



The Surf Zone Ichthyoplankton Adjacent to an Intermittently Open Estuary, with Evidence of Recruitment during Marine Overwash Events

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The composition, structure and seasonality of ichthyoplankton in the surf zone adjacent to the mouth of the intermittently open East Kleinemonde Estuary (33°32'S, 27°03'E) were investigated over a period of 2 years. Altogether 451 fishes, representing at least 21 taxa from 14 families, were collected. The assemblage was dominated by postflexion larvae of euryhaline marine species that are dependent on estuaries as nursery areas. The sparid *Rhabdosargus holubi* was the most abundant taxon and constituted more than 77% of the total catch. A distinct modal size class was identified for *R. holubi*, while the mean individual size of this and other abundant taxa was comparable to the observed recruitment size range reported from a wide variety of estuarine nursery habitats in southern Africa. Periodic regression analyses revealed significant peaks in abundance of larval *R. holubi* during late winter (August), at dawn and dusk, at new and full moon (spring tides), and on the flood stage of the tidal cycle. Evidence for estuarine immigration during marine overwash events (surging rough seas that enter the estuary) is provided by (1) the stranding of postflexion larvae in the region of the closed estuary mouth following these events, and (2) back extrapolation from length modes within the estuary to coincide with such an event. The advantages and disadvantages of such a recruitment strategy are discussed. © 2001 Academic Press

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Introduction

Studies conducted in southern Africa and elsewhere have shown that the majority of fish species found in estuaries recruit from the marine environment at a late larval or early juvenile stage of development (Neira *et al.*, 1992; Tzeng & Wang, 1992; Whitfield & Kok, 1992; Warlen, 1994). Opportunities for marine-spawned larvae to recruit into most southern African estuaries is impeded because approximately 70% of them are cut off from the sea for extended periods by sand bars across the mouth. Whitfield (1992a) classifies these as temporarily open/closed estuaries. In some regions along the South African coastline (e.g. KwaZulu-Natal) these estuaries usually open annually in response to seasonal precipitation (Harrison & Whitfield, 1995). However, rainfall along the south-eastern coastal belt of the Eastern Cape Province is highly variable and not as strongly seasonal (Kopke, 1988), and mouth opening events occur sporadically throughout the year (Cowley, 1998). Probably in consequence, temporarily open/closed estuarine

systems have lower species diversity than permanently open estuaries (Begg, 1984; Bennett, 1989; Whitfield *et al.*, 1989).

Despite the absence of recent mouth openings, newly recruited juveniles of marine-spawning taxa (e.g. Mugilidae and Sparidae) are often recorded in temporarily open/closed estuaries. This puzzle is only resolved if recruitment also takes place during barrier overwash conditions. These overwash events usually occur during rough sea conditions when pulses of surging waves enter the closed estuary.

The importance of overwash events for recruiting and emigrating fishes associated with temporarily open/closed estuaries has received insufficient scientific attention (Whitfield, 1992b). Most studies on larval fishes in southern Africa have been conducted in either the offshore and nearshore marine environments (e.g. Olivar & Fortuno, 1991; Tilney & Buxton, 1994; Beckley & Connell, 1996) or within estuaries (Melville-Smith & Baird, 1980; Beckley, 1985; Whitfield, 1989a,b), with few studies focusing on the link with surf zone ichthyoplankton (Whitfield, 1989c; Harris & Cyrus, 1996). Although work in the

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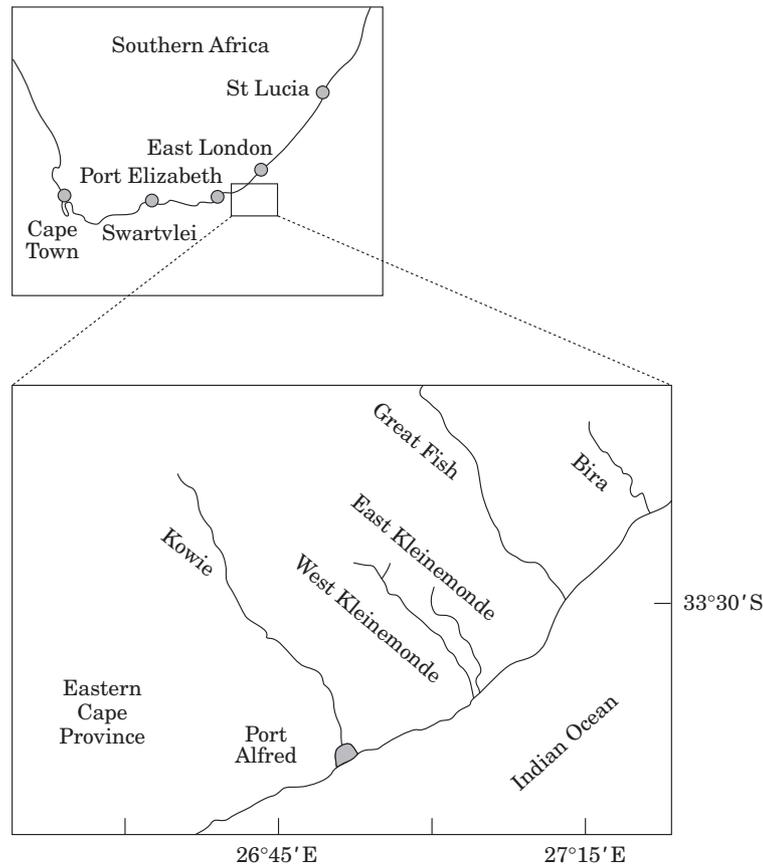


FIGURE 1. Map of southern Africa showing the location of the East Kleinemonde and adjacent estuaries.

surf zone faces difficulties and dangers associated with sampling these high-energy environments, the surf zone is an important transit region for larvae recruiting from nearshore spawning areas into estuarine nursery areas.

The aim of this study was to investigate the ichthyoplankton species composition, seasonality and abundance in the surf zone adjacent to the mouth of the predominantly closed East Kleinemonde Estuary on the south-eastern Cape coast. This work also provides evidence of postflexion larval immigration to estuaries during marine overwash events.

Material and methods

Sampling procedure

Surf zone. Ichthyoplankton samples were collected in the surf zone adjacent to the mouth of the East Kleinemonde estuary (33°32'S, 27°03'E; Figure 1) between August 1994 and September 1996. Sampling was conducted subject to safety considerations; consequently data are not representative of extreme weather or wave conditions. Despite these limitations,

sampling was conducted on a total of 45 days, representing every month except June 1995 and April 1996 during the 2-year sampling period. Larval fish collections were made using a floating plankton sled fitted with a 500 μm nylon mesh net, which sampled the upper 30 cm of the water column. The net, with a mouth area of 0.17 m^2 was attached to a 3 m rope and towed through the surf zone, parallel to the shoreline in water ranging from 0.5 to 1.5 m in depth. The net was towed at a rate of approximately 1 m s^{-1} for a duration of exactly 2 min. The mean volume of water passing through the net for each haul was estimated at approximately 20 m^3 (i.e. by multiplying the length of the sampling transect and the cross sectional area of the net). On 84% of sampling days, five tows were conducted, and on the remaining days two to four were taken. All samples were preserved in formalin.

Beach morphology in the mouth region of the East Kleinemonde estuary is classified as an intermediate type with a ridge-runnel or low tide terrace (Short & Wright, 1983). Initial trials revealed that sampling during the low tide period was impractical due to a lack of water depth. Hence, most samples were collected at or near high tide when sea conditions were

fairly calm, with very little or no longshore current (side wash) and light winds.

Physical data collected on each sampling day included time of day, state of tide, wave height, wind speed and direction, and temperature (to the nearest 0.5 °C). The state of the tide for purposes of analysis was assessed from sampling time and the South African Navy tide tables. Most samples were taken during daylight, and there were also two 24 h sampling sessions (11–12 February and 15–16 May 1995) using the same methods. On each of these occasions weather conditions were very calm and a triplicate series of 2 min hauls was taken every 3 h over a full diel period (i.e. 24 hauls per cycle).

Overwash samples. Following marine overwash events on 4 and 5 November 1998, fish larvae were collected in isolated pools on the sandbar in the mouth region of the closed East Kleinemonde and Bira estuaries (Figure 1). These pools became isolated from the sea as the tide receded after the overwash events and dried up quickly (<1 h) as the water drained into the sand. Eight pools were inspected, seven at Bira and one at Kleinemonde. Any larvae present in the pools were collected for later analysis in the laboratory.

Sample analyses

All fish were measured to the nearest 0.1 mm body length (BL) using a dissecting microscope with an ocular micrometer and identified to the lowest possible taxon using van der Elst and Wallace (1976), Melville-Smith (1978), Brownell (1979), Smith and Heemstra (1986), and Olivar and Fortuno (1991).

Statistical analyses

Periodic regression (Bliss, 1958; Batschelet, 1981), also summarized in Bell *et al.* (2001), was used to evaluate cyclic trends in relative abundance. Abundances from each tow were transformed to $\ln(\text{number}+1)$ and regressed against angular transforms of seasonal, lunar, daily and tidal periods (along with second harmonics for all periodic variables). Although the seasonal component was of principal interest, inclusion of other variables is beneficial because, generally, the effect of x_1 on y_1 , when $x_2, x_3 \dots x_n$ also affect y , is most accurately estimated in a procedure that includes x_2 to x_n (i.e. the estimate of the effect of x_1 is better because it is corrected for the effects of x_2 and x_n). The incidental benefit is that the effects of x_2 to x_n are estimated as well as that of x_1 .

Each model was evaluated by examining the remaining trend in residuals with respect to the

independent variables (in the case of periodic variables, their linear equivalents were plotted). Normality of residuals was evaluated by normal probability plots (Wilkinson, 1987).

Results

Surf zone samples

The catch composition and abundance of ichthyoplankton sampled in the surf zone adjacent to the mouth of the East Kleinemonde Estuary are given in Table 1. A total of 451 fishes, representing at least 21 taxa from 14 families were collected from 251 plankton hauls. The family Sparidae dominated the total catch composition with almost 85%, while Mugilidae, Soleidae, Monodactylidae and Atherinidae contributed 4.4%, 4.2%, 2% and 1.1%, respectively. Each remaining family comprised less than 1%. The numerically dominant species (*Rhabdosargus holubi*) accounted for more than 77% of the overall catch. The other dominant taxa included unidentified Mugilidae (4.4%), *Diplodus sargus capensis* (4.2%), *Heteromycteris capensis* (3.6%), *Monodactylus falciformis* (2%) and a single unidentified sparid species (1.8%). Less abundant taxa collectively comprised only 6.4% of the total catch (Table 1).

Mean ichthyoplankton densities in the surf zone were 9 per 100 m³ (all taxa), and 7 per 100 m³ for *R. holubi* (Table 1). A maximum concentration of 325 larvae per 100 m³ for the dominant species was recorded in August 1995.

Using Whitfield's (1998) estuary-association categorization, the taxonomic composition of surf zone ichthyoplankton indicated a high degree of estuarine dependence. Euryhaline marine species (category II) comprised almost 95% of the total catch with *R. holubi* being the most abundant species in category IIa. Other taxa in this category included *M. falciformis* (2%), *Elops machnata* (0.7%) and the unknown contribution of *Mugil cephalus* to the catch of Mugilidae. Species in category IIb included *H. capensis* (3.6%) and *Solea bleekeri* (0.7%), with taxa not dependent on estuaries (category III) contributing only 0.4% to the total catch (excluding the possible contribution of the 14 unidentified specimens). A few larvae of category I species were also recorded from the surf zone during this study (Table 1).

All specimens, except for five *Atherina breviceps*, one *R. holubi* and one mugilid, were postflexion larvae according to Kendall *et al.* (1984). The dominant length classes, ranging from 9 to 14 mm BL, were similar for the three numerically dominant taxa (Figure 2). The mean body lengths of the estuarine dependent species sampled in the Kleinemonde surf

TABLE 1. Ichthyoplankton catch composition (ranked according to family abundance) and mean densities (number per 100 m³) recorded from the surf zone adjacent to the mouth of the East Kleinemonde Estuary between August 1994 and September 1996

Family	Species	Number caught	Mean density (N per 100 m ³)	Estuary-dependence category
Sparidae	<i>Rhabdosargus holubi</i>	350	7.0	IIa
	<i>Diplodus sargus capensis</i>	19	0.4	IIc
	<i>Sarpa salpa</i>	2	*	IIc
	Unidentified (1 species)	8	*	(?)
Mugilidae	Unidentified (several species)	20	0.4	IIa, b & Vb
Soleidea	<i>Heteromycteris capensis</i>	16	0.3	IIb
	<i>Solea bleekeri</i>	3	*	IIb
Monodactylidae	<i>Monodactylus falciformis</i>	9	0.2	IIa
Atherinidae	<i>Atherina breviceps</i>	6	0.1	Ib
Blenniidae	Unidentified (1 species)	3	*	(?)
Clupeidae	<i>Gilchristella aestuaria</i>	1	*	Ia
	Unidentified (1 species)	2	*	(?)
Elopidae	<i>Elops machnata</i>	3	*	IIa
Gobiidae	<i>Psammogobius knysnaensis</i>	3	*	Ia
Clinidae	<i>Clinus superciliosus</i>	1	*	Ib
	Unidentified (1 species)	1	*	(?)
Tetraodontidae	Unidentified (1 species)	2	*	III(?)
Bothidae	Unidentified (1 species)	1	*	(?)
Syngnathidae	<i>Syngnathus acus</i>	1	*	Ib
Total		451	9.0	

The estuary-dependence category for each species are according to Whitfield (1998), where Ia=resident estuarine species which have not been recorded spawning in the marine or freshwater environment, Ib=resident estuarine species which also have marine or freshwater breeding populations, IIa=euryhaline marine species which breed at sea but juveniles are dependent on estuaries as nursery areas, IIb=euryhaline marine species that have juveniles occurring mainly in estuaries but are also found at sea, IIc=euryhaline marine that have juveniles occurring in estuaries but are usually more abundant at sea, III=marine species which occur in estuaries in small numbers but are not dependent on these systems (*denotes a mean density of less than 0.1 per 100 m³).

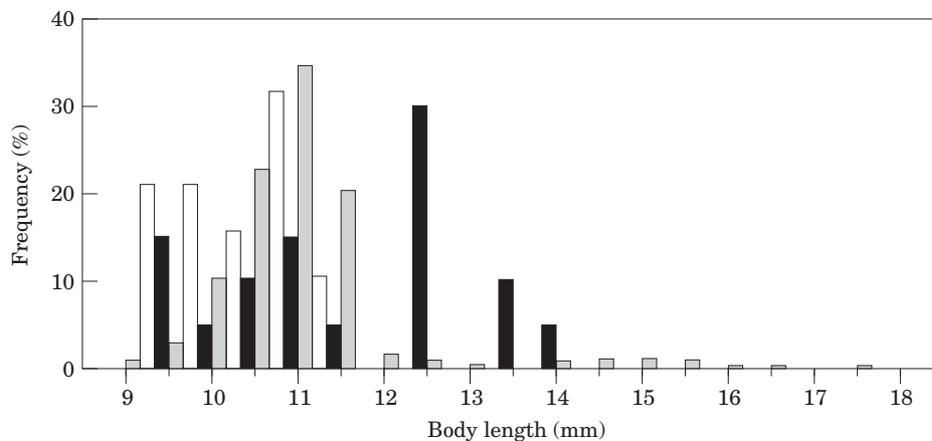


FIGURE 2. Ichthyoplankton length frequency distribution of the three most abundant taxa sampled in the surf zone adjacent to the mouth of the East Kleinemonde estuary (N =total number of fish samples). □ *Rhabdosargus holubi* ($N=349$); □ *Diplodus sargus capensis* ($N=19$); ■ Mugilidae ($N=19$).

zone were consistent with studies conducted in other southern African estuaries (Table 2).

Periodic regression identified seasonal, lunar, daily and tidal influences on *R. holubi* larval abundance in

the Kleinemonde surf zone. The contribution of the seasonal variable (time of year) was lowest between November and April, with a distinct peak at 9 August [Figure 3(a); $P<0.001$]. Also important were time

TABLE 2. A comparison of ichthyoplankton size ranges (mm BL) of five common taxa recorded from the Kleinemonde surf zone and other estuarine localities in South Africa (* = total length)

Reference	Locality	Species				
		<i>R. holubi</i>	<i>D. s. capensis</i>	Mugilidae	<i>H. capensis</i>	<i>M. falciformis</i>
This study	Kleinemonde	9.3–21.0	9.0–11.4	9.2–18.5	6.3–8.0	4.6–6.1
Beckley (1985)	Surf zone	mean = 11.3	mean = 10.2	mean = 11.6	mean = 7.4	mean = 5.3
Harris (1996)	Swartkops estuary	9.0–13.0	9.0–10.0	12.0–14.0	7.0–10.0	
	Richards Bay harbour	6.5–11.0		9.5–11.0		
	Durban harbour	7.5–11.0		9.2–10.0		
Harris and Cyrus (1995)	St Lucia estuary	6.0–12.2		5.0–23.5		
Harrison and Whitfield (1990)	Sundays estuary	mostly < 15		mostly < 15		
Melville-Smith (1978)	Swartkops estuary	7.0–20.0*			7.0–10.0*	6.0–11.0*
Whitfield (1989a)	Swartvlei estuary	9.0–10.0		8.0–11.0	6.0–8.0	4.0–7.0
Whitfield (1994b)	Great Fish estuary	5–10 (>50%) 10–15 (>40%) 15–20 (<10%)		mostly 15–30		
	Sundays estuary	mostly 10–15		mostly 15–30		
	Kariega estuary	mostly 10–15		mostly 15–30		

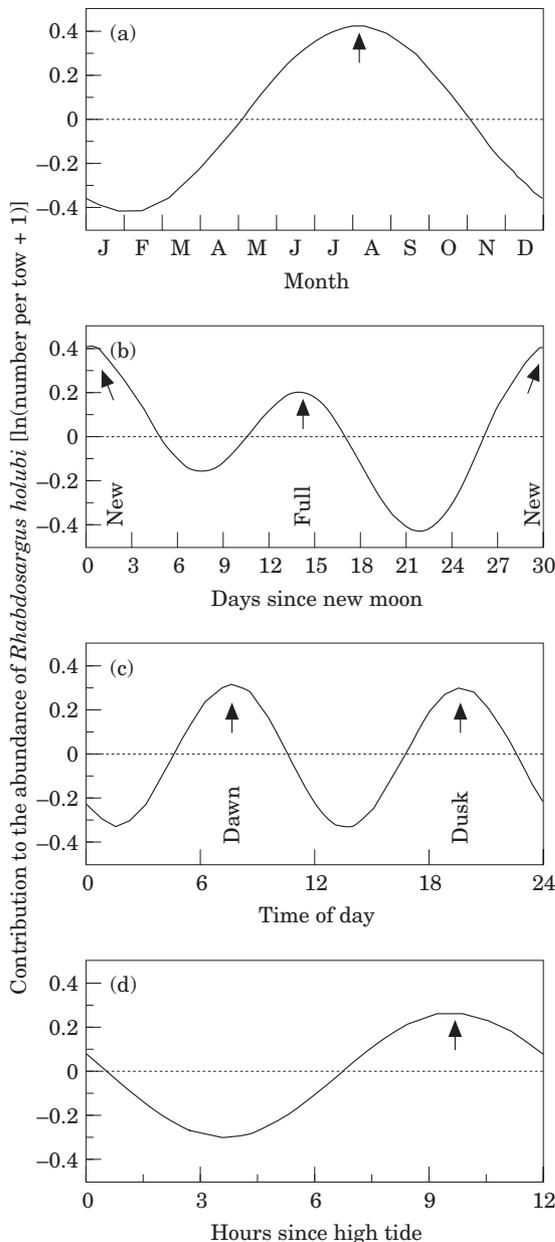


FIGURE 3. The contribution of each periodic variable to the abundance of *Rhabdosargus holubi* larvae in the Kleinemonde surf zone [values expressed as $\ln(\text{number per tow} + 1)$]. Over the full cycle of any periodic variable, by definition, its mean contribution (y) is zero. The time scales (x) differ among plots and are arranged from longest (A) to shortest (D). Arrows indicate the location of peak contributions.

of day, lunar month and hours since high tide [Figure 3(b,c,d)], with peak contributions to abundance near (1) dawn and dusk ($P < 0.05$); (2) new and full moon spring tides ($P < 0.01$); and (3) the peak of the flood tide (approximately 10 h after the last high tide; $P < 0.05$).

The periodic regression equation for *R. holubi* ($N = 251$, $R^2 = 0.329$, $P = 0.0001$) is:

$$\begin{aligned}
 y = \ln(1 + \text{abundance}) = & 0.284 - 0.252 \sin \text{RDOY}^{***} \\
 & - 0.395 \cos \text{RDOY}^{***} + 0.192 \sin \text{RHDOY}^{***} \\
 & - 0.044 \cos \text{RHDOY} + 0.167 \sin \text{RLU}^{**} \\
 & + 0.147 \cos \text{RLU}^* + 0.107 \sin \text{RHLU} \\
 & + 0.31 \cos \text{RHLU}^{***} - 0.016 \sin \text{RTOD} \\
 & + 0.021 \cos \text{RTOD} - 0.178 \sin \text{RHTOD} \\
 & - 0.232 \cos \text{RHTOD} - 0.232 \sin \text{RSncHiTide}^* \\
 & + 0.109 \cos \text{RSncHiTide} + 0.007 \sin \text{RHSncHiTide} \\
 & + 0.157 \cos \text{RHSncHiTide}^*,
 \end{aligned}$$

where R denotes angular transform to radians; H denotes second harmonic (e.g. 12 h cycle is second harmonic of diel 24 h cycle). Primary independent time variables are: DOY, day of year (0–364.99); LU, time since new moon on 29.5 day cycle; TOD, decimal time of day (0–1); SncHiTide, time since high tide (12.5 h cycle). *** indicates $P < 0.001$ (very highly significant), ** indicates $P < 0.01$ (highly significant), * indicates $P < 0.05$ (significant).

Seasonality peaks in August were found also for both *Diplodus sargus capensis* ($P < 0.05$) and the mugilids ($P < 0.01$) but not for the other species collected (for some of these species there was insufficient data for analysis).

Overwash samples

Overwash samples were dominated by three taxa (*Rhabdosargus holubi*, *Monodactylus falciformis* and Mugilidae). A sample collected near the mouth of the East Kleinemonde Estuary contained 170 stranded fishes, while two samples (145 and 89 fish) were collected near the mouth of the Bira Estuary. Despite a much lower diversity (only three taxa), the catch composition and size range of the overwash samples were similar to those collected in the surf zone (Table 3).

The presence of fish in temporary, rapidly draining beach pools suggested that wave surges during the overwash event aided the transport and hence introduction (recruitment) of postflexion larvae into the closed East Kleinemonde and Bira estuaries. This is supported by length frequency data of fishes sampled within the East Kleinemonde Estuary (after Cowley, 1998). Back-extrapolated growth of a distinct size cohort of *R. holubi* indicated that recruitment within the reported size range (Table 2) could only have coincided with a period during which there were no mouth openings. The only access opportunities during this time were a series of marine overwash

TABLE 3. Composition and size range (mm BL) of fish collected during this study in the overwash (Kleinemonde and Bira data combined) and surf zone samples

Species		Number caught	% catch composition	Mean BL (mm)	Length range
<i>Rhabdosargus holubi</i>	Surf zone	350	77.6	11.3	10–12.1
	Overwash	368	91.1	10.2	9.0–12.1
<i>Monodactylus falciformis</i>	Surf zone	9	2	5.3	4.6–6.1
	Overwash	10	2.5	5.8	5.4–6.1
Mugilidae	Surf zone	20	4.4	11.6	9.2–18.5
	Overwash	26	6.4	13.3	11.0–22.1
Others	Surf zone	72	16.0	—	—
	Overwash	0	0	—	—

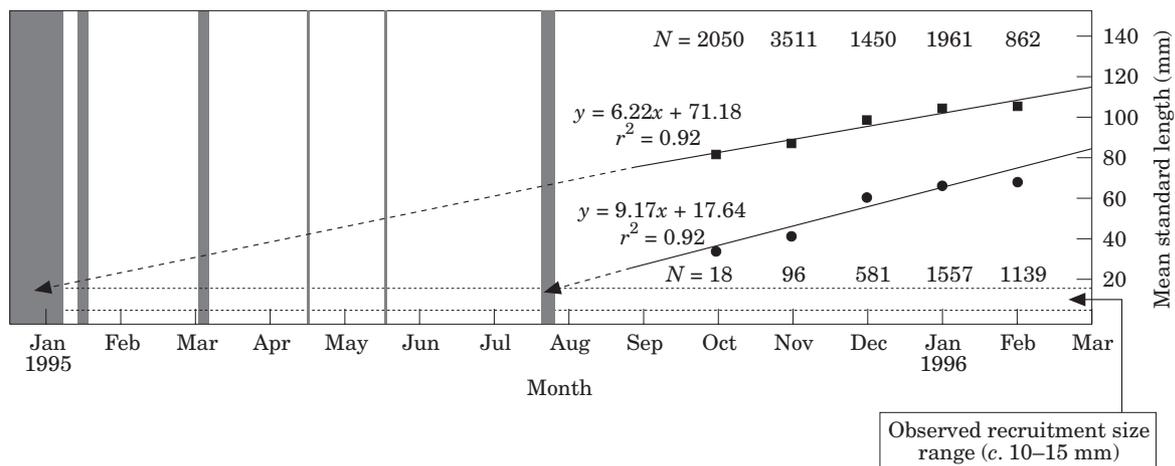


FIGURE 4. The observed growth curves (solid lines) of two *Rhabdosargus holubi* size cohorts caught in the East Kleinemonde estuary between October 1995 and February 1996 (after Cowley, 1998), with back extrapolation to reveal periods of recruitment that coincide with either open mouth conditions (solid bar) or marine overwash events (shaded bars).

events over six consecutive days in late July 1995 (Figure 4).

Discussion

The diversity of ichthyoplankton recorded during this study (21 taxa, 14 families) was similar to that found in the surf zone adjacent to the warm-temperate Swartvlei estuary (26 taxa, 16 families; Whitfield, 1989c), but considerably less diverse than that reported from the subtropical St Lucia estuary region (88 taxa, 47 families; Harris & Cyrus, 1996). The difference at St Lucia is ascribed to the higher contribution of tropical offshore spawning species (category III). The predominance of estuarine dependent (category I and II) species at Kleinemonde (95%) is consistent with the findings of Whitfield (1989c) at Swartvlei, where they accounted for >80% of the surf zone ichthyoplankton. Harris and Cyrus (1996) found that species with some degree of estuarine association

comprised only 36% in terms of the number of taxa, but were the dominant category in terms of abundance of larvae (60%) in the surf zone at St Lucia. The collection of the resident estuarine species (*Gilchristella aestuaria*) in the Kleinemonde surf zone indicates that the larvae are sometimes washed out of the estuary when it is open, and suggests a possible mode of gene flow between estuaries.

During their early life histories, estuary-associated fishes are known to occupy a wide variety of habitats within the coastal environment (Hoss & Thayer, 1993). This study supports the view (Whitfield, 1989c) that, for postlarvae, the surf zone is a waiting area for estuary access. Firstly, the dominance of category II species (estuarine; see Table 1) and rarity of category III species (marine) indicates that the larval fish assemblage of the Kleinemonde surf zone consists mainly of species that are in search of an estuarine nursery habitat. Secondly, the size ranges are consistent amongst surf zone, overwash, and the

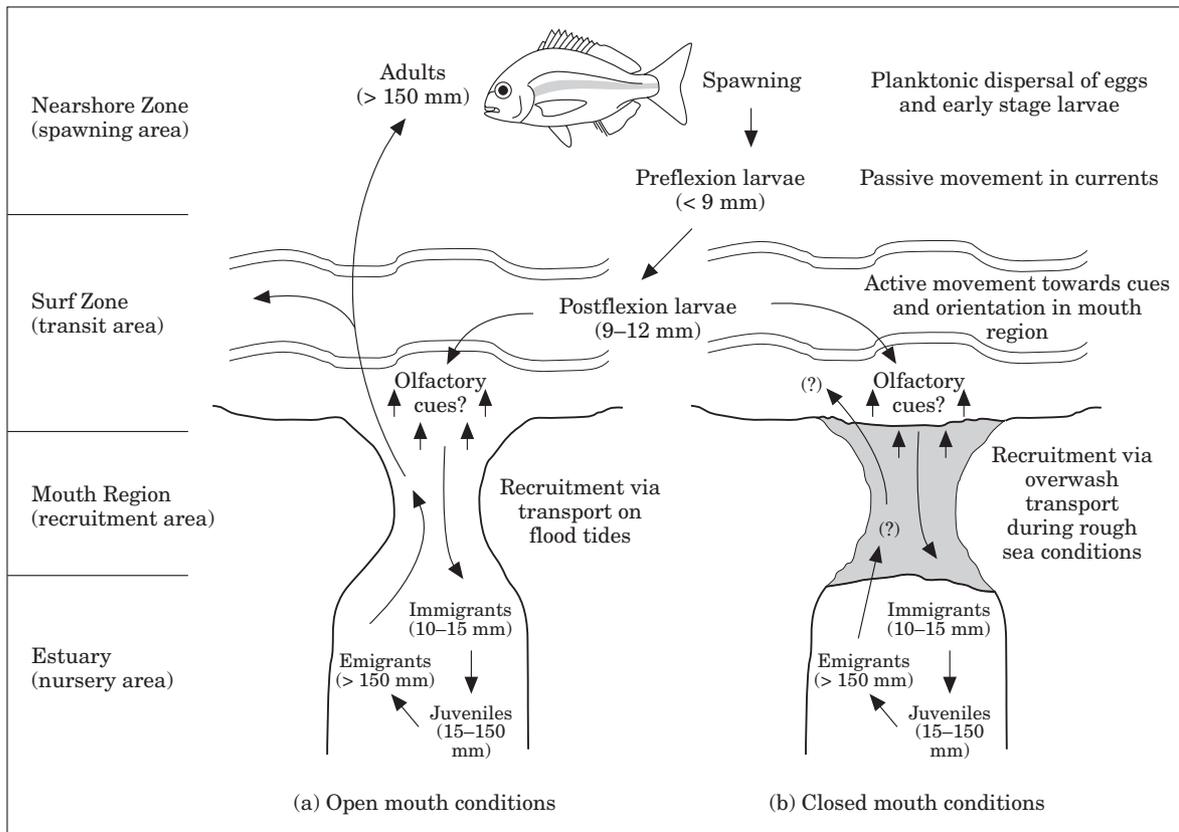


FIGURE 5. A diagrammatic representation of the life-cycle and proposed recruitment strategy of *Rhabdosargus holubi* into the East Kleinemonde estuary under (a) open mouth conditions and (b) closed mouth conditions.

lower limit found in estuaries (Tables 2, 3). The absence of larger specimens in the surf zone may be attributed to net avoidance, postlarval mortality, or already having left the surf zone.

High ichthyoplankton densities have been reported in spring and summer in both the surf zone (Whitfield, 1989c) and estuaries (Whitfield, 1989a; Warlen & Burke, 1990; Neira & Potter, 1994; Harris & Cyrus, 1995). These temporal peaks tend to coincide with greater planktonic food sources and higher water temperatures. It has been suggested that these fishes have timed their spawning to match the spatial and temporal coincidence of larvae and food items (Dickey-Collas *et al.*, 1996). However, the occurrence of fish larvae throughout the year, particularly of species associated with estuaries, is also documented (Melville-Smith & Baird, 1980; Yoklavich *et al.*, 1992).

Ichthyoplankton densities of the dominant species (*Rhabdosargus holubi*) within the surf zone at Kleinemonde showed a statistically significant peak during the late winter (August). This is consistent with Harris and Cyrus (1996) who recorded that this

species peaks in abundance during June and August at St Lucia. Whether or not such timing is adaptive depends on its match with, among other factors, opportunities to gain entry to the estuary. For the indicated peak in *R. holubi* larval abundance, the overall survival potential (assuming a daily survival of 90%) of a spawned cohort is approximately 10% when considering overwash events as the sole entry opportunity while, in contrast, the same potential for mouth openings alone is less than 0.001% (see Figure 4 in Bell *et al.*, 2001). From this comparison it is apparent that the timing of the peak in *R. holubi* larval abundance in the Kleinemonde surf zone is more consistent with an adaptation to take advantage of overwash events than openings.

Besides the influence of reproductive seasonality, aggregations of estuarine associated ichthyoplankton in the inshore zone have been allied to a number of physical and environmental factors. The characteristics of estuarine discharge water, including elevated nutrient levels, decreased salinity and increased turbidity may be important in eliciting a recruitment response for different fish species (Martin *et al.*, 1992;

Grimes & Kingsford, 1996; Harris & Cyrus, 1996). Whitfield (1994) hypothesized that estuarine water seeping through the sand bar of a temporarily open/closed estuary contains dissolved organic and/or inorganic olfactory cues, thus aiding the orientation of estuarine dependent larvae towards this habitat.

This study shows that *R. holubi* uses overwash events as an alternative means to access an estuary during closed mouth conditions. The significance of these overwash events as a recruitment opportunity is underscored by the fact the mouth of the East Kleinemonde Estuary was open to sea on only 43 days (2.6% of the time) between March 1993 and August 1997, while overwash events occurred on an additional 421 days (Cowley, 1998). Thus *R. holubi* and other species (e.g. *Monodactylus falciformis*) make use of two access routes into the East Kleinemonde Estuary. Firstly, under open mouth conditions, post-flexion larvae move from the surf zone directly into the estuary and secondly, under closed mouth conditions, postflexion larvae can remain in the surf zone until there is an opportunity to enter the estuary via overwash wave transport (see text, Figure 5). It is evident that there is some mortality in attempting to cross the barrier bar but this mortality must be considered in the context of increasing cumulative mortality in the surf zone.

In summary, the evidence to support overwash as an estuary access route is as follows: species composition and size ranges in the surf zone (this study), stranded fish in temporary beach pools near estuaries (this study), movement of larvae over a barrier bar into an estuary (Whitfield, 1992b), and back-extrapolation of fish length modes to indicate that recruitment coincided with overwash events (this study). Therefore, the importance of overwash to estuarine recruitment cannot be dismissed. Future work is needed to determine the relative importance of this mechanism to recruitment. Other important questions concern the behavioural response of larvae to high seas, whether their response is stronger when near estuary mouths, and what mortality is behaviourally induced as a result of attempting to enter estuaries during adverse sea conditions.

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References

- Batschelet, E. 1981 Circular statistics in biology. In *Mathematics in Biology* (Sibson, R. & Cohen, J., eds). Academic Press, London. 371 pp.
- Beckley, L. E. & Connell, A. D. 1996 Early life history of *Pomatomus saltatrix* off the east coast of South Africa. *Marine and Freshwater Research* 47(2), 319–322.
- Begg, G. W. 1984 The comparative ecology of Natal's smaller estuaries. *Natal Town and Regional Planning Report* 62, 182 pp.
- Bell, K. N. I., Pepin, P. & Brown, J. A. 1995 Seasonal, inverse cycling of length- and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* (Pisces) in Dominica, West Indies. *Canadian Journal of Fisheries and Aquatic Science* 52, 1535–1545.
- Bell, K. N. I., Cowley, P. D. & Whitfield, A. K. 2000 Seasonal variation in frequency of access to estuaries: implications for recruitment strategies. *Estuarine, Coastal and Shelf Science* (2001).
- Bennett, B. A. 1989 A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the south-western Cape, South Africa. *South African Journal of Marine Science* 8, 43–55.
- Bliss, C. I. 1958 Periodic regression in biology and climatology. *Bulletin of the Connecticut Agricultural Experimental Station, New Haven* 615, 1–55.
- Brownell, C. L. 1979 Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* 40, 1–84.
- Cowley, P. D. 1998 Fish population dynamics in a temporarily open/closed South African estuary. PhD thesis, Rhodes University, Grahamstown, South Africa. 145 pp.
- Dickey-Collas, M., Gowen, R. J. & Fox, C. J. 1996 Distribution of larval and juvenile fish in the western Irish Sea: relationship to phytoplankton, zooplankton biomass and recurrent physical features. *Marine and Freshwater Research* 47(2), 169–181.
- Grimes, C. B. & Kingsford, M. J. 1996 How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? *Marine and Freshwater Research* 47(2), 191–208.
- Harris, S. A. & Cyrus, D. P. 1995 Occurrence of fish larvae in the St. Lucia estuary, KwaZulu-Natal, South Africa. *South African Journal of Marine Science* 16, 333–350.
- Harris, S. A. & Cyrus, D. P. 1996 Larval and juveniles fishes in the surf zone adjacent to the St. Lucia estuary mouth, KwaZulu-Natal, South Africa. *Marine and Freshwater Research* 47(2), 465–482.
- Harrison, T. D. & Whitfield, A. K. 1995 Fish community structure in three temporarily open/closed estuaries on the Natal coast. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* 64, 1–80.
- Harrison, T. D. & Whitfield, A. K. 1990 Composition, distribution and abundance of ichthyoplankton on the Sundays River estuary. *South African Journal of Zoology* 25, 161–168.
- Hoss, D. E. & Thayer, G. W. 1993 The importance of habitat to the early life history of estuarine dependent fishes. *American Fisheries Society Symposium* 14, 147–158.
- Kendall, A. W., Ahlstrom, E. H. & Moser, H. G. 1984 Early life history stages of fishes and their characters. In *Ontogeny and Systematics of Fishes* (Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, A. W. & Richardson, S. L., eds). *Special Publication of the American Society of Ichthyology and Herpetology* 1, 11–22 (Proceedings of an International Symposium in La Jolla, California, August 1983).
- Kopke, D. 1988 The climate of the Eastern Cape. In *Towards an environmental plan for the Eastern Cape* (Bruton, M. N. & Gess, F. W., eds). Rhodes University, Grahamstown.
- Martin, T. J., Cyrus, D. P. & Forbes, A. T. 1992 Episodic events: the effects of cyclonic flushing on the ichthyoplankton of St Lucia estuary on the southeast coast of Africa. *Netherlands Journal of Sea Research* 30, 273–278.

- 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. *South African Journal of Zoology* **15**(2), 72–78.
- Neira, F. J. & Potter, I. C. 1994 The larval fish assemblage of the Nornalup-Walpole Estuary, a permanently open estuary on the southern coast of western Australia. *Australian Journal of Marine and Freshwater Research* **45**, 1193–1207.
- Neira, F. J., Potter, I. C. & Bradley, J. S. 1992 Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary. *Marine Biology* **112**(1), 1–16.
- Olivar, M. P. & Furtuno, J. M. 1991 Guide to ichthyoplankton of the Southeast Atlantic (Benguela Current Region). *Scientia Marina* **55**(1), 1–383.
- Short, A. D. & Wright, L. D. 1983 Physical variability of sandy beaches. In *Sandy Beaches as Ecosystems* (McLachlan, A. & Erasmus, T., eds). Junk Publishers, The Hague 757 pp.
- Smith, M. M. & Heemstra, P. C. (eds) 1986 *Smiths' Sea Fishes*. Macmillan Publishers, Johannesburg. 1047 pp.
- Tilney, R. L. & Buxton, C. D. 1994 A preliminary ichthyoplankton survey of the Tsitsikamma National Park. *South African Journal of Zoology* **29**, 204–211.
- Tzeng, W.-N. & Wang, Y.-T. 1992 Structure, composition and seasonal dynamics of the larval and juvenile fish community in the mangrove estuary of Tanshui River, Taiwan. *Marine Biology* **113**(3), 481–490.
- van der Elst, R. P. & Wallace, J. H. 1976 Identification of the juvenile mullet of the east coast of South Africa. *Journal of Fish Biology* **9**, 371–374.
- Warlen, S. M. 1994 Spawning time and recruitment dynamics of larval Atlantic menhaden, *Brevoortia tyrannus*, into a North Carolina estuary. *Fishery Bulletin, Washington* **92**(2), 420–433.
- Warlen, S. M. & Burke, J. S. 1990 Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. *Estuaries* **13**(4), 453–461.
- Whitfield, A. K. 1989a Fish larval composition, abundance and seasonality in a southern African estuarine lake. *South African Journal of Zoology* **24**(3), 217–224.
- Whitfield, A. K. 1989b Ichthyoplankton interchange in the mouth region of a southern African estuary. *Marine Ecology Progress Series* **54**, 25–33.
- Whitfield, A. K. 1989c Ichthyoplankton in a southern African surf zone: nursery area for the postlarvae of estuarine associated fish species? *Estuarine, Coastal and Shelf Science* **29**, 533–547.
- Whitfield, A. K. 1992a A characterization of southern African estuarine systems. *South African Journal of Aquatic Science* **18**(1/2), 89–103.
- Whitfield, A. K. 1992b Juvenile fish recruitment over an estuarine sand bar. *Ichthos* **36**, 23.
- Whitfield, A. K. 1994 Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. *Marine Ecology Progress Series* **105**, 257–267.
- Whitfield, A. K. 1998 Biology and Ecology of Fishes in Southern African Estuaries. *Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology* **2**, 223 pp.
- Whitfield, A. K. & Kok, H. M. 1992 Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southern coast of South Africa. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* **57**, 1–17.
- Whitfield, A. K., Beckley, L. E., Bennett, B. A., Branch, G. M., Kok, H. M., Potter, I. C. & Van der Elst, R. P. 1989 Composition, species richness and similarity of ichthyofaunas in eelgrass *Zostera capensis* beds of southern Africa. *South African Journal of Marine Science* **8**, 251–259.
- Wilkinson, L. 1987 *SYSTAT: The system for statistics*. Evanston, Illinois: Systat Inc.
- Yoklavic, M. M., Stevenson, M. & Caillet, G. M. 1992 Seasonal and spatial patterns of ichthyoplankton abundance in Elkhorn Slough, California. *Estuarine, Coastal and Shelf Science* **34**, 109–126.