

## Fish abundance in the Wilderness and Swartvlei lake systems: changes relative to environmental factors

Ian A. Russell

National Parks Board, P.O. Box 176, Sedgefield, 6573 Republic of South Africa

Received 10 March 1995; accepted 6 November 1995

Fish communities throughout the Wilderness and Swartvlei lake systems were sampled in the winters of 1991 and 1993 using gill and seine nets. Gill net catches indicated substantial increases in the abundance of large juveniles and adults of the majority of marine fish species in both systems. Seine net catches indicated increases in the abundance of juvenile *Liza richardsonii*, but a decline in the abundance of other fish species. The recruitment of most fish is unlikely to have been negatively affected by the recorded fluctuations in salinity or turbidity. The senescence of macrophytes, however, may have increased exposure of recruiting *Monodactylus falciformis* and *Rhabdosargus holubi* to piscivorous birds and fish. The artificial breaching of estuaries during optimum fish recruitment periods in 1991 and 1992 may have contributed to the recorded increases in the abundance of fish in 1993. A longer duration tidal phase in the Swartvlei system during 1992 and 1993, compared to the Wilderness lake system, did not result in greater abundance of fish sampled. There appears to be no justification for the artificial maintenance of permanently tidal conditions in the Swartvlei and Touw River estuaries on the grounds of benefit for the maintenance of viable fish communities.

Several environmental factors have been noted to influence the abundance of marine fish in estuaries (Whitfield & Kok 1992), including the open/closed condition of the estuary (Bennett, Hamman, Branch & Thorne 1985; Bennett 1989), salinity (Blaber 1974), turbidity (Cyrus & Blaber 1987c), pollution (Blaber, Hay, Cyrus & Martin 1984), incidence and severity of floods (Marais 1982), impoundment of influent rivers (Plumstead 1990) and habitat diversity (Blaber 1978). Of these factors, Whitfield & Kok (1992) consider the open/closed condition of an estuary to be the major determinant of fish species diversity and abundance. The National Parks Board (NPB) manipulates several environmental factors in the Wilderness and Swartvlei lake systems, principally by artificially breaching the sandbars at the Touw River and Swartvlei estuary mouths. One of the primary reasons for opening these estuaries is to prevent flooding of surrounding residential properties in the towns of Wilderness and Sedgefield. Consequently these estuaries are, at times, opened during periods that are not optimal for recruitment of marine fish and/or when the water levels are lower than recommended minima [Swartvlei estuary = 2 m above msl (CSIR 1978; Whitfield, Allanson & Heinecken 1983), Touw River estuary = 2,1–2,4 m above msl (CSIR 1981; 1982)]. The breaching of estuaries at low water levels can result in premature closure (Whitfield & Kok 1992) owing to reduced scour of accumulated marine sediments. Therefore, NPB has come under increasing public criticism that their management actions are having a detrimental impact on fish communities, and proposals have been made that the estuaries be managed such that they remain permanently tidal (*Sedgefielder* March 1992; *Knysna Plett Herald* 21 May 1992, 2 July 1992).

Several authors have documented changes in marine fish communities in South African estuaries arising from mouth opening and closing (Bennett *et al.* 1985; Kok & Whitfield 1986), and compared fish communities in nearby permanently open and seasonally open estuaries (Bennett 1989; Whitfield & Kok 1992). The primary aim of the present study was to investigate the influence of the management policy of artificial breaching of the Swartvlei and Touw River estuary mouths on the abundance of marine fish in the Swartvlei and

Wilderness lake systems. To facilitate this assessment it was also necessary to investigate changes in other environmental factors (*viz.* water turbidity, salinity, submerged aquatic plant biomass and predator pressure) which could potentially influence the distribution and abundance of marine fish in the lake systems.

### Study area

The Wilderness and Swartvlei lake systems are situated on the Cape south coast and form the core conservation area of the Wilderness National Park. The Wilderness system comprises three lakes (Rondevlei, Langvlei, Eilandvlei) interconnected by shallow channels, and the Touw River estuary which connects with Eilandvlei via the sinuous Serpentine channel (Figure 1). Eilandvlei has a maximum depth of 6,5 m, Langvlei 4,0 m and Rondevlei 6,0 m, while the Touw River estuary varies between 1 and 3,5 m (Hall, Whitfield & Allanson 1987). The Swartvlei system comprises two waterbodies: Swartvlei and Swartvlei estuary (Figure 1). Maximum depth in the Swartvlei estuary is 4,0 m, with a narrow central channel bordered by intertidal sand flats of varying widths (Kok & Whitfield 1986). Swartvlei has a mean depth of 5,5 m and a maximum depth of 16,7 m (Howard-Williams & Allanson 1981).

The Wilderness system is fed by three rivers, the Touw River, Duiwe River and Langvlei spruit, whereas the Diep, Klein Wolwe, Hoëkraal and Karatara rivers flow into the Swartvlei system. All these rivers arise in forested mountain catchments in the Outeniqua mountains. They flow predominantly over Table Mountain sandstone and are low in dissolved solids and stained with humates (Roberts & Allanson 1977). Mean annual rainfall in the catchments is between 900 and 1000 mm p.a. (Adamson 1975) with no identifiable seasonal variation (Whitfield *et al.* 1983).

The estuaries are subject to wide variations in hydrology resulting from frequent mouth closure by south-westerly wave conditions and longshore sand transport (Whitfield *et al.* 1983) and erratic river inflow (Heydorn & Tinley 1980). Periodic heavy rains in the river catchments result in flooding of the estuaries and 'breaching' of the sand bar across the

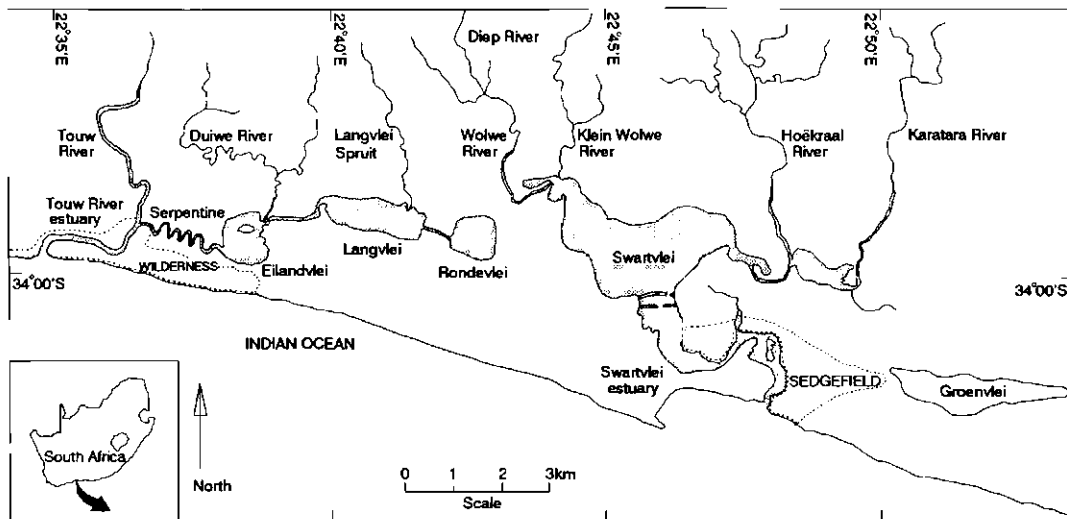


Figure 1 Map of Wilderness and Swartvlei lake systems showing localities mentioned in the text.

estuary mouths.

Salinities in the estuaries are highly variable, being above  $30 \text{ g kg}^{-1}$  prior to and immediately after mouth closure, and declining to  $<5 \text{ g kg}^{-1}$  depending on the inflow from the lakes (Whitfield *et al.* 1983; Allanson & Whitfield 1983). A reverse salinity gradient exists in the Wilderness system, with Rondevlei, being the furthest from the sea, having a higher salinity than Langvlei, which in turn is higher than Eilandvlei. Salinities in these lakes are variable though generally do not exceed  $15 \text{ g kg}^{-1}$  (Allanson & Whitfield 1983). In Swartvlei lake, surface salinities vary between  $1 \text{ g kg}^{-1}$  and  $20 \text{ g kg}^{-1}$ , whereas bottom salinities range between  $12 \text{ g kg}^{-1}$  and  $20 \text{ g kg}^{-1}$  (Howard-Williams & Allanson 1978).

Water temperature varies with season, ranging from  $10\text{--}14^\circ\text{C}$  in winter and  $25\text{--}29^\circ\text{C}$  in summer (Whitfield *et al.* 1983; National Parks Board unpublished data), although water temperatures in the lower portions of the estuaries can occasionally decline to  $13^\circ\text{C}$  during summer owing to the inflow of cold upwelled water from the sea (Schumann, Perrens & Hunter 1982).

Dissolved oxygen varies in response to biological activity, with higher oxygen values being associated with the presence of aquatic plants (Kok & Whitfield 1986). In the Swartvlei estuary, the closing of the mouth has been found to have no effect on mean dissolved oxygen values in the channels (Liptrot 1978). De-oxygenated conditions have been recorded in the Swartvlei estuary in localized areas (Liptrot 1978), either in the deeper portions of the estuary, or alternatively along the channel edges amongst decomposing organic matter.

Aquatic macrophytes are widespread in all of the waterbodies, and consist predominantly of pure and mixed stands of *Ruppia cirrhosa*, *Potamogeton pectinatus*, Charophyta and filamentous algae (*Cladophora* spp. and *Cocconeis* spp.) (Howard-Williams & Liptrot 1980; Weisser & Howard-Williams 1982; Whitfield *et al.* 1983). *Zostera capensis* is abundant in the lower reaches of the Swartvlei estuary (Whitfield *et al.* 1983) and occurs sporadically in the Touw River estuary. Aquatic macrophytes do not generally occur in waters deeper than 3,0 m (Whitfield 1984). The lakes are fringed by a narrow margin of emergent aquatic plants (*Phragmites aus-*

*tralis*, *Scirpus littoralis*, *Typha latifolia*) with these species being sparsely distributed along the estuaries.

## Methods

The fish communities of the two lake systems were extensively sampled on two occasions, firstly between 29 July 1991 and 8 October 1991 (prior to which the systems were open for only short durations), and secondly between 22 June 1993 and 31 July 1993 (prior to which the systems were open for most of the spring and summer of 1992). Eighteen sample sites were located in a stratified random manner with two sites in each estuary, three sites in each of the lakes of the Wilderness lake system (Rondevlei, Langvlei and Eilandvlei), and four sites in Swartvlei. Two types of fish sampling apparatus were used. A set of six multifilament gill nets, measuring  $40 \text{ m} \times 2 \text{ m}$  with bar mesh sizes of 35, 45, 57, 73, 95 and 114 mm, were set parallel to the shoreline at approximately 2 m depth at 09h00, and lifted at 09h00 the following day. Nets were emptied at approximately 15h00 and when being lifted. A purse seine net ( $40 \text{ m} \times 2 \text{ m} \times 2 \text{ mm}$  bar mesh) with 50-m warps was used at least twice at each sample site. Where sample sites were unsuitable for seine netting owing to the presence of underwater obstructions or the absence of a suitable landing area, the closest suitable sampling locality was used. All fish caught were transported to the NPB laboratories at Rondevlei, identified according to Smith & Heemstra (1986), counted, and fork-length (FL) measured to the nearest millimetre. The number of specimens caught was expressed as catch per unit effort (CPUE) which is equivalent to 100 m gill net/24 h, and 100 m seine net with every effective haul constituting 40 m seine net effort.

Differences between the number of fish caught in different surveys were evaluated on a unit effort basis using *t* statistics.

Salinity and turbidity of surface waters were measured monthly from January 1991 to December 1993 at 37 different localities: Rondevlei (five localities), Langvlei (five localities), Eilandvlei (five localities), Swartvlei lake (six localities), Swartvlei estuary (eight localities) and Touw River estuary (eight localities). Salinity was determined in the field at 30 cm depth with a YSI Model 33 S-C-T meter. Turbidity

was measured with a Hach 16800 turbidimeter with samples collected at 30 cm depth.

Standing biomass of submerged aquatic plants was determined in May and June of 1991, 1992 and 1993. Stratified random sampling was used to position six littoral transect lines around Swartvlei, four transect lines around each of the lakes in the Wilderness lake system, and five transect lines in the Touw River and Swartvlei estuaries. The limits of each transect line in the lakes were defined as the inner edge of the emergent macrophyte zone and the 2 m depth contour. In Swartvlei and Touw River estuaries, transect lines extended from shore to shore, and were orientated perpendicular to the banks. A macrophyte sampler designed by Howard-Williams & Longman (1976) was used to sample a 0,0625 m<sup>2</sup> area at five sample points along the length of each transect line. Samples were sorted into six groups (*P. pectinatus* and *R. cirrhosa*; *Z. capensis*; *Najas marina*; Characeae; epiphytic and epipsammic algae; detritus) after all attached bivalves had been removed. All samples were weighed to the nearest gram on an electronic balance after oven-drying at 55°C until no further weight loss was observed.

## Results

### Marine fish communities

Predominantly adult or large juvenile (1+ years) fish were

collected in gill nets, whereas predominantly small juvenile (0+ years) fish were collected by seine netting. Gill net catches of fish in both lake systems were dominated by Mugilidae in both 1991 and 1993, with *Monodactylus falciformis* and *Rhabdosargus holubi* also being relatively abundant (Table 1). No major changes occurred in the relative abundances of species, though significant (Table 2) increases occurred in the total CPUE in gill nets of large juvenile and adult fish in both the Wilderness (Figure 2a; 220%) and Swartvlei (Figure 3a; 190%) systems.

Seine net catches indicated substantial changes in the relative abundance of juvenile fish (Table 1). Seine net catches in both lake systems in 1991 were dominated by juvenile *R. holubi* (Wilderness system 52%; Swartvlei system 92%), whereas in 1993 catches were dominated by juvenile (<40 mm FL) Mugilidae (Wilderness system 96%; Swartvlei system 63%). Total CPUE of juveniles in the Wilderness system between 1991 and 1993 remained essentially unchanged (Figure 2a). In the Swartvlei system, however, a substantial decline in total CPUE of juvenile fish occurred (Figure 3a), resulting primarily from a reduction in the CPUE of *R. holubi* (Table 1).

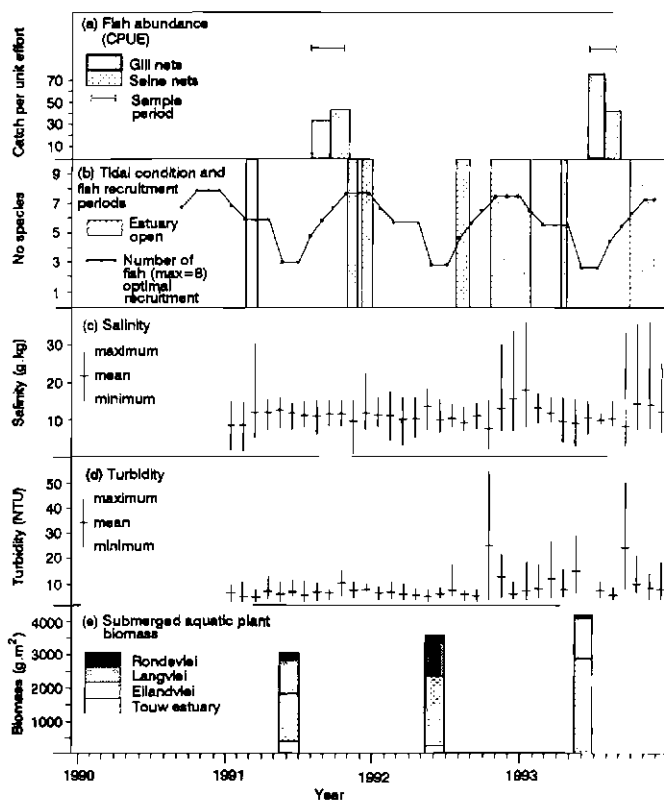
Two abundant fish species (*Liza richardsonii*, *R. holubi*) caught in both Wilderness and Swartvlei systems both showed polymodal length frequency distributions (Figures 4 & 5). The low abundance of 0+ juvenile (<75 mm; Ratte 1977) *L. richardsonii* in the Swartvlei system (Figures 4c &

**Table 1** Catch per unit effort (100 m gill net per 24 h; 100 m seine net) of marine fish captured in surveys undertaken in the Wilderness and Swartvlei systems during 1991 and 1993

Family	Gill nets				Seine net			
	Wilderness		Swartvlei		Wilderness		Swartvlei	
	1991	1993	1991	1993	1991	1993	1991	1993
<b>Ariidae</b>								
<i>Galeichthys feliceps</i>	-	-	1,0	9,2	-	-	-	-
<b>Carangidae</b>								
<i>Lichia amia</i>	-	0,3	0,1	1,7	-	-	-	0,2
<b>Haemulidae</b>								
<i>Pomadasys commersonii</i>	-	0,1	1,7	1,4	0,5	-	-	-
<b>Monodactylidae</b>								
<i>Monodactylus falciformis</i>	5,5	10,7	10,3	14,0	1,0	0,2	5,8	1,0
<b>Mugilidae</b>								
<i>Liza dumerilii</i>	2,4	0,3	5,6	2,2	-	-	-	-
<i>Liza richardsonii</i>	14,7	18,5	11,9	35,4	10,2	41,2	0,8	15,2
<i>Liza tricuspidens</i>	3,9	0,4	0,3	0,6	6,3	-	-	4,2
<i>Myxus capensis</i>	0,7	0,4	-	-	-	-	-	-
<i>Mugil cephalus</i>	2,5	30,8	1,5	4,7	0,1	0,1	-	-
<b>Pomatomidae</b>								
<i>Pomatomus saltatrix</i>	0,1	-	-	-	-	-	-	-
<b>Sciaenidae</b>								
<i>Argyrosomus hololepidotus</i>	-	-	-	0,2	-	-	-	-
<b>Sparidae</b>								
<i>Lithognathus lithognathus</i>	0,3	0,7	0,5	1,7	3,2	-	-	0,4
<i>Rhabdosargus holubi</i>	4,1	14,4	15,1	20,1	22,8	1,5	72,1	3,3
<i>Rhabdosargus sarba</i>	-	-	-	0,1	-	-	-	-
<b>Total</b>	<b>34,2</b>	<b>76,6</b>	<b>48,1</b>	<b>91,3</b>	<b>44,1</b>	<b>43,0</b>	<b>78,8</b>	<b>24,3</b>

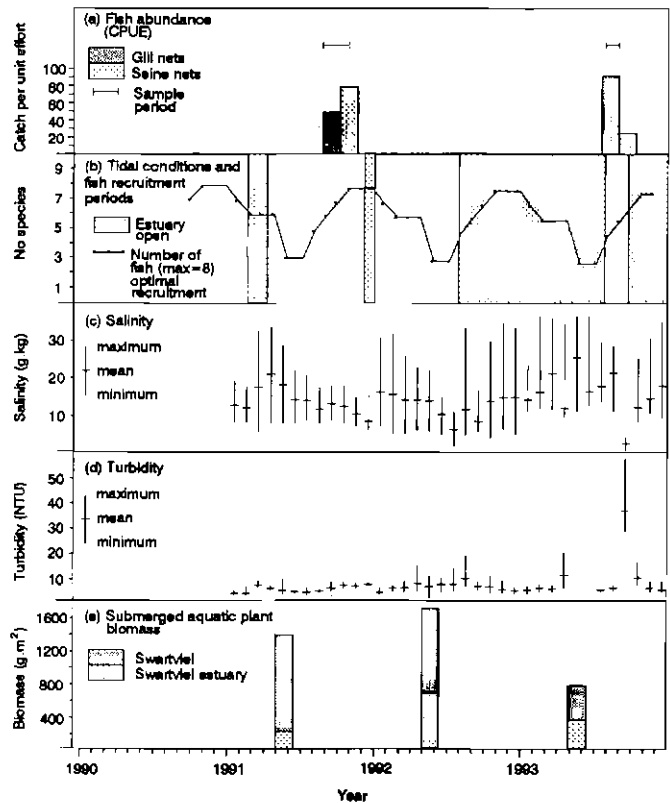
**Table 2** Summary of *t* tests on changes in catch per unit effort of marine fish in the Swartvlei and Wilderness lake systems between surveys undertaken in 1991 and 1993

System	Method	<i>t</i>	d.f.	<i>p</i>	Difference
Swartvlei	Gill nets	2,5861	10	< 0,05	significant
Wilderness	Gill nets	2,2793	20	< 0,05	significant
Swartvlei	Seine net	1,6462	7	> 0,1	not significant
Wilderness	Seine net	0,4401	6	> 0,5	not significant



**Figure 2** Changes in various biological, chemical and physical components of the Wilderness lake system between 1990 and 1993 depicted by changes in (a) the catch per unit effort (100 m gill net per 24 h; 100 m seine net) of marine fish, (b) the tidal condition of the Touw River estuary, (c) salinity, (d) turbidity, and (e) biomass of submerged aquatic plants. Data on periods of optimal fish recruitment (2b) adapted from Whitfield & Kok (1992).

4d) indicated poor recruitment into this system in both 1991 and 1993, whereas substantial recruitment occurred in the Wilderness system, particularly in 1993 (Figures 4a & 4b). Assuming that 0+ juvenile *R. holubi* in the Swartvlei and Wilderness lake systems have an average monthly growth increment of 8 mm, as observed in the Sundays River (Beckley 1984), Swartkops (Winter 1979) and Knysna (Whitfield & Kok 1992) estuaries, the abundance of 0+ juveniles in the Wilderness system indicated strong recruitment in both 1991 (Figure 5a) and 1993 (Figure 5b). Proportionally fewer 0+ juvenile *R. holubi* were recorded in the Swartvlei system, particularly in 1991 (Figure 5c), indicating lower recruitment success. The length distribution of 0+ juvenile *R. holubi* in both Wilderness and Swartvlei systems during 1993 (Figures 5b & 5d) indicated that this year-class was dominated by



**Figure 3** Changes in various biological, chemical and physical components of the Swartvlei system between 1990 and 1993 depicted by changes in (a) the catch per unit effort (100 m gill net per 24 h; 100 m seine net) of marine fish, (b) the tidal condition of the Swartvlei estuary, (c) salinity, (d) turbidity, and (e) biomass of submerged aquatic plants. Data on periods of optimal fish recruitment (3b) adapted from Whitfield & Kok (1992).

older (8 to 12-month-old) individuals. Thus recruitment of *R. holubi* commenced almost immediately after the Swartvlei and Touw River estuaries were opened in July 1993, with a marked decline in recruitment success later in the open phases.

#### Opening and closing of estuary mouths

The date on which the Touw River and Swartvlei estuaries opened, as well as the length of time they remained open, varied from year to year (Figures 2b & 3b). The Touw River estuary, in 1991, prior to fish surveys, was open on only one brief (30 days duration) occasion, before which it had been closed for 14 months. Similarly in the Swartvlei estuary, prior to the 1991 fish surveys, there was only a single short duration (48 days) open phase which was both preceded and fol-

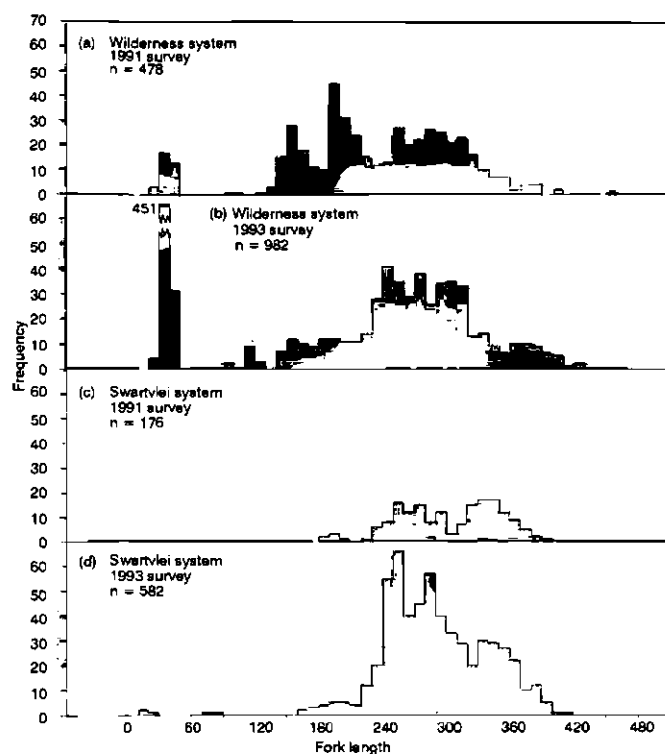


Figure 4 Size composition of *Liza richardsonii* captured in the Wilderness lake system during (a) 1991 and (b) 1993 surveys, and Swartvlei system during (c) 1991 and (d) 1993 surveys.

lowed by extended closed phases. Brief openings occurred in both estuaries towards the end of 1991 during periods that were optimal for the recruitment of most fish species (Figures 2b & 3b). Both estuaries were again opened in mid-1992 after which Swartvlei estuary remained tidal for 364 days, closing shortly after the commencement of the 1993 fish survey. The Touw River estuary, however, remained open for substantially less time with open phases totalling 144 days.

### Salinity

Salinities in the Wilderness and Swartvlei systems were strongly influenced by the tidal condition. During open phases salinities tended to increase owing to the influx of marine water, and decreased during closed phases owing to freshwater inflows (Figures 2c & 3c). The greatest variability in salinity was recorded in the estuaries. In the Touw River estuary average salinity during the closed phase was generally below  $15 \text{ g kg}^{-1}$  with low concentrations ( $2 \text{ g kg}^{-1}$ ) recorded on occasion (January & February 1991). In Swartvlei estuary steady declines in salinity were recorded during closed phases though average salinity generally did not fall below  $10 \text{ g kg}^{-1}$  except briefly during periods of high rainfall in July 1992 and September 1993. Strong axial salinity gradients occurred in both estuaries during open phases (mean  $\pm$  SE and range: Swartvlei estuary =  $17,4 \pm 7,8$ ;  $1,0$ – $28,7 \text{ g kg}^{-1}$  Touw River estuary =  $18,7 \pm 10,0$ ;  $0,6$ – $32,0 \text{ g kg}^{-1}$ ).

Salinity in Swartvlei during 1991 and 1992 was relatively stable, ranging between  $5$  and  $8 \text{ g kg}^{-1}$ . An approximate  $4 \text{ g kg}^{-1}$  increase in salinity occurred during 1993 following an extended open phase in the system. Heavy rainfall in the Swartvlei catchment during September 1993 resulted in a

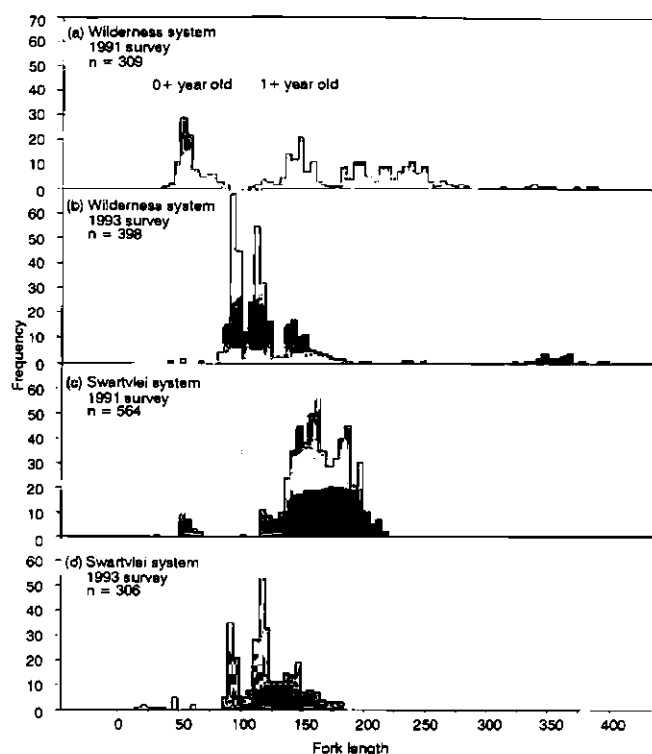


Figure 5 Size composition of *Rhabdosargus holubi* captured in the Wilderness lake system during (a) 1991 and (b) 1993 surveys, and Swartvlei system during (c) 1991 and (d) 1993 surveys.

brief (<60 days) though substantial ( $12,3 \text{ g kg}^{-1}$ ) decline in salinity.

Salinity in lakes of the Wilderness lake system remained relatively constant both spatially and temporally, with only minor variations occurring depending on freshwater inflows and the movement of water between waterbodies. A reverse salinity gradient persisted throughout the study period, with the highest salinities recorded in Rondevlei ( $13$  to  $16 \text{ g kg}^{-1}$ ), followed by Langvlei ( $8$  to  $12 \text{ g kg}^{-1}$ ) and Eilandvlei ( $6$  to  $8 \text{ g kg}^{-1}$ ).

### Turbidity

Turbidity in all waterbodies was generally low (Figures 2d & 3d), with substantial increases occurring during periods of high runoff from the catchments (October 1992 — Wilderness lake system; September 1993 — both lake systems). High turbidities resulted largely from the input of suspended sediments from the catchments. Only in Rondevlei were turbidity levels higher than  $10 \text{ NTU}$  frequently recorded, which were primarily a consequence of algal blooms.

### Aquatic plants

Marked changes occurred in the above ground biomass of aquatic plants in all waterbodies, with the exception of Langvlei. In the Touw River estuary there was a virtual complete dieback of aquatic plants between 1991 and 1993. Substantial increases occurred in the biomass of *Potamogeton/Ruppia* and detritus in Eilandvlei, whereas algal blooms in Rondevlei in 1993 are thought to have resulted in an extensive dieback of *Potamogeton/Ruppia*. There was an overall increase in the biomass of submerged aquatic plants in the

Wilderness system over the three year sample period (Figure 2e). The reinstatement of tidal action in Swartvlei estuary during 1992 and 1993 resulted in a dieback of *Potamogeton/Ruppia* beds, and an increase in the abundance of filamentous algae and *Z. capensis*. In Swartvlei there was a marked reduction in the biomass of *Chara* spp. whereas the biomass of *Potamogeton/Ruppia* remained relatively unaltered. Overall there was a substantial decrease in the biomass of submerged aquatic plants over the three year sample period (Figure 3e).

## Discussion

Estuarine systems are highly dynamic (Day 1981), with the interactions existing in both space and time between physical, chemical and biological components being highly complex (Allanson 1981). This complexity of functioning is typified in estuarine fish communities, the status and productivity of which are governed by a variety of environmental factors. Fish species, however, are tolerant of both biotic and abiotic changes in the environment, with only severe changes of long duration having significant effects (Day & Grindley 1981). This study revealed that significant changes had occurred in the abundance of fish in the Swartvlei and Wilderness lake systems, despite their resilience to environmental changes. The question of importance to environmental managers is which factors are likely to have contributed to these changes, and how these cause and effect relationships influence the way in which the Swartvlei and Wilderness lake systems should be managed.

Several of the environmental factors listed above (see introduction) which could potentially influence the abundance of fish in estuaries (impoundments, flood severity, pollution) can be discounted as probable causes for observed community changes as few or no changes occurred during the study period. Emphasis is thus placed on those environmental factors where change is potentially highly variable, or where changes result either directly or indirectly from management actions.

**Salinity.** Most fish species recorded in the Swartvlei and Wilderness lake systems are strong osmoregulators, capable of surviving both low and high salinities (Whitfield, Blaber & Cyrus 1981). Salinity tolerances of fish given by Day, Blaber & Wallace (1981) and Whitfield *et al.* (1981) differ, particularly with respect to the lower salinity concentrations. Using the lower salinity value given by these authors as the lower salinity tolerance of a species, it is apparent that all fish species recorded in the Wilderness lake system, with the exception of *Liza tricuspidens*, would be capable of tolerating the low salinities (2 g kg<sup>-1</sup>) periodically recorded in Eilandvlei and the Touw River estuary. The narrower salinity tolerance range of *L. tricuspidens* could explain its low abundance in the Swartvlei and Wilderness lake systems. The survival of other fish species in the Swartvlei and Wilderness lake systems is, however, unlikely to have been negatively affected by the recorded salinity fluctuations.

Studies in South African (Marais 1988; Whitfield 1994) and North American (Allen & Barker 1990) estuaries have illustrated positive correlations between the numbers and abundance of marine fish and decreasing salinity. Similarities in the axial salinity gradients in the Touw River and Swartvlei estuaries, however, suggest that salinity differences between

the Wilderness and Swartvlei systems do not provide an explanation for different levels of recruitment success of fish. It is possible, however, that inputs of fresh water from the Touw River close to the estuary mouth of the Wilderness lake system could, during high inflow periods, provide stronger cues for recruiting euryhaline fishes than occur in the Swartvlei system where fluvial inputs are first mixed with saline lake water.

**Turbidity.** The effects of suspensoids on fish can be either detrimental or beneficial, depending on the concentration of suspended particles, and the timing and duration of exposure (Bruton 1985). Moderate suspensoid concentrations appear to be beneficial to fish in estuaries by reducing clarity and hence the risk of predation from piscivorous birds and fish (Blaber 1981), increasing habitat diversity (Blaber & Blaber 1980) and the abundance of food (Whitfield 1983), and acting as a navigational aid to fish entering estuaries (Blaber & Blaber 1980).

The turbidity tolerances and preferences of fish in southern Cape estuaries are unknown. It is reasonable to conclude, however, that the range of tolerance amongst southern Cape species would be similar to those studied in KwaZulu/Natal estuaries, with relatively few species being turbidity intolerant or indifferent to turbidity, and the majority being tolerant of moderate turbidities (Blaber & Blaber 1980). Turbidity levels recorded in the Swartvlei and Wilderness lake systems during non-flood conditions were sufficiently low that even turbidity intolerant species (<10 NTU; Cyrus & Blaber 1987a; 1987b) were unlikely to have been detrimentally influenced. Cyrus & Blaber (1987a; 1987b) established that juveniles of the majority of fish entering northern KwaZulu/Natal estuaries show a preference for moderately turbid waters (>10 NTU), thus elevated turbidities during flood events in the Wilderness lake system in October 1992 may have been beneficial for recruiting species.

Overall it appears unlikely that turbidity levels recorded in both Wilderness and Swartvlei systems during the study period would have had a detrimental impact on fish communities.

**Submerged aquatic plant biomass.** Aquatic plants form an important component of the habitat of several fish species, with juveniles of species such as *M. falciformis* and *R. holubi* occurring mainly in the vicinity of macrophyte beds (Whitfield 1984). Two major reasons have been forwarded why juvenile fishes are attracted to macrophyte beds: firstly these areas provide refuge from predators, and secondly the large biomass of invertebrates and epiphytes on macrophytes provide an assured food supply (Whitfield 1984). Changes in the abundance of macrophytes would thus be expected to result in change in the abundance of fish species attracted to macrophyte beds. This cause and effect relationship was noted by Whitfield (1984) who recorded significant decreases in the total CPUE of *M. falciformis* (92%) and *R. holubi* (91%) caught in gill nets in Swartvlei following the senescence of macrophyte beds between 1979 and 1982. No such reductions from gill net returns were recorded in this study indicating minimal impact of changes in macrophyte biomass on the abundance of fish. The absence of reductions in gill net catches of *M. falciformis* and *R. holubi* in 1993 may be due to

the fact that macrophyte beds still persisted in all waterbodies with the exception of the Touw River estuary. This contrasted with the situation in Swartvlei in 1982 where no aquatic plants were present in the littoral zone (Whitfield 1984). A further contributing factor could be that the 1993 gill net catches, which predominantly represent 1+ fishes which utilized the extensive macrophyte beds in 1992 and earlier, were too soon after 1992 for fish stocks to reflect the decline in aquatic plants.

Reduction in CPUE of juvenile *M. falciformis* and *R. holubi* from seine nets in both Swartvlei and Wilderness lake systems did indicate a decline in recruitment. Predation may have been a significant factor in reducing the abundance of fish, particularly *M. falciformis* and *R. holubi*. Reduction in available cover resulting from the senescence of macrophyte beds, particularly in the estuaries, may have increased exposure of recruiting *M. falciformis* and *R. holubi* to existing avian and fish predators.

*Opportunities for breeding and recruitment.* The timing and duration of the open phases in periodically closed estuaries are recognized as major determinants of fish species diversity and abundance (Wallace & van der Elst 1975). Increases in the abundance of fish following mouth opening have been recorded in southern African estuaries (Whitfield 1980; Kok & Whitfield 1986), with declines during extended closed phases indicating a breakdown in the recruitment process. Comparisons of fish communities in permanently open and periodically opened estuaries (Bennett 1989; Whitfield, Beckley, Bennett, Branch, Kok, Potter & Van der Elst 1989; Whitfield & Kok 1992) have also indicated that the CPUE of marine migrants is higher in the former systems.

The recruitment of most species in southern Cape estuaries occurs predominantly during spring and summer (September to March) (Marais 1976; van der Horst & Erasmus 1978; 1981; Kok 1981; Kok, Whitfield, Ratte & Coetzee 1981; Lasiak 1983), with November to January being optimum for most species (Whitfield & Kok 1992). This was confirmed by Whitfield (1989) who found the larvae of several summer recruiting species to be absent from the nearshore marine environment during winter. Open mouth conditions in both Swartvlei and Touw River estuaries during early 1991 did not occur in the optimum recruitment period for several fish species (*Lichia amia*, *Mugil cephalus*, *L. tricuspidens*, *Lithognathus lithognathus*), whereas in subsequent summers both estuaries were open during periods which were optimum for the recruitment of most fish. It is therefore suggested that the opening of the Swartvlei and Touw River estuaries during optimum recruitment periods in the 1991/92 and 1992/93 summers may have contributed to the recorded increases in the abundance of fish in 1993.

Tidal conditions are required for sufficient duration to enable reproductively active adults to emigrate and spawn, and recruitment of fry back into the estuary. The premature formation of a sand bar across the mouth of an estuary would retard these processes, thereby directly affecting the composition of the fish community. Whitfield (1992) has recorded postlarval *R. holubi* and Mugilidae entering the temporarily closed Haga Haga estuary (Eastern Cape) when the sand bar at the mouth was being overtopped. Although waves frequently overtop the sandbars at mouths of the Swartvlei and

Touw estuaries, particularly at high tide shortly after the estuaries have closed, it is unknown whether juvenile fish gain access to these estuaries by this means.

The length of time between spawning and recruitment for fish in Cape estuaries, and hence minimum time an estuary should remain tidal for effective recruitment to take place is unknown. In the Mhlanga estuary (KwaZulu/Natal), Whitfield (1980) recorded the recruitment of juveniles of two marine fish species within six weeks of the estuary being opened after an 11 month closed phase. The duration of the open phase necessary for recruitment, however, may well be shorter than six weeks as the Mhlanga estuary usually closes within ten days of opening (Whitfield 1980), and yet several fish species persist within in the estuary, albeit with some species being uncommon. Increases in the abundances of large juvenile and adult fish collected in the Swartvlei and Wilderness lake systems in 1993 indicated that recruitment had been successful in 1992. Thus even short duration openings (30–40 days) could be adequate for the maintenance of viable fish communities. This is supported by the observation that recruitment of *R. holubi* into the Wilderness and Swartvlei lake systems during 1993 commenced almost immediately after the estuary mouths had been opened. Data presented in this paper also indicate that recruitment of marine fish species can be as successful in an estuary that is open for only a portion (129 days) of the year (Wilderness lake system) as in one which is opened for a whole year (Swartvlei system), provided that the opening takes place during optimum recruitment times. These observations lend weight to the argument that there is no justification for the artificial maintenance of permanently tidal conditions in the Swartvlei and Touw River estuaries on the grounds of this being essential for the maintenance of fish communities. Consequently, as observed by Kok & Whitfield (1986) a closed phase during winter is unlikely to have a major impact on the population dynamics of fish within these systems.

No single environmental factor could be identified as being the major determinant of changes in the abundances of fish in the Swartvlei and Wilderness lake systems. Biotic changes were most likely the result of variation in a suite of environmental variables, including the opening of estuaries during periods favourable for fish migration and breeding. Of importance to managers, however, is the conclusion that, contrary to popular belief, permanently tidal conditions are not required for effective conservation of fish communities. Fish which utilize the Wilderness and Swartvlei systems during part of their life cycles are well adapted to cope with the stochastic nature of the estuarine environment. Consequently, as long as the estuary mouths are wisely managed to enable periodic emigration and subsequent immigration, water quality maintained within environmentally acceptable limits, and vibrant aquatic plant communities maintained to provide food and cover, a viable and diverse fish community should ensue.

### Acknowledgments

The National Parks Board is thanked for funding the project and for permission to publish results. Numerous persons assisted in the field and laboratory with various aspects of this project, though assistance provided by J. Filmlater, J. Grootboom, L. James and P. Mitchell in particular is gratefully

acknowledged. Dr R. Randall and N. Geldenhuys provided invaluable support throughout this research programme. Drs N. Hanekom and R. Randall and two anonymous referees are thanked for constructive comments on the manuscript.

## References

- ADAMSON, P.T. 1975. Extension of monthly runoff records in the catchments of the Wit Els, Diep and Karatara rivers. Department of Water Affairs, Pretoria.
- ALLANSON, B.R. 1981. The coastal lakes of southern Africa. In: Estuarine ecology with particular reference to southern Africa, (ed.) J.A. Day. A.A. Balkema, Cape Town.
- ALLANSON, B.R. & WHITFIELD, A.K. 1983. The Limnology of the Touw River Floodplain. South African National Scientific Programmes Report No 79. CSIR, Pretoria.
- ALLEN, D.M. & BARKER, D.L. 1990. Interannual variations in larval fish recruitment to estuarine epibenthic habitats. *Mar. Ecol. Prog. Ser.* 63: 113–125.
- BECKLEY, L.E. 1984. The ichthyofauna of the Sundays estuary, South Africa, with particular reference to the juvenile marine component. *Estuaries* 7: 248–250.
- 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. *S. Afr. J. mar. Sci.* 8: 43–55.
- BENNETT, B.A., HAMMAN, K.C.D., BRANCH, G.M. & THORNE, S.C. 1985. Changes in the fish fauna of the Bot River estuary in relation to opening and closure of the estuary mouth. *Trans. Roy. Soc. S. Afr.* 45: 449–464.
- BLABER, S.J.M. 1974. Osmoregulation in juvenile *Rhabdosargus holubi* (Steindachner) (Pisces: Sparidae). *J. Fish Biol.* 6: 797–800.
- BLABER, S.J.M. 1978. Fishes of the Kosi system. *Lammergeyer* 24: 28–41.
- BLABER, S.J.M. 1981. The zoogeographic affinities of estuarine fishes in south-east Africa. *S. Afr. J. Sci.* 77: 305–307.
- BLABER, S.J.M. & BLABER, T.G. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. *J. Fish Biol.* 17: 143–162.
- BLABER, S.J.M., HAY, D.G., CYRUS, D.P. & MARTIN, T.J. 1984. The ecology of two degraded estuaries on the north coast of Natal, South Africa. *S. Afr. J. Zool.* 19: 224–240.
- BRUTON, M.N. 1985. The effects of suspensoids on fish. *Hydrobiol.* 125: 221–241.
- CSIR, 1978. Hydrouliese studie van die Swartvlei Estuarium: Effek van bestaande en voorgestelde brûe op die waterbeweging. Vol I. Ingenieurs verslag. CSIR Report C/SEA 7805/1, Coastal Engineering and Hydraulics Division, National Research Institute for Oceanology, Council for Scientific and Industrial Research, Stellenbosch. 20pp, 21 figures.
- CSIR, 1981. Wilderness Report No. 1. Evaluation of prototype data and the application of a numeric model to the Wilderness lakes and Touws River floodplain. CSIR Report C/SEA 8113. Coastal Engineering and Hydraulics Division, National Research Institute for Oceanology, Council for Scientific and industrial Research, Stellenbosch.
- CSIR, 1982. Wilderness Report No. 2. Evaluation of prototype flood conditions and application of the numeric model to conditions when the estuary mouth was open. CSIR Report C/SEA 8255. Coastal Engineering and Hydraulics Division, National Research Institute for Oceanology, Council for Scientific and Industrial Research, Stellenbosch.
- CYRUS, D.P. & BLABER, S.J.M. 1987a. The influence of turbidity on juvenile marine fishes in estuaries. Part 1. Field studies at Lake St. Lucia on the southeastern coast of Africa. *J. Exp. Mar. Biol. Ecol.* 109: 53–70.
- CYRUS, D.P. & BLABER, S.J.M. 1987b. The influence of turbidity on juvenile marine fishes in estuaries. Part 2. Laboratory studies, comparisons with field data and conclusions. *J. Exp. Mar. Biol. Ecol.* 109: 71–91.
- CYRUS, D.P. & BLABER, S.J.M. 1987c. The influence of turbidity on juvenile marine fish in estuaries of Natal, South Africa. *Contl. Shelf Res.* 7: 1411–1416.
- DAY, J.H. 1981. The estuarine fauna. In: Estuarine ecology with particular reference to southern Africa, (ed.) J.A. Day. A.A. Balkema, Cape Town. pp. 77–100.
- DAY, J.H., BLABER, S.J.M. & WALLACE, J.H. 1981. Estuarine fishes. In: Estuarine ecology with particular reference to southern Africa, (ed.) J.A. Day. A.A. Balkema, Cape Town.
- DAY, J.H. & GRINDLEY, J.R. 1981. The estuarine ecosystem and environmental constraints. In: Estuarine ecology with particular reference to southern Africa, (ed.) J.A. Day. A.A. Balkema, Cape Town.
- HALL, C.M., WHITFIELD, A.K. & ALLANSON, B.R. 1987. Recruitment, diversity and the influence of constrictions on the distribution of fishes in the Wilderness lakes system, South Africa. *S. Afr. J. Zool.* 22: 163–169.
- HEYDORN, A.E.F. & TINLEY, K.L. 1980. Estuaries of the Cape. Part 1. Synopsis of Cape coast — Natural features, dynamics and utilization. CSIR Research Report 380, CSIR, Pretoria.
- HOWARD-WILLIAMS, C. & LONGMAN, M. 1976. A quantitative sampler for submerged aquatic macrophytes. *J. Limnol. Soc. S. Afr.* 2: 31–33.
- HOWARD-WILLIAMS, C. & ALLANSON, B.R. 1978. Swartvlei Project Report, Part II. The limnology of Swartvlei with special reference to production and nutrient dynamics in the littoral zone. Institute for Freshwater Studies Special Report No. 78/3. Grahamstown. 280pp.
- HOWARD-WILLIAMS, C. & ALLANSON, B.R. 1981. An integrated study on littoral and pelagic primary production in a southern African coastal lake. *Arch. Hydrobiol.* 92: 507–534.
- HOWARD-WILLIAMS, C. & LIPROT, M.R.M. 1980. Submerged macrophyte communities in a brackish South African estuarine-lake system. *Aquat. Bot.* 9: 101–116.
- KOK, H.M. 1981. Studies on the juvenile fishes of Cape south coast estuaries. In: The Touw River Floodplain. Part III, The chemical and biological environment and the impact of man, (eds.) A. Jacot Guillarmod & B.R. Allanson. Institute for Freshwater Studies, Grahamstown.
- KOK, H.M. & WHITFIELD, A.K. 1986. The influence of open and closed mouth phases on the marine fish fauna of the Swartvlei estuary. *S. Afr. J. Zool.* 21: 309–315.
- KOK, H.M., WHITFIELD, A.K., RATTE, T. & COETZEE, D. 1981. Recommendations regarding fish stocks in the Wilderness System. In: The Touw River Floodplain. Part I, Summary and Recommendations (eds.) A. Jacot Guillarmod & B.R. Allanson. Institute for Freshwater Studies, Grahamstown.
- LASIAK, T.A. 1983. Aspects of the reproductive biology of the southern mullet, *Liza richardsonii*, from Algoa Bay, South Africa. *S. Afr. J. Zool.* 18: 89–95.
- LIPROT, M.R. 1978. Community metabolism and phosphorous dynamics in a seasonally closed South African estuary. Unpublished M.Sc. thesis, Rhodes University, Grahamstown.
- MARAIS, J.F.K. 1976. The nutritional ecology of mullets in the Swartkops estuary. Unpublished Ph.D. thesis, University of Port Elizabeth.
- MARAIS, J.F.K. 1982. The effects of river flooding on the fish populations of two eastern Cape estuaries. *S. Afr. J. Zool.* 17: 96–104.
- MARAIS, J.F.K. 1988. Some factors that influence fish abundance in South African estuaries. *S. Afr. J. mar. Sci.* 6: 67–77.
- PLUMSTEAD, E.F. 1990. Changes in ichthyofaunal diversity and



- abundances within the Mbashe estuary, Transkei, following construction of a river barrage. *S. Afr. J. mar. Sci.* 9: 399–407.
- RATTE, T.W. 1977. Age and growth of the mullet *Mugil richardsonii* (Smith) in the Berg River estuary. Internal Research Report, Department of Nature and Environmental Conservation, Provincial Administration of the Cape of Good Hope: pp. 45–58.
- ROBARTS, R.D. & ALLANSON, B.R. 1977. Meromixis in the lake-like upper reaches of a South African estuary. *Arch. Hydrobiol.* 80: 531–540.
- SCHUMANN, E.H., PERRINS, L.A. & HUNTER, I.T. 1982. Upwelling along the Cape south coast. *S. Afr. J. Sci.* 78: 238–242.
- SMITH, M.M. & HEEMSTRA, P.C. (eds.) 1986. *Smith's Sea Fishes*. 1st edition. Southern Book Publishers, Johannesburg. 1048 pp, 144 pls.
- VAN DER HORST, G. & ERASMUS, T. 1978. The breeding cycle of male *Liza dumerili* (Teleostei: Mugilidae) in the mouth of the Swartkops estuary. *Zoologica Afr.* 13: 259–273.
- VAN DER HORST, G. & ERASMUS, T. 1981. Spawning time and spawning grounds of mullet with special reference to *Liza dumerili* (Steindachner, 1869). *S. Afr. J. Sci.* 77: 73–78.
- 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. S. Afr.* 42: 1–63.
- WEISSER, P.J. & HOWARD-WILLIAMS, C. 1982. The vegetation of the Wilderness lakes system and the macrophyte encroachment problem. *Bontebok* 2: 19–40.
- 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 fish. *S. Afr. J. Sci.* 79: 362–365.
- WHITFIELD, A.K. 1984. The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a southern African coastal lake. *Estuar. coast. mar. Sci.* 18: 315–329.
- WHITFIELD, A.K. 1989. Ichthyoplankton in a southern African surf zone; nursery area for the postlarvae of estuarine associated fish species? *Estuar. coast. mar. Sci.* 29: 533–547.
- WHITFIELD, A.K. 1992. 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 different freshwater inputs. *Mar. Ecol. Prog. Ser.* 105: 257–267.
- WHITFIELD, A.K., ALLANSON, B.R. & HEINECKEN, T.J.F. 1983. Report No. 22: Swartvlei (CMS11). In: *Estuaries of the Cape*. Part II. Synopses of available information on individual systems. CSIR Research Report 421, (eds.) A.E.F. Heydorn & J.R. Grindley. CSIR, Stellenbosch.
- 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. *S. Afr. J. mar. Sci.* 8: 251–259.
- WHITFIELD, A.K., BLABER, S.J.M., & CYRUS, D.P. 1981. Salinity ranges of some southern African fish species occurring in estuaries. *S. Afr. J. Zool.* 16: 151–155.
- 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* No. 57. 39pp.
- 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, Port Elizabeth.