampling session, predicted times for high tide in Algoa Bay were 12h00 and 00h15 and low tide 18h12 and 06h45. Tidal height had a range of 0,9 m and tidal current velocity in the estuary mouth reached  $0,8 \text{ m s}^{-1}$  (Figure 4). Surface and bottom current velocity,



**Figure 4** Physical and biological data from Session 2 (— surface, - - - bottom if it differs from the surface value).

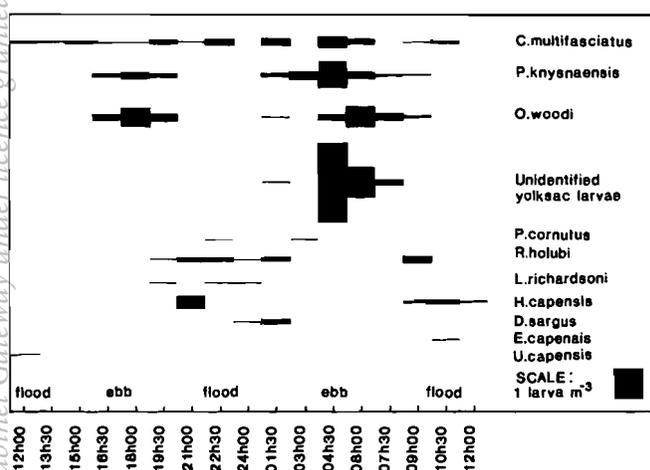
temperature and salinity measurements were all lower than those measured during Session 1. Temperature decreased on the flood-tide and salinity increased whilst on the ebb-tide temperatures increased and salinity decreased (Figure 4).

Egg density in the plankton tows was extremely low, ranging from 0–2,1 eggs  $\text{m}^{-3}$  with a mean of 0,3 eggs  $\text{m}^{-3}$  (Figure 4). There was an efflux of unidentified eggs at sunset on the ebb-tide. Larval and juvenile densities ranged from 0–6,6  $\text{m}^{-3}$  with a mean of 0,7  $\text{m}^{-3}$  (Figure 4). Densities of larvae and juveniles in the plankton tows in the surface and bottom water followed the same pattern and were not found to be significantly different (Wilcoxon paired sample test  $p > 0,05$ ).

The larvae and juveniles in the plankton tows comprised 11 species, one of which remained unidentified as the larvae were still in the yolk-sac stage. In terms of frequency of occurrence, *Caffrogobius multifasciatus* larvae were found in 56% of all samples. Numerically (based on density values), the unidentified yolk-sac larvae (1–2 mm) constituted 37% of the total, *Omobranchus woodi* (2–4 mm) 20%, *Psammogobius knysnaensis* (2–3 mm) 17%, *Caffrogobius multifasciatus* (2–18 mm) 13% and the other seven species, collectively, 13%. Figure 5 shows *Psammogobius knysnaensis* and *Omobranchus woodi* to be abundant on the ebb-tide whilst *Rhabdosargus holubi* (9–12 mm), *Liza richardsoni* (12–14 mm), *Heteromycteris capensis* (7–8 mm) and *Diplodus sargus* (9–10 mm) were most abundant on the night flood-tide. Mean number of species per sample was significantly higher during the night ( $\bar{x} = 2,8$ ) than during the day

**Table 1** Abundance, frequency and size of fish captured by seine-netting during two 24-h sampling sessions in the mouth of the Swartkops estuary (<sup>a</sup>common names taken from Smith 1975)

| Name                               | Common name <sup>a</sup> | October 1980 |               |                      | October 1981 |               |                      |
|------------------------------------|--------------------------|--------------|---------------|----------------------|--------------|---------------|----------------------|
|                                    |                          | Number       | Frequency (%) | Length range (TL mm) | Number       | Frequency (%) | Length range (TL mm) |
| <i>Rhabdosargus holubi</i>         | Cape stumpnose           | 233          | 82            | 11–140               | 2826         | 82            | 10–16                |
| <i>Liza richardsoni</i>            | southern mullet          | 50           | 59            | 10–342               | 797          | 71            | 12–285               |
| <i>Spondylisoma emarginatum</i>    | steentjie                | 309          | 94            | 9–14                 | 1            | 6             | 13                   |
| <i>Diplodus sargus</i>             | blacktail                | 223          | 88            | 7–32                 | 200          | 71            | 10–140               |
| <i>Sarpa salpa</i>                 | strepie                  | 53           | 29            | 15–60                | 230          | 47            | 18–52                |
| <i>Heteromycteris capensis</i>     | Cape sole                | 40           | 35            | 7–55                 | 403          | 71            | 8–50                 |
| <i>Etrumeus teres</i>              | redeye round-herring     | 352          | 35            | 22–44                | 151          | 12            | 17–34                |
| <i>Engraulis capensis</i>          | Cape anchovy             | 139          | 53            | 9–34                 | 34           | 12            | 16–30                |
| <i>Sardinops ocellata</i>          | South African pilchard   | 194          | 65            | 14–31                | –            | –             | –                    |
| <i>Atherina breviceps</i>          | Cape silverside          | 44           | 29            | 51–83                | 77           | 65            | 42–89                |
| <i>Gilchristella aestuarii</i>     | estuarine round-herring  | 45           | 12            | 37–66                | 1            | 6             | 56                   |
| <i>Psammogobius knysnaensis</i>    | Knysna sandgoby          | 15           | 53            | 7–52                 | 20           | 65            | 7–59                 |
| <i>Caffrogobius multifasciatus</i> | prison goby              | 1            | 6             | 41                   | 22           | 29            | 11–25                |
| <i>Parablennius cornutus</i>       | horned blenny            | 71           | 59            | 4–23                 | 1            | 6             | 19                   |
| <i>Trachurus capensis</i>          | maasbanker               | 5            | 18            | 11–25                | 1            | 6             | 15                   |
| <i>Syngnathus acus</i>             | longnose pipefish        | 2            | 12            | 57                   | 2            | 6             | 59–74                |
| <i>Monodactylus falciformis</i>    | Cape moony               | 2            | 12            | 6                    | 12           | 29            | 7–10                 |
| <i>Lithognathus mormyrus</i>       | sand steenbras           | 1            | 6             | 76                   | –            | –             | –                    |
| <i>Clinus superciliosus</i>        | super klipfish           | 1            | 6             | 24                   | 25           | 29            | 16–27                |
| <i>Rhabdosargus globiceps</i>      | white stumpnose          | 1            | 6             | 21                   | –            | –             | –                    |
| <i>Lithognathus lithognathus</i>   | white steenbras          | 1            | 6             | 19                   | 3            | 12            | 11–14                |
| <i>Argyrosomus hololepidotus</i>   | kob                      | 1            | 6             | 7                    | –            | –             | –                    |
| <i>Diplodus cervinus</i>           | zebra                    | 1            | 6             | 7                    | –            | –             | –                    |
| <i>Amblyrhynchotes honckenii</i>   | evileyed blaasop         | –            | –             | –                    | 4            | 18            | 50–76                |
| <i>Mugil cephalus</i>              | flathead mullet          | –            | –             | –                    | 2            | 6             | 27–28                |
| <i>Chorisochismus dentex</i>       | rocksucker               | –            | –             | –                    | 1            | 6             | 10                   |
| <i>Pomadasys olivaceum</i>         | piggy                    | –            | –             | –                    | 10           | 29            | 12–49                |
| <i>Valamugil buchani</i>           | bluetail mullet          | –            | –             | –                    | 2            | 12            | 20–21                |
| <i>Pomatomus saltatrix</i>         | elf                      | –            | –             | –                    | 1            | 6             | 201                  |
| <i>Myxus capensis</i>              | freshwater mullet        | –            | –             | –                    | 1            | 6             | 41                   |
| <i>Liza dumerili</i>               | groovy mullet            | –            | –             | –                    | 5            | 18            | 202–260              |
| <i>Coracinus multifasciatus</i>    | banded galjoen           | –            | –             | –                    | 1            | 6             | 20                   |
| <i>Elops machnata</i>              | tenpounder               | –            | –             | –                    | 1            | 6             | 39                   |
| <i>Chaetodon marleyi</i>           | double butterflyfish     | –            | –             | –                    | 1            | 6             | 21                   |
| <i>Myliobatis aquila</i>           | eagleray                 | –            | –             | –                    | 1            | 6             | 400                  |

**Figure 5** Density of fish larvae and juveniles in the plankton samples of Session 2 (surface and bottom samples averaged).

( $\bar{x} = 1,9$ ) ( $t$  test for independent sample means  $p < 0,05$ ) but mean densities at night ( $\bar{x} = 1,0 \text{ m}^{-3}$ ) were not significantly higher than during the day ( $\bar{x} = 0,5 \text{ m}^{-3}$ ) ( $t$ -test for indepen-

dent samples means  $p > 0,05$ ). In the seine-net catches, a total of 4 848 fish of 30 species was captured (Table 1). *Rhabdosargus holubi* occurred in 82% of the hauls, *Liza richardsoni*, *Heteromycteris capensis* and *Diplodus sargus* each in 70% and *Sarpa salpa* in 47%. Juveniles of the pelagic species *Engraulis capensis* and *Etrumeus teres* were also captured.

## Discussion

Fish occurring in South African estuaries have been divided into categories by Wallace, Kok, Beckley, Bennett, Blaber & Whitfield (1984) on the basis of the extent to which their juveniles are dependent on estuaries. In the present context, these categories can be condensed into three groups, namely resident estuarine species, marine species utilizing estuaries as nursery areas and incidental marine species. The influx and efflux of larvae and juveniles of these groups to and from estuaries are likely to differ as follows:

- Resident estuarine species spawn in the estuary and their larvae should occur regularly in the plankton but may be lost from the estuary on the ebb-tide as estuarine water flows seaward;

- (ii) In the case of marine species spawning at sea but utilizing the estuary as a nursery area, larvae and juveniles should enter on the flood-tide;
- (iii) Incidental marine species are likely to have an irregular influx and efflux of larvae.

Examination of the tidal distribution of ichthyoplankton in the mouth of the Swartkops estuary during the sampling sessions, reveals that three such patterns can be distinguished.

Species falling into the first group include *Caffrogobius multifasciatus*, *Psammogobius knysnaensis* (Gobiidae) and *Omobranchus woodi* (Blenniidae), all small species with demersal eggs (Gilchrist & Hunter 1919; Breder & Rosen 1966) which are known to spawn in the Swartkops estuary (Melville-Smith & Baird 1980). Larvae of these species, together with those of *Gilchristella aestuarius* from the upper reaches, dominate the ichthyoplankton of the Swartkops estuary (Melville-Smith & Baird 1980). The larvae of *Caffrogobius multifasciatus*, *Psammogobius knysnaensis* and *Omobranchus woodi* captured in the plankton tows during the present study, were all very small (95% < 5 mm) and occurred frequently in the samples. Larvae of *Caffrogobius multifasciatus* were particularly abundant during Session 1 with a large efflux on the ebb-tide. Although reduced, their density was also relatively high on the early morning flood-tide, probably as a result of transport back into the estuary of some of these larvae. *Psammogobius knysnaensis* and *Omobranchus woodi* showed marked effluxes of larvae on the ebb-tide in Session 2.

Melville-Smith, Baird & Wooldridge (1981), when investigating tidal movements of larvae of the estuarine species *Gilchristella aestuarius* in the middle reaches of the Sundays estuary, also found that densities increased on the ebb-tide and decreased on the flood-tide. In the middle reaches of the Sundays estuary, current velocity was stratified and *Gilchristella aestuarius* larvae and some estuarine copepods (Wooldridge & Erasmus 1980) were found to concentrate in the slower-moving bottom water to prevent themselves from being carried seawards. However, in the mouth of the Swartkops estuary, current velocities are not significantly different between surface and bottom (1 m above substratum) waters (paired sample *t* test  $p > 0,05$ ) and such a mechanism for avoiding being swept out to sea on the ebb-tide would be to no avail.

In the second group of fish, flood-tide immigration of larval and juvenile *Rhabdosargus holubi*, *Heteromycteris capensis*, *Spondylisoma emarginatum* and in lower densities *Liza richardsoni*, *Monodactylus falciformis*, *Diplodus sargus* and *Atherina breviceps* was significantly greater than the ebb-tide efflux (Spearman's rank correlation  $p < 0,05$ ). All these marine species occur as juveniles in the Swartkops estuary (Winter 1979; Beckley 1983a) although the extent to which they depend on the estuary as a nursery area differs (Wallace *et al.* 1984). The sparids, mullet and soles had definitive fin elements and their size (7–14 mm) corresponds with that of one- to two-month-old specimens reared at 15°C by Brownell (1979).

The seine-net catches, which were concentrated on the bank near the mouth, also contained similar sized juvenile sparids, mullet and soles during flood-tides. Despite the absence of these juveniles from plankton samples during the ebb-tides, they were captured in more than 70% of ebb-tide seine-net samples. There is thus a possibility that juveniles migrate to the banks during the ebb-tide to avoid being swept back to sea. Wooldridge & Erasmus (1980) found that two mysid spe-

cies maintained position in the estuary in this way and Emmerson (1983) suggested that zoea 6 *Palaemon pacificus* also use this mechanism whilst immigrating into the Swartkops estuary. Quantitative cross-channel measurements of current velocities and juvenile fish densities would, however, be necessary to confirm that juvenile marine fish use this mechanism as well.

The larvae of several marine species which occur incidentally in estuaries were also captured. *Sardinops ocellata*, *Engraulis capensis* and *Etrumeus teres* are pelagic shoaling species and the occurrence of their larvae in the ichthyoplankton and seine-net catches in the mouth of the Swartkops estuary was unexpected. Larvae and juveniles of these species are, however, abundant in the inshore ichthyoplankton of Algoa Bay and collectively comprised 47% of the total catch in a two-year survey (Beckley 1983b). Their presence in the estuary, particularly the night ebb-tide in Session 1, may possibly be accounted for by them having been swept into the estuary on the preceding spring flood-tide and becoming temporarily trapped in a plug of tidal water. The presence of *Trachurus capensis* and *Umbrina capensis* is also regarded as incidental.

*Clinus superciliosus*, *Syngnathus acus* and *Parablennius cornutus* do not fit easily into any of the three groupings outlined above. *Clinus superciliosus* and *Syngnathus acus* are complicated cases as these species exhibit reproductive specializations (viviparity and possession of a male brood pouch, respectively) and breed in both estuaries and the sea (Day, Blaber & Wallace 1981). *Parablennius cornutus* is unknown from the Swartkops estuary, except for three larval specimens (Melville-Smith 1978). However, there has not been an investigation of the cryptic fish occupying the rocky areas of the north bank near the mouth, where this blenny could occur. On the other hand, larvae of this species are also abundant in the inshore plankton (Beckley 1983b) and the larvae in the mouth of the estuary during Session 1 could thus also be due to an influx on the spring-tide, similar to that suggested for clupeid and engraulid larvae.

Finally, the movement of fish larvae and juveniles in the mouth of the Swartkops estuary is concluded to be largely by passive drift, though active swimming may be utilized by some marine migrants. The larvae of the estuarine resident species, because of their small size and absence of fin elements, appear to be entirely at the mercy of tidal currents and many are lost from the estuary on the ebb-tide. Conversely, marine species are swept into the estuary on the flood-tide and it is suggested that these juveniles, because of their larger size and definitive fin elements, can actively prevent themselves from being flushed back out to sea by migrating to the banks to avoid the mainstream ebb current.

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## References

- AKATSU, S., OGASAWARA, Y. & YASUDA, F. 1977. Spawning behaviour and development of eggs and larvae of the striped fingerfish, *Monadactylus sebae*. *Japan. J. Ichthyol.* 23: 208–214.
- BECKLEY, L.E. 1983a. The ichthyofauna associated with *Zostera capensis* Setchell in the Swartkops estuary, South Africa. *S. Afr. J. Zool.* 18: 15–24.
- BECKLEY, L.E. 1983b. Community structure of ichthyoplankton off sandy beaches in Algoa Bay, South Africa. In: Sandy beaches as ecosystems, (eds) McLachlan, A. & Erasmus, T. p. 747, W. Junk, The Hague, Netherlands.
- BLABER, S.J.M. & BLABER, T.G. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. *J. Fish Biol.* 17: 143–162.
- BREDER, C.M. & ROSEN, D.E. 1966. Modes of reproduction in fishes. T.F.H. Publications, Jersey City, U.S.A.
- BROWNELL, C.L. 1979. Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. *Ichthyol. Bull. J.L.B. Smith Inst. Ichthyol.* 40: 1–84.
- CLARK, J., SMITH, W.G., KENDALL, A.W. & FAHAY, M.P. 1969. Studies of estuarine dependence of Atlantic coastal fishes. *U.S. Fish & Wildlife Service Tech. paper* 28: 1–132.
- CREUTZBERG, F. 1958. Use of tidal streams by migrating eelers (*Anguilla vulgaris* Turt.). *Nature* 181: 857–858.
- DAY, J.H., BLABER, S.J.M. & WALLACE, J.H. 1981. Estuarine fishes. In: Estuarine ecology with particular reference to southern Africa, (ed.) Day, J.H. pp. 197–221, A.A. Balkema, Cape Town, South Africa.
- 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.
- GILCHRIST, J.D.F. & HUNTER, H. 1919. Reproduction of fishes in Table Bay. *Trans. roy. Soc. S. Afr.* 8: 1–16.
- GUNTER, G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. In: Estuaries (ed.) Lauff, G.H. pp. 621–638, American Association for the Advancement of Science, Washington, U.S.A.
- HAIGH, E.H. 1972. Development of *Trachurus trachurus* (Carangidae), the South African maasbanker. *Ann. S. Afr. Mus.* 59: 47–70.
- JONES, P.W., MARTIN, F.D. & HARDY, J.D. 1978. Development of the fishes of the mid-Atlantic bight — an atlas of egg, larval and juvenile stages. U.S. Dept. of the Interior, U.S.A.
- LOUW, A.E. & O'TOOLE, M.J. 1977. Larval development of *Sardinops ocellata* (Pisces: Clupeidae). *Ann. S. Afr. Mus.* 72: 125–145.
- MARAIS, J.F.K. & BAIRD, D. 1980. Seasonal abundance, distribution and catch per unit effort of fishes in the Swartkops estuary. *S. Afr. J. Zool.* 15: 66–71.
- MELVILLE-SMITH, R. 1978. Aspects of the ecology of fish larvae in the Swartkops estuary, Port Elizabeth. M.Sc. thesis, University of Port Elizabeth, South Africa.
- MELVILLE-SMITH, R. & BAIRD, D. 1980. Abundance, distribution and species composition of fish larvae in the Swartkops estuary. *S. Afr. J. Zool.* 15: 72–78.
- MELVILLE-SMITH, R., BAIRD, D. & WOOLDRIDGE, T. 1981. The utilization of tidal currents by the larvae of an estuarine fish. *S. Afr. J. Zool.* 16: 10–13.
- PACHECO, A.C. & GRANT, G.C. 1973. Immature fishes associated with larval Atlantic menhaden at Indian River inlet, Delaware 1958–61. In: Proceedings of a workshop on egg, larval and juvenile stages of fish in Atlantic coast estuaries, (ed.) Pacheco, A.C. pp. 78–117. *Middle Atlantic Coastal Fisheries Centre Tech. publ.* No. 1.
- RANZI, S. 1933. Sparidae. In: Uova, larve e stadi giovanili di Teleostei. *Fauna & Flora Del Golfo di Napoli Monogr.* 38: 332–382.
- REDDERING, J.S.V. & ESTERHUYSEN, K. 1981. The sedimentary ecology of the Swartkops estuary. Unpublished ROSIE report No. 1, Dept. Geology, University of Port Elizabeth, South Africa.
- SMITH, J.L.B. 1965. The sea fishes of southern Africa. Central News Agency, Cape Town, South Africa.
- SMITH, M.M. 1975. Common and scientific names of the fishes of southern Africa. Part I. Marine fishes. *J.L.B. Smith Inst. Ichthyol. Spec. Publ.* 14: 1–178.
- VAN DER ELST, R. & WALLACE, J.H. 1976. Identification of the juvenile mullet of the east coast of South Africa. *J. Fish Biol.* 9: 371–374.
- WALLACE, J.H. 1975. The estuarine fish of the East coast of South Africa. III Reproduction. *Investl. Rep. oceanogr. Res. Inst.* 41: 1–51.
- WALLACE, J.H., KOK, H.M., BECKLEY, L.E., BENNETT, B., BLABER, S.J.M. & WHITFIELD, A.K. 1984. South African estuaries and their importance to fishes. *S. Afr. J. Sci.* 80: 203–207.
- WALLACE, J.H. & VAN DER ELST, R.P. 1975. The estuarine fishes of the East coast of South Africa. IV Occurrence of juveniles in estuaries. V Ecology, estuarine dependence and status. *Investl. Rep. oceanogr. Res. Inst.* 42: 1–63.
- WHITFIELD, A.K. 1980. Factors influencing the recruitment of juvenile fishes into the Mhlanga estuary. *S. Afr. J. Zool.* 15: 166–169.
- WHITFIELD, A.K. 1983. Factors influencing the utilization of southern African estuaries by fishes. *S. Afr. J. Sci.* 79: 362–365.
- WINTER, P.E.D. 1979. Studies on the distribution, seasonal abundance and diversity of the Swartkops estuary ichthyofauna. M.Sc. thesis, University of Port Elizabeth, South Africa.
- WOOLDRIDGE, T. 1983. Ecology of beach and surf zone mysid shrimps in the eastern Cape, South Africa. In: Sandy beaches as ecosystems, (eds) McLachlan, A. & Erasmus, T. pp. 449–460, W. Junk, The Hague, Netherlands.
- WOOLDRIDGE, T. & ERASMUS, T. 1980. Utilization of tidal currents by estuarine zooplankton. *Estuar. cstl. mar. Sci.* 11: 107–114.