
**DYNAMICS OF EARLY STAGE FISHES ASSOCIATED WITH
SELECTED WARM TEMPERATE ESTUARIES
IN SOUTH AFRICA**

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NADINE AMELIA STRYDOM

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GENERAL ABSTRACT

Early stage fishes, namely larvae and early juveniles, were collected from 12 estuaries and associated habitats in the warm temperate region of South Africa between July 1998 and December 2000. This study served to provide new information and expand on existing knowledge of early stage fish assemblages associated with various types of Eastern Cape estuaries. A total of 65 536 predominantly postflexion fish larvae were collected. Together with early juveniles, taxa comprised 72 species from 25 teleost fish families. Surf zones associated with two intermittently open estuaries showed that estuary-dependent marine species predominated in this zone. Early stage fishes responded positively during natural estuary opening events and concentrated along the estuary outflow plume, suggesting that cueing from estuary and/or river water may be taking place. A habitat study in the Swartkops Estuary, using light traps, showed that newly recruited larval fishes concentrated along the margins of the estuary and unlike their older juvenile counterparts, were poorly represented in eelgrass beds. A multi-estuary comparison, including seven permanently open and five intermittently open estuaries, indicated that early stage fish assemblages were more diverse than indicated by past investigations. Early stage fishes were also shown to concentrate in the mesohaline regions of these estuaries. Studies of estuaries with altered freshwater flow regimes were also included in the research. A regulated release of dam water in the euhaline Kromme Estuary failed to induce a cueing response from estuary-dependent marine fish larvae. This project showed that large amounts of freshwater are required to reverse the negative effects of river impoundments. The release study did show that estuary-resident fishes were sensitive to small natural pulses of freshwater and responded by spawning. However, excessive river supply through an inter-basin water transfer scheme was shown to have a flushing effect on the larvae and early juveniles of the estuary-resident *Gilchristella aestuaria* in the upper reaches of the Great Fish Estuary. This effect was evident in comparisons with the freshwater starved Kariega Estuary where concentrations of *G. aestuaria*, a species usually more abundant in freshwater rich estuaries, were considerably higher. This finding suggests that freshwater minima and maxima be considered when assessing and managing estuarine systems.

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CHAPTER 1

GENERAL INTRODUCTION

Estuarine and marine ichthyoplankton research in South Africa: a perspective

South African research on larval fishes commenced in the early 1900s when J.D.F. Gilchrist published the first comprehensive accounts of marine fish eggs and fish larvae (Gilchrist 1903, 1904). His work culminated in a series of scientific works dealing with fish eggs and larvae (Gilchrist 1914, 1916, 1918, 1921, Gilchrist & Hunter 1919). The marine environment enjoyed most of the initial scientific attention with considerably less effort directed towards estuaries. Following Gilchrist's efforts, taxonomic and ontogenetic work recommenced in the mid 1900s, focusing mainly on commercially exploited fish species (e.g. Mathews & De Jager 1951, Davies 1954, De Jager 1955). However, research efforts were sporadic with extended periods revealing a complete absence of larval fish work.

Research on offshore (Castle 1968, 1969 *inter alia*) and commercially important (Haigh 1972, Louw & O'Toole 1977, King, *et al.* 1978 *inter alia*) marine species continued in the late 1960s and 1970s and dominated the literature on larval fishes. Ichthyoplankton investigations gained momentum in subsequent years, both in estuarine (see below) and nearshore marine habitats (Brownell 1979), while ocean-based ecological (e.g. Beckley & Van Ballegooyen 1992, Tilney & Buxton 1994, Wood 1998, Beckley & Leis 2000) and descriptive (e.g. Olivar & Fortuño 1991, Olivar *et al.* 1999) larval fish work continued.

The first comprehensive estuary based work on larval fishes was conducted in the late 1970s (Melville-Smith 1978). Melville-Smith & Baird (1980) published the first intensive larval fish ecology study in a South African estuary, conducted in the Swartkops Estuary on the warm temperate Eastern Cape Province coast. This project was followed by a similar investigation in the nearby Kromme Estuary (Melville-Smith 1981). Melville-Smith *et al.* (1981) further contributed to estuarine ichthyoplankton work with their investigation into the utilisation of tidal currents by larvae of an estuarine resident fish species. The trophic importance of roundherring larvae, *Gilchristella aestuaria*, were also considered by Wooldridge & Bailey (1982) in a zooplankton survey of the Sundays Estuary. Beckley (1985) conducted the first study on tidal exchange of ichthyoplankton through the Swartkops

Estuary mouth. Thereafter, Whitfield (1989a) investigated larval fish composition, abundance and seasonality in the Swartvlei estuarine lake that included an assessment of ichthyoplankton interchange in the mouth region of the same estuary (Whitfield 1989b). An investigation of the Sundays Estuary concentrating on the composition, distribution and abundance of ichthyoplankton (Harrison & Whitfield 1990) was followed by an assessment of the effects of differing freshwater inputs on ichthyoplankton and 0+ juvenile abundance in three separate estuarine systems (Whitfield 1994). The first estuarine ichthyoplankton work in the subtropical KwaZulu-Natal region was undertaken by Martin *et al.* (1992), focusing on the flushing effects of cyclone-induced floods in the St Lucia Estuary. Harris & Cyrus (1995) continued estuarine work in this region by assessing the occurrence of larval fishes in the St Lucia Estuary. This research was followed by investigations into the composition of larval fish at the mouth of the Kosi Estuary (Harris *et al.* 1995), and in addition, the abundance and seasonality of such assemblages in the Richards Bay Harbour (Harris & Cyrus 1997) and the Durban Bay Harbour (Harris & Cyrus 1999). Concurrently, estuarine larval fish work was conducted by Strydom (1998) in the warm temperate Gamtoos Estuary. This study focused on larval fish dynamics in the mouth region of the estuary and incorporated preliminary investigations into the diel, tidal and lunar implications for larval fish abundance and distribution.

South African estuarine larval fish work has also extended into the adjacent nearshore and surf zone regions where the nursery function of these habitats in association with estuarine habitats was evaluated. Work by Lasiak (1981, 1986) and Wallace *et al.* (1984) drew attention to these areas as nursery areas for young fishes, particularly estuary-dependent species. Beckley (1986) conducted the first ichthyoplankton study in the Algoa Bay nearshore region with particular relation to the utilization of the coastal zone by juvenile fish. Whitfield (1989c) went on to assess the nursery function of the surf zone for estuary associated larval fish species in Swartvlei Bay. Harris & Cyrus (1996) conducted the initial KwaZulu-Natal work focusing on similar aspects. Their work focused on larval and juvenile fishes in the surf adjacent to the St Lucia Estuary. Cowley *et al.* (2001) and Bell *et al.* (2001) have recently expanded the very limited database on surf zone utilization by larval stages of estuary-dependent species. This work provided initial evidence of larval fish recruitment, and the seasonal timing thereof, into closed estuaries during marine over-wash events. Harris

et al. (2001) investigated larval fish diversity along an ocean-estuarine gradient in Northern KwaZulu-Natal and have expanded on limited available information linking these habitats and highlighting the coupling and importance of these habitats for estuary-dependent larval fishes.

Estuarine and adjacent nearshore ichthyoplankton work has been supplemented by the descriptions of larval developmental stages for a few estuarine and estuarine-associated marine fish species (e.g. O'Toole & King 1974, Melville-Smith 1978, Brownell 1979, Olivar 1986, Neira *et al.* 1988, Cambray & Bok 1989, Beckley 1989, 1990, Olivar & Fortuño 1991, Haigh & Whitfield 1993). Generic information can be obtained from international descriptive works (e.g. Leis & Carson-Ewart 2000, Neira *et al.* 1998) but despite their scientific value, these national and international descriptions cover relatively few species. There is still insufficient information on the identification of many species of larval fishes that occur in South African estuaries and near-shore marine environments, particularly along the Eastern Cape coast of South Africa, highlighting the need for baseline research on ichthyoplankton taxonomy.

Rationale for this study

Estuaries worldwide are important nursery areas for juveniles of many species of estuarine and marine fishes (Weinstein 1979, Day *et al.* 1981, Dando 1984, Wallace *et al.*, 1984). This is a direct result of these species being represented in estuaries predominantly by juveniles. Although some species of fish do enter estuarine nursery areas as juveniles, more recent research shows that others enter as larvae (Beckley 1985, Roper 1986, Whitfield 1989b, Gaughan *et al.* 1990). The nursery function of estuaries therefore commences not only at the juvenile phase for estuary-dependent marine fishes, but also at the postflexion larval stage for some of these species. In estuaries, both nationally (Whitfield 1989b, Harris & Cyrus 1995, Harris *et al.* 1995) and internationally (e.g. Claridge *et al.* 1986, Miskiewicz 1986, Tzeng & Wang 1992, Neira & Potter 1994), postflexion larvae and early juveniles of estuary-dependent marine fish species recruit into estuarine nurseries from nearshore and offshore spawning grounds.

The recruitment of postflexion larval fish into estuarine nurseries include larvae of marine species as well as those of certain estuary-resident species whose preflexion larvae undergo a marine phase (Whitfield 1989b). These larvae later return to the estuary as postflexion larvae or early juveniles. Estuaries are also important nursery areas for the larvae of estuary-resident species whose life cycles are completed within the estuarine environment. Despite the importance of these habitats as nursery areas for early developmental stages of estuary-dependent fishes, little information exists on the intricacies of estuary use by these fishes or on the factors driving the recruitment process into both permanently open and intermittently open estuaries.

Prior to entering estuaries, larvae use surf zones as intermediary nursery habitats. The importance of these surf habitats for early stage fishes is poorly studied and very little comparative work exists between surf zones off permanently open and intermittently open estuaries. For example, estuary-dependent larval and juvenile fishes appear to be responding to cues from the estuarine or riverine environment, thus facilitating the recruitment process from surf zones into estuaries but more information is needed to support this hypothesis. Fish do possess a highly developed sense of smell (Stabell 1992) and estuarine/riverine water entering the marine environment could act as a cue in guiding estuary-dependent larvae towards appropriate nursery habitats (Boehlert & Mundy 1988). Freshwater flow into estuaries has been positively linked to recruitment of these fishes (Whitfield 1994) and it is therefore important to further investigate this process in an attempt to understand the forces driving and affecting fish recruitment into surf zones and estuaries.

Once larvae and early juveniles enter estuaries, very little is known about the distribution of these early stage fishes within their newly acquired nursery. Lower reaches habitat studies have tended to focus on older juvenile stages (Beckley 1983), and it is not known whether larvae and early juveniles occupy the same habitats after initial entry into the system. Moreover, once early stage fishes have successfully entered an estuary, very little is known about their abundance and distribution throughout the estuary, particularly when influenced by varying estuary type and existing physico-chemical conditions.

One of the most important factors governing the physico-chemical and hydrodynamic properties of estuarine waters in South Africa is river inflow (Allanson & Baird 1999). Catchment size and river characteristics result in various types of downstream estuaries that vary significantly in terms of salinity, turbidity and freshwater inflow. Limited information is available on the early stage fishes utilising these various types of estuaries. These studies however, are single estuary studies and do not give holistic comparative views on the biology and ecology of early stage fishes using these estuaries. Past investigations have also largely concentrated on permanently open estuaries leaving early stage fishes in intermittently open estuaries poorly studied (Dundas 1994). Moreover, spatial and temporal variations characteristic of past investigations make comparisons with these works difficult. A regional multi-estuary study will provide much needed comparative information pertaining to early stage fish use and association with varying permanently and intermittently open estuary types.

South Africa is an arid country characterized by a high demand for freshwater with a resultant high degree of catchment manipulation (Davies & Day 1986). Consequently, extensive alterations to the freshwater supply of many estuaries have occurred that invariably altered the biological functioning of these systems (Schlacher & Wooldridge 1996, Grange *et al.* 2000). Despite the widespread occurrence of these activities, very little is known about the influence of freshwater supply alterations to the larval and juvenile fishes relying on downstream estuaries as nursery areas. River inflow also influences the state of the estuary mouth and therefore the estuary type. Early stage fishes are found in all types of estuaries along the South African coastline but very little quantitative or qualitative work has been conducted to determine the influence of estuary type, or anthropogenic changes to these estuaries, on the composition and abundance of early stage fishes utilizing these systems (Harris & Cyrus 2000).

Aims and Objectives

South African estuaries have been classified by Whitfield (1998) into five principal types, viz. permanently open estuaries, intermittently open estuaries (temporarily closed), estuarine bays, estuarine lakes and river mouths. The warm temperate Eastern Cape Province includes permanently open, temporarily open/closed estuaries and river mouths, but permanently open

and intermittently open systems dominate the region. The Eastern Cape Province boasts the highest number of estuaries countrywide with respect to the biogeographical classification of the S.A. coast. The warm temperate region supports 123 estuarine systems compared to the 117 subtropical systems to the northeast and 10 cool temperate systems in the west (Whitfield 1998).

The scope of the present study includes the two dominant estuary types found in the Eastern Cape Province and spans 12 estuaries (seven permanently open and five intermittently open) of varying sizes and physico-chemical properties. These estuaries are investigated in a holistic approach together with case studies in selected estuarine systems and associated habitats. Permanently open and intermittently open systems in the Eastern Cape display considerable physico-chemical variability, much of which is mainly linked to the fluctuating freshwater supply entering these systems (Whitfield & Wooldridge 1994). The focus of this work is firstly, to quantify and qualify the larval and early juvenile fish assemblages associated with and utilising these estuaries and, secondly, to further understand the influence of variable freshwater input and the resultant estuarine variability, on the early stage fish assemblages utilising these systems.

The aims of the present study are to assess the:

- Composition of early stage fish assemblages in the surf zone adjacent to the intermittently open Kabeljous and Van Stadens estuaries (Chapter 2).
 - Utilization of habitat by postflexion larval fishes and early juveniles in a shallow tidal creek of the Swartkops Estuary (Chapter 3).
 - Species composition, diversity, abundance and distribution of larval and early juvenile fishes in selected permanently open and intermittently open estuaries (Chapter 4).
 - Effects of a single regulated release of freshwater into the euhaline Kromme Estuary on larval fish recruitment (Chapter 5).
 - Influence of altered freshwater flow regimes on larval and early juvenile *Gilchristella aestuaria* (Pisces: Clupeidae) abundance in the upper reaches of the Kariega and Great Fish estuaries (Chapter 6).
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Thesis structure

A series of independent studies are presented in this thesis. The chapters are interwoven around the influence of estuarine type, and associated physico-chemical and hydrodynamic functioning, on early stage (larvae and early juveniles) fish assemblages associated with these systems and habitats. This thesis is presented as a collection of scientific papers, published, in press or submitted for publication. This results in a limited degree of repetition in the introduction, methods and study areas of each section. This collective work is preceded by a general introduction and followed by a synthesis and conclusion.

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CHAPTER 2

OCCURRENCE OF EARLY STAGE FISHES IN THE SURF ZONE ADJACENT TO TWO INTERMITTENTLY OPEN ESTUARIES, SOUTH AFRICA

(This work has been submitted to the journal *Environmental Biology of Fishes*)

SYNOPSIS

Early stage fishes were monitored in the surf zone adjacent to two warm temperate, intermittently open estuaries in South Africa. Sampling was conducted on the new moon spring low tide adjacent to the Kabeljous and Van Stadens estuaries on two consecutive days and two consecutive months per season over one year. A total of 2739 larval and early juvenile fishes were collected in 96 samples. The surf zone adjacent to the Van Stadens Estuary yielded 321 individuals representing 13 taxa and 7 fish families. The Kabeljous Estuary catches yielded 2418 individuals representing 25 taxa and 14 families. Family composition in both surf zones was dominated by Mugilidae, Sparidae and Soleidae. The mugilid *Myxus capensis*, in a postflexion or early juvenile stage of development, and the sparid *Rhabdosargus holubi*, in a postflexion stage of development, were the most abundant species caught during the study. Surf zone catches were dominated almost exclusively by species displaying a degree of dependence on estuaries during the early phase of their life cycle. Most fish encountered were at the postflexion stage. Early stage fishes were more abundant during the summer and autumn months with density peaking several fold during estuary opening events, particularly in the surf zone adjacent to the Kabeljous Estuary. Salinity showed a significant relationship with fish density during this event and catches were concentrated along the current-driven estuarine plume in the marine environment rather than proximity to the estuary mouth. Van Stadens catches also increased notably during the smaller opening events. Surf zone salinity played no statistically significant role in these increased catches. This result suggests that either very small amounts of estuarine water entering the surf zone elicits an accumulation response by estuary-dependent larval fishes or that some olfactory characteristic of estuary / river water, other than salinity per se, is aiding the cueing process.

INTRODUCTION

The recruitment of early stage fishes into estuaries and the importance of these habitats as nursery areas have been particularly well studied internationally (e.g. Roper 1986, Boehlert & Mundy 1988, Neira & Potter 1992) but to a much lesser degree in South Africa (e.g. Beckley 1985, Whitfield 1989a, Strydom & Whitfield 2000). Despite the available information on recruitment of young fishes into estuaries, there is a paucity of information describing the factors driving this process. Many researchers have linked recruitment to various physico-chemical factors, with salinity gradients (Whitfield 1989a), temperature (Miller 1988), turbidity (Blaber & Blaber 1980) and catchment odours (Miles 1968) among the probable cues driving recruitment of early stage fishes. Many researchers conform to the broad school of thought that olfaction is the primary sense behind the recruitment process (Boehlert & Mundy 1988, Stabell 1992,) but conclusive evidence is lacking.

Surf zones have been identified as important accumulation areas and transient routes for estuary-dependent species (Boehlert & Mundy 1988, Potter *et al.* 1990). Larvae of estuary-dependent marine fishes move from offshore spawning grounds, initially passively but later by active migration to surf zones (Boehlert & Mundy 1988). These larvae make use of various physical events such as flooding tides (Beckley 1985, Whitfield 1989a), tidal fronts (Kingsford & Suthers 1996), non-local forcing (Pietrafesa & Janowitz 1988) and overtopping events, in the case of intermittently open estuaries (Cowley *et al.* 2001) to facilitate the final stage of recruitment into estuaries.

International focus on the relationship between surf zones and larval fishes has been concentrated in areas such as Japan (e.g. Senta & Kinoshita 1985), the Gulf of Mexico (e.g. Ruple 1984) and Australia (e.g. Doherty & McIlwain 1996). Research on early stage fishes in South African surf zones is limited to isolated investigations (Whitfield 1989b, Harris & Cyrus 1996, Harris *et al.* 2001, Cowley *et al.* 2001) despite the importance of these areas for the recruitment process into both permanently and intermittently open estuaries. Past investigations traditionally targeted juvenile fish (Lasiak 1981, 1986, Bennett 1989) that were thought to be the primary users of surf zone habitats. Moreover, investigations by Miskiewicz (1986), Gaughan *et al.* (1990) and Warlen & Burke (1990) indicate that fishes recruit into estuaries at earlier developmental stages than previously thought.

The concentration of estuary-dependent fishes in surf zones adjacent to intermittently open estuaries poses some interesting, yet unanswered questions (Whitfield 1989b, Cowley *et al.* 2001). Whitfield (1989b) suggested that the accumulation of large numbers of estuary-dependent species in the surf adjacent to an intermittently open estuary was due to seepage through the sand bar at the mouth, but this has not been fully investigated. The driving forces behind these accumulations are poorly understood, as are the responses of these early stage fish assemblages to natural opening events of intermittently open estuaries. The present study focuses on identifying the assemblage structure of early stage fishes in the surf zone adjacent to two intermittently open estuaries in South Africa with particular emphasis on the physical factors affecting these assemblages. The study incorporates a comparison of catches before, during and after natural estuary opening events into the surf zone.

MATERIAL AND METHODS

Study area

The surf zone sites used in this study are adjacent to the intermittently open Van Stadens and Kabeljous estuaries that open into St Francis Bay (Figure 1). This region lies within a warm temperate climatic zone. The coastline consists of long open sandy beaches that are of an intermediate type and subject to continuous wave action (McLachlan *et al.* 1981). Surf zones usually range from 100 to 300 m in width with breaking wave heights ranging from less than 1 m to approximately 5 m. Tides are semidiurnal with a maximum spring tidal range of 2.1 m (McLachlan *et al.* 1981).

The Van Stadens Estuary (33°58'1"S, 25°13'20"E) has a catchment area of 271 km² and is subject to mean annual precipitation of 707 mm and mean annual run-off of 21.41 x 10⁶ m³ (Crowther 1987). The Kabeljous Estuary (34°00'20"S, 24°56'15"E) has a catchment area of 238 km² and is subject to mean annual precipitation of 450 mm and mean annual run-off of 27 x 10⁶ m³ (Reddering & Esterhuysen 1984). Freshwater supply to these systems varies according to upriver abstraction with the Van Stadens Estuary generally having a higher freshwater input and lower salinity range than the Kabeljous system. Frequent rainfall prior to the study period resulted in the usually euhaline Kabeljous Estuary becoming more mesohaline, similar to the conditions that usually prevail in the Van Stadens system.

Field sampling and laboratory analyses

The Van Stadens and Kabeljous surf zones were sampled with a small-mesh seine net on two consecutive days over the new moon phase, in two consecutive months in each season from February – December 2000. All sampling was confined to daylight on the new moon spring low tide due to the difficulties of operating a net in a high-energy surf zone. Each surf zone area consisted of four sampling sites (Figure 1). Two sites were situated opposite the mouth of each estuary and two sites were situated 1 km away from each mouth on either side. Three replicates were collected at each site by pulling a modified beach-seine net across 25m parallel to the coast. In total, 75m of surf water were sampled at each site. This data series spanned a total of eight days and 96 samples for each surf zone. Catches are expressed as catch per unit effort (CPUE) which refers to the number of fish collected in a single 25 m seine haul.

The net was 1.5 m high x 4.5 m wide with a bar mesh aperture size of 0.5 mm. This net was designed for catching larval fish and consisted of a small beach seine-net fitted with a central tapering cone (similar to a WP2 plankton net with mouth diameter of 0.57 m) that ended in a tied cod end. The cone resulted in the concentration of larvae at the tapered cod end and allowed for easy removal of larvae. Any larvae adhering to the sides of the beach-seine net or the cone were also easily washed down into the cod end for removal. The approximate volume of surf water filtered by each haul was 150 m³, as the entire net was not submerged during hauls. Approximately 20 cm remained above the water surface. Samples were preserved on site with 5 % formaldehyde in seawater. Whole samples were processed in the laboratory and early stage fish removed. Fish were identified to the lowest possible taxon according to Brownell (1979), Moser *et al.* (1984), Leis & Trnski (1989), Olivar & Fortuño (1991), Smith & Heemstra (1995) and Neira *et al.* (1998). At each site on each occasion, temperature, salinity and turbidity measurements were taken. Temperature (°C) was measured on site with a standard mercury thermometer. Salinity (‰) and turbidity (Formazin Attenuation Units or FAU) were measured in the laboratory using a WTW Multiline P4 Meter and Hach DR/890 Colorimeter respectively.

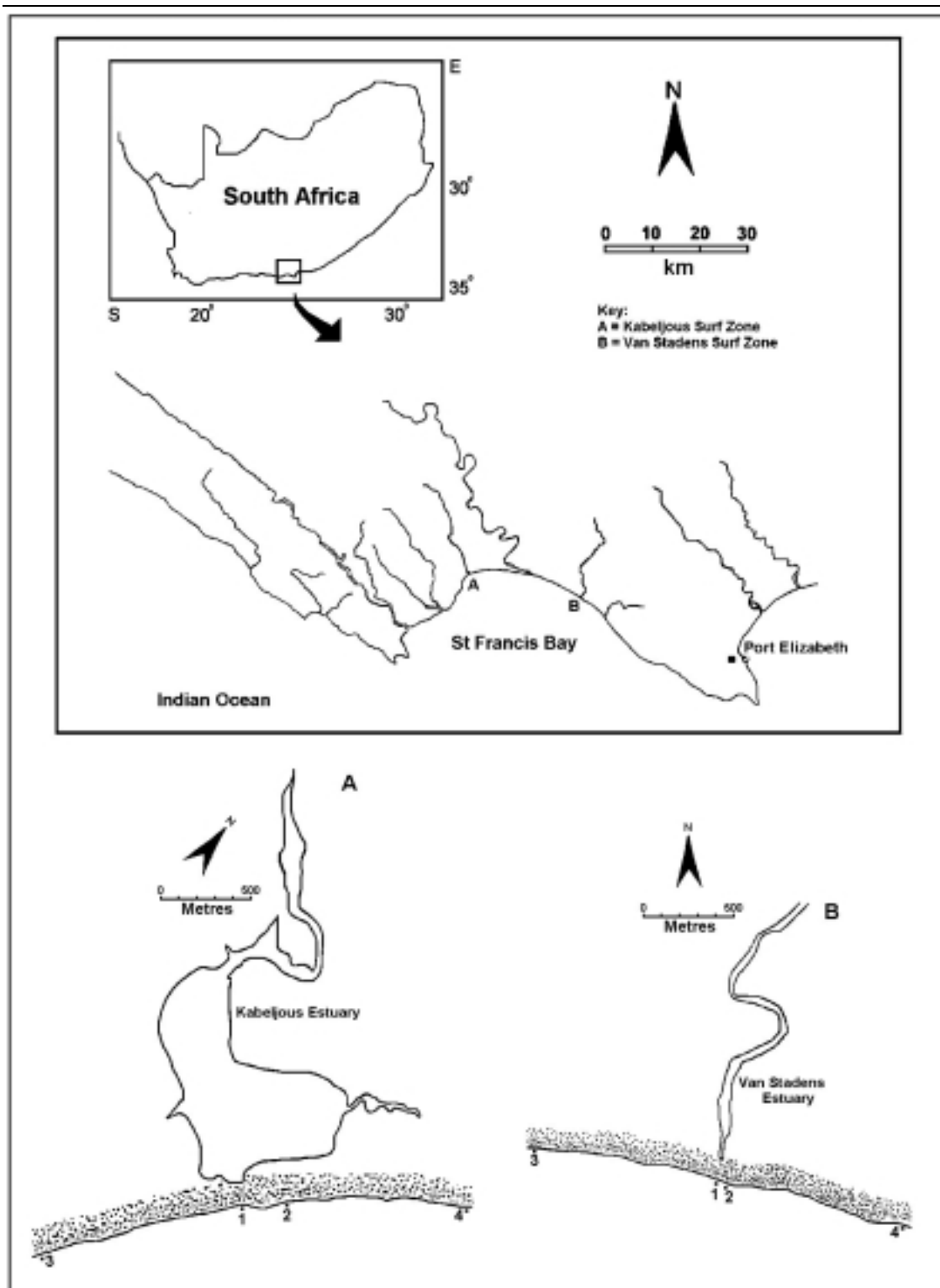


Figure 1. Geographical position of St Francis Bay showing location of sampling sites (1-4) in the Van Stadens and Kabeljous surf zone.

All terminology pertaining to larval fish follows that of Kendall *et al.* (1984). The term "larva" is used to designate all stages in the early life history from hatching to the attainment of a full fin ray complement, squamation and the subsequent loss of all larval characters, at which stage the "larva" becomes a "juvenile". The term "larva" is further divided into yolk-sac, preflexion, flexion and postflexion larval stages. The term "early stage fishes" is used to collectively refer to larvae and early juveniles. Distinction is made in the text between these stages where necessary. Larvae and early juveniles were measured to the nearest 0.1 mm body length (BL), which represents notochord length in preflexion and flexion stage larvae, and standard length in postflexion larvae and juveniles. Measurements were made using an eyepiece micrometer for larvae <10 mm and Vernier calipers for larger specimens.

Estuary association categories

Early stage fishes that were positively identified were categorized according to the degree to which the species is dependent on South African estuaries (Whitfield 1998).

Category	Description
Ia.	Estuarine species that breed only in estuaries
Ib.	Estuarine species that breed in estuaries and the marine environment
IIa	Euryhaline marine species that usually breed at sea but the juveniles are dependent on estuaries as nursery areas
IIb.	Euryhaline marine species that usually breed at sea, with the juveniles occurring in estuaries but also being found at sea.
IIc.	Euryhaline marine species that usually breed at sea, with the juveniles occurring in estuaries but being more abundant at sea
III.	Marine stragglers not dependent on estuaries
V.	Catadromous species

Data analyses

All frequency data were square-root-transformed and continuous physical data were log transformed to conform to normality and homogeneity of variances. All transformed data failed to meet the assumptions of parametric statistical tests and non-parametric methods were used. Heterogeneity of variance and non-normality of data were attributed to the patchy

nature of early stage fish assemblages in the surf zone and to the occurrence of estuary opening events in the surf zone data set. In all statistical analyses a significance level of $P < 0.05$ was used. Exceptions were made in tests that included multiple comparisons. The Bonferroni adjustment to the level of significance was used for multiple comparisons to ensure that the overall level of significance did not exceed 0.05. Log-linear models were used to investigate interactive relationships between fish CPUE and estuary, collection month and site. Summed frequencies were used for each site for these analyses.

Data were further analysed using standard non-parametric tests to isolate significant effects. Significant differences between physical variables and CPUE of larval fishes between surf zones were evaluated using the Mann-Whitney U-test. CPUE data were evaluated at the total species and individual species levels and included a focus on estuary-dependent species during open and closed phases of the estuaries. The Kruskal Wallis test was used to assess differences in CPUE and physical data between collection month, seasons and sites within each surf zone. Data were assessed at the total species and estuary-dependent species levels. Multiple linear stepwise regressions were used to ascertain whether environmental variables displayed any significant relationships with fish density. These regressions were assessed using total species and dominant species (occurring in numbers equal or greater than 10) between and within surf zones associated with the different estuaries.

RESULTS

Environmental variability

Salinity ranged from 31.1 – 35.0 ‰ in the Van Stadens surf zone and 31.4 – 35.2 ‰ in the Kabeljous surf during the entire study period (Fig. 2). Reductions in salinity occurred during two estuary-opening events in the Van Stadens surf in March and November of the study year. The March opening resulted in a maximum recorded reduction of surf salinity to 34.6 ‰ throughout the surf sites sampled and the smaller November opening resulted in a reduction to 31.1 ‰ only at site 1, directly opposite the estuary outflow. Kabeljous surf salinity was reduced at all sites during the single large March opening, with reductions of between 2 – 4 ‰ recorded. At site 3, salinity was reduced to the minimum in this range (31.4

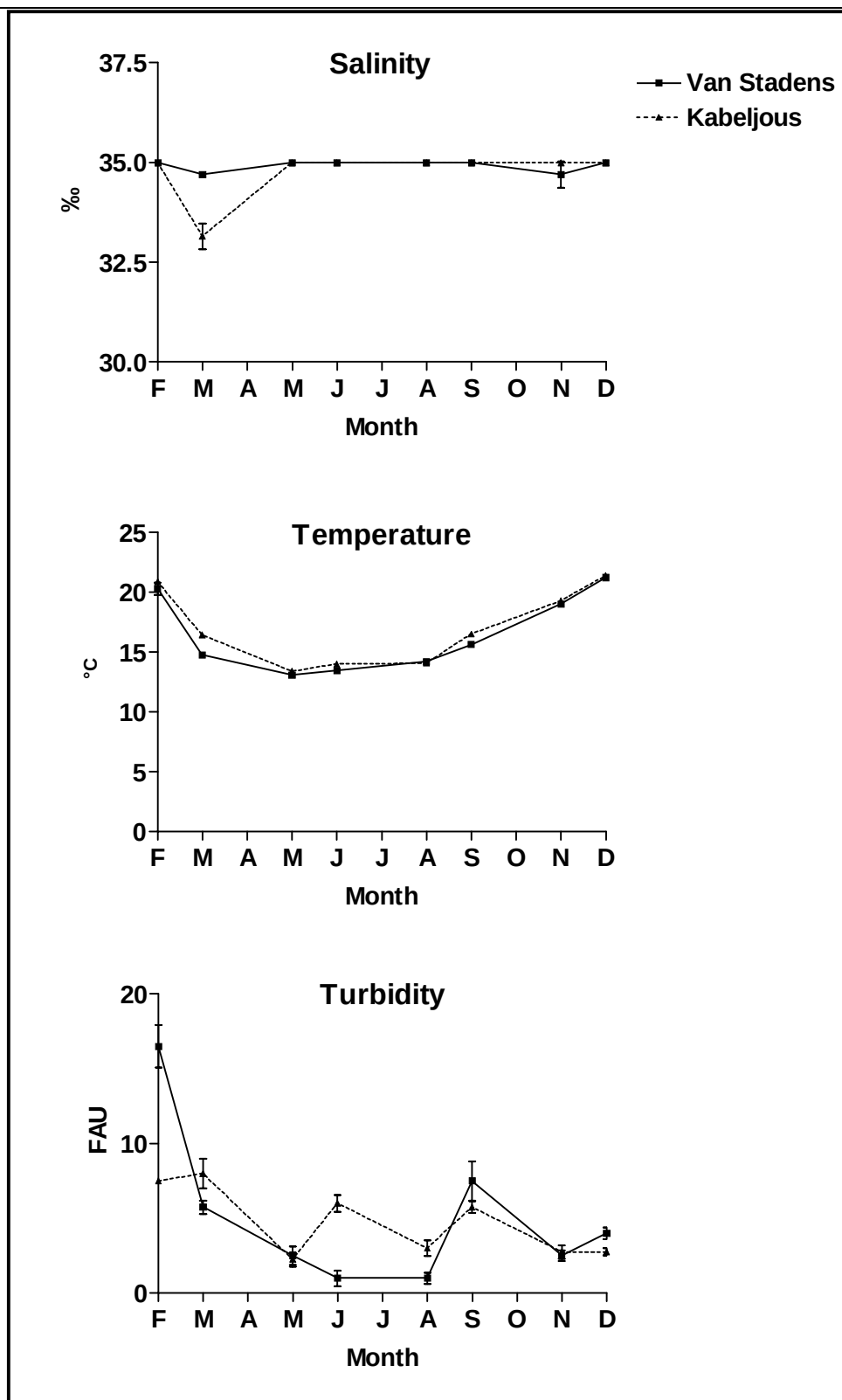


Figure 2. Mean (! S.E.) salinity, temperature and turbidity recordings for Van Stadens and Kabeljous surf zones.

‰). Temperature ranged between 13 and 22 °C in both surf zones and Van Stadens turbidity ranged slightly higher at 0 – 24 FAU whereas Kabeljous turbidities ranged from 0 – 13 FAU.

Physical variables were compared between surf zones with only salinity showing a significant difference ($P < 0.05$). Comparisons were also made between collection trips and sites for each individual surf zone. Salinity remained constant throughout the year in both surf zones except during the March opening events where there were significant differences ($P < 0.05$ in salinity between sites off both estuaries). Salinity in the Van Stadens surf during this month was however not statistically different from other months sampled, indicating that the opening events experienced during March and November were small in magnitude. Recordings for collection trips and sites in the Van Stadens surf indicated that temperature and turbidity were significantly different ($P < 0.01$) throughout the year. A similar trend was observed between the Kabeljous surf sites. During the winter months, temperature and turbidity differences between sites in both surf zones were less pronounced.

Multiple linear stepwise regressions of physical variables with CPUE of estuary-dependent species indicated that salinity displayed a significant ($P < 0.01$) relationship with fish CPUE. Data were then separated and individual surf zones analysed. No significant relationship with environmental variables and fish CPUE was observed in the Van Stadens surf zone but this relationship was highly significant ($P < 0.01$) with salinity in the Kabeljous surf zone and was responsible for the over-riding effect of salinity in the data set as a whole. Regression statistics for the surf zones are shown in Table 1.

Dominant species were also regressed against physical variables to assess any significant relationships with individual species between and within each surf zone (Table 1). Van Stadens catches revealed only three species that showed a significant relationship between CPUE and a physical variable, i.e. *Diplodus sargus capensis* CPUE showed a significant relationship with turbidity, *Heteromyceteris capensis* CPUE indicated patterns associated with temperature and the engraulid *Engraulis japonicus* CPUE showed a positive relationship with decreases in salinity. Kabeljous catches showed significant relationships between 13 species and salinity (Table 1).

Table 1. Stepwise multiple linear regression statistics of fish density versus environmental variables for all taxa, estuary-dependent taxa and dominant individual species. $\text{adj}R^2$ = adjusted coefficient of determination; R = Correlation coefficient; F = F-statistic; sa = Salinity, te = Temperature, tu = Turbidity; Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant.

	VAN STADENS				KABELJOUS			
	$\text{adj}R^2$	R	F	Significant variable	$\text{adj}R^2$	R	F	Significant variable
All taxa	-0.010	0.147	0.680	ns	0.596	0.780	47.777	sa***
Estuary dependent taxa	-0.012	0.138	0.595	ns	0.599	0.782	48.295	sa**
Dependent species								
<i>Myxus capensis</i>	0.003	0.188	1.120	ns	0.622	.0796	53.161	sa***
<i>Liza richardsonii</i>	0.004	0.190	1.159	ns	0.115	0.378	5.108	sa***
<i>Mugil cephalus</i>	0.001	0.180	1.033	ns	-0.013	0.137	0.590	ns
<i>Rhabdosargus holubi</i>	-0.012	0.140	0.611	ns	0.474	0.701	29.571	sa***
<i>Rhabdosargus globiceps</i>	-	-	-	-	0.449	0.683	26.762	sa***
<i>Diplodus sargus capensis</i>	0.142	0.412	6.271	tu***	0.179	0.453	7.914	sa***
<i>Atherina breviceps</i>	-0.032	0.012	0.004	ns	0.108	0.369	4.826	ns
<i>Heteromycteris capensis</i>	0.042	0.270	2.409	te*	0.778	0.886	112.029	sa***
<i>Solea bleekeri</i>	-0.023	0.096	0.284	ns	0.694	0.839	72.725	sa***
<i>Monodactylus falciformis</i>	-	-	-	-	0.584	0.773	45.387	sa***
<i>Psammogobius knysnaensis</i>	-0.023	0.096	0.284	ns	0.406	0.652	22.670	sa***tetu*
<i>Gilchristella aestuaria</i>	-	-	-	-	0.273	0.544	12.892	sa***
Independent species								
<i>Engraulis japonicus</i>	0.075	0.323	3.570	sa**	0.231	0.505	10.5170	sate**tu***

Species composition and estuary association

A total of 2739 fish larvae and early juveniles were collected in the surf zones adjacent to the Van Stadens and Kabeljous estuaries during the entire study. Catches were represented by 321 and 2418 specimens respectively. Catches in the Van Stadens surf zone yielded seven fish families represented by 13 species (Table 2). Dominant families in the Van Stadens surf were the Mugilidae (66.7%), Sparidae (15.6%), Soleidae (12.5%) and Engraulidae (3.1%). Kabeljous surf zone catches yielded 14 families represented by 25 species with an additional two unidentified species (Table 2). Catches were dominated by Mugilidae (59.4%) but the Atherinidae made a large contribution to total catch (21%) with smaller contributions by the Sparidae (5.3%), Soleidae (5.8%), Gobiidae (3.9%), Monodactylidae (1.4%), Engraulidae (1.3%) and the Clupeidae (1.1%). Early stage fishes caught were predominantly at the postflexion stage of development. All developmental stages encountered for individual species caught are shown in Table 2.

Surf zone catches were dominated almost exclusively by estuary-dependent species of varying degrees (categories I, II and V). Van Stadens surf catches consisted of 96.3% estuary-dependent species and Kabeljous surf catches similarly, consisted of 97.5% estuary-dependent species. Estuary association categories for early stage fishes caught in this study are shown in Table 2 with percentage contributions shown for the Van Stadens and Kabeljous surf zones in Figure 3.

Table 2. Species composition, total catch, length, estuary association and developmental stages for fishes caught in the Van Stadens (VS) and Kabeljous (KB) surf zones by means of modified beach seine net. Pr = preflexion, F = Flexion, Po = postflexion, Ju = early juvenile.

Family	Species	VS	KB	Total catch		Body length (mm)		Developmental stage	Estuary association
		No.	No.	No	%	Mean	Range		
Ambassidae	<i>Ambassis dussumieri</i>	-	6	6	0.2	10.03	8.16-12.24	Po	Ib?
Atherinidae	<i>Atherina breviceps</i>	3	508	511	18.7	9.9	6.12-21.20	Pr,F,Po,Ju	Ib?
Blenniidae	<i>Parablennius cornutus</i>	1	3	4	0.1	15.64	14.80-15.92	Po	III
	Blenniid 3	1	-	1	<0.1	3.23		Pr	?
	Blenniid 4	-	1	1	<0.1	4.59		Pr	?
	Clinid 6	-	2	2	<0.1	9.35	9.30-9.40	Po	?
Clupeidae	<i>Gilchristella aestuaria</i>	-	24	24	0.9	17.54	11.56-24.0	Po,Ju	Ia
	<i>Sardinops sagax</i>	-	2	2	<0.1	41.48	40.60-43.10	Ju	III
Cynoglossidae	<i>Cynoglossus capensis</i>	-	1	1	<0.1	9.35		Pr	III
Engraulidae	<i>Engraulis japonicus</i>	10	31	41	1.5	6.48	2.89-19.0	Pr,F,Po	III
Gobiidae	<i>Caffrogobius</i> sp. 1	-	4	4	0.1	10.71	10.62-10.97	Po	?
	<i>Caffrogobius</i> sp. 2	-	5	5	0.2	7.65	4.76-9.69	F,Po	?
	Gobiid 5	-	5	5	0.2	5.61	5.42-5.68	F	?
	<i>Psammogobius knysnaensis</i>	1	80	81	3.0	6.63	5.78-8.16	Po	Ib?
	<i>Monodactylus falciformis</i>	-	33	33	1.2	5.76	5.10-6.29	Po	Ila
Mugilidae	<i>Liza richardsonii</i>	11	89	100	3.7	18.75	11.90-34.4	Po,Ju	Iic
	<i>Mugil cephalus</i>	7	3	10	0.4	21.36	18.10-24.50	Po,Ju	Ila
	<i>Myxus capensis</i>	196	1345	1541	56.3	10.61	8.33-32.90	Po,Ju	V
	<i>Heteromycteris capensis</i>	39	99	138	5.0	6.93	5.61-11.05	Po	Iib
Sparidae	<i>Solea bleekeri</i>	1	41	42	1.5	4.49	3.57-6.80	Po	Iib
	<i>Diplodus sargus capensis</i>	2	14	16	0.6	11.22	7.14-39.90	Po,Ju	Iic
	<i>Rhabdosargus globiceps</i>	-	41	41	1.5	14.03	9.69-23.80	Po,Ju	Iic
	<i>Rhabdosargus holubi</i>	48	72	120	4.4	11.30	9.35-32.40	Po,Ju	Ila
	<i>Syngnathus acus</i>	-	1	1	<0.1	10.54		Po	Ib
Terapontidae	<i>Terapon jarbua</i>	1	2	3	0.1	10.37	9.86-11.05	Po	Ila
Tetraodontidae	<i>Amblyrhynchotes honckenii</i>	-	1	1	<0.1	87.89		Ju	III

Table 2. continued...

Family	Species	VS	KB	Total catch		Body length (mm)		Developmental stage	Estuary association
		No.	No.	No	%	Mean	Range		
Unidentified	Species 6	-	2	2	<0.1	8.67		Po	?
	Species 7	-	3	3	0.1	4.43	4.42-4.76	Po	?

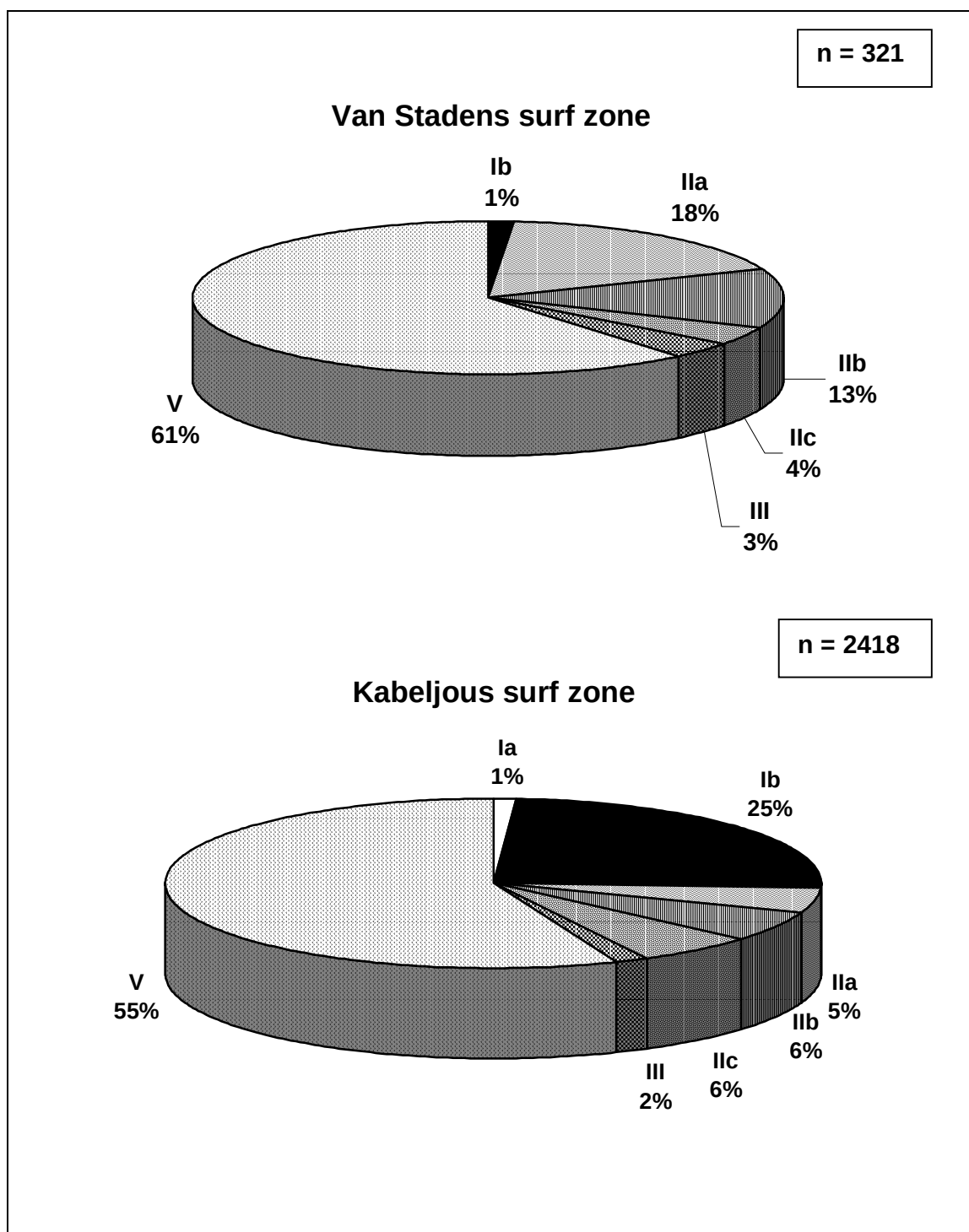


Figure 3. Estuary association categories for early stage fishes collected in the Van Stadens and Kabeljous surf zones between February and December 2000.

Temporal and spatial trends in fish density

Log-linear modeling was used to detect interactive relationships between CPUE (Figure 4) and time-space variables (estuary, collection month and site). CPUE data for the combined Van Stadens and Kabeljous surf zones showed highly significant interactions ($P < 0.01$) with all combinations of variables used for model testing. Surf zones were also modeled separately and highly significant interactions ($P < 0.01$) were found with all models tested (Table 3).

Catches in the Van Stadens and Kabeljous surf zones were significantly different ($P < 0.01$). Mean CPUE for the two study areas are shown in Figure 4. Considerably higher catches were made in the Kabeljous surf with *Liza richardsonii*, *Rhabdosargus globiceps*, *Atherina breviceps*, *Monodactylus falciformis*, *Psammogobius knysnaensis*, *Caffrogobius* sp. and *Gilchristella aestuaria* all occurring in significantly ($P < 0.05$) higher concentrations in the Kabeljous surf zone (Table 2). Total CPUE for estuary-dependent species also varied significantly ($P < 0.01$) between the two surf zones with the Kabeljous catches being higher than those of the Van Stadens (Figure 5).

Surf zone catches were compared between sites and between surf zones during open and closed phases of the estuaries. Sites were coded as mouth sites and away sites to assess any possible cueing response to both opening events and/or possible seepage. Sites were also coded as sites to the east and sites to the west to assess the effects of localized current flow on possible cueing responses. No significant differences between sites were observed throughout the entire study period. The data set was split between surf zones and reanalyzed. Surf zone catches during the closed phase of both estuaries also indicated no significant differences between sites. Open phase catches did however show a highly significant difference ($P < 0.05$) between east and west based sites in the surf zone adjacent to the open Kabeljous Estuary. Open and closed phase total CPUE between estuaries for individual species are shown in Figure 5. Catches also varied significantly ($P < 0.01$) between fieldtrips in both Van Stadens and Kabeljous surf zones for all species and exclusively estuary-dependent species. Seasonal variation also significantly influenced CPUE in the Van Stadens ($P < 0.05$) and Kabeljous ($P < 0.01$) surf zones.

Table 3. Test statistics for log-linear analysis of relationships between CPUE of early stage fishes and various effects (estuary, collection month and site).

Model tested	Pearson Chi-square All taxa	Pearson Chi-square Estuary-dependent taxa	df	Significance
Combined surf zones				
Estuary	30368.50	30806.44	62	P < 0.001
Trip	9552.812	9604.707	56	P < 0.001
Site	19423.46	19488.30	60	P < 0.001
Estuary-Trip	4511.366	4518.881	48	P < 0.001
Estuary-Site	10642.27	10464.76	56	P < 0.001
Trip-site	1969.732	1921.911	32	P < 0.001
Van Stadens				
Trip	378.6184	304.9297	24	P < 0.001
Site	978.8517	952.8920	28	P < 0.001
Kabeljous				
Trip	4132.749	4213.950	24	P < 0.001
Site	9663.420	9511.864	28	P < 0.001

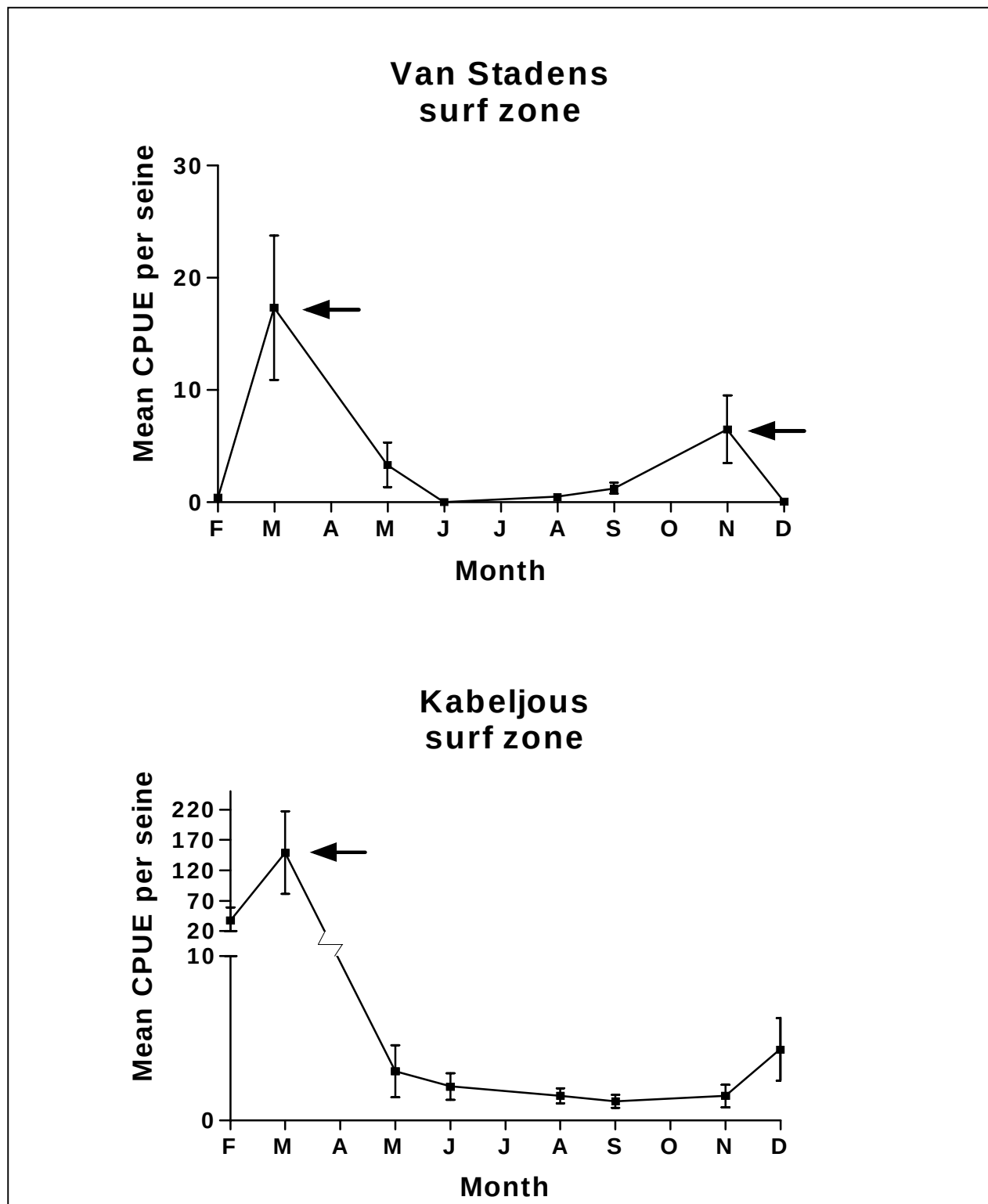


Figure 4. Mean CPUE for early stage fishes in the Van Stadens and Kabeljous surf zones between February and December 2000. Arrows indicate natural estuary opening events.

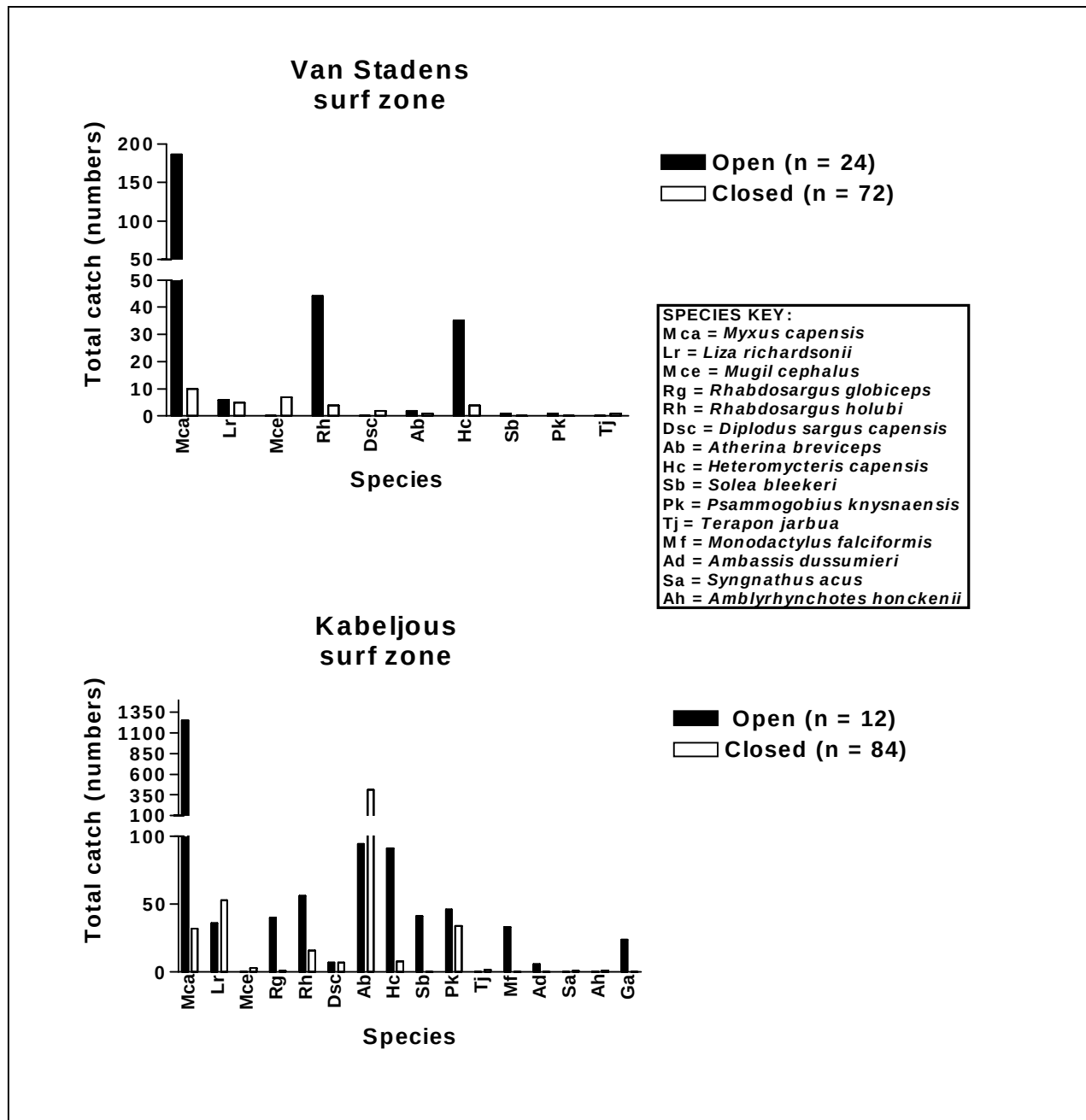


Figure 5. Total CPUE for estuary-dependent larval and early juvenile fishes caught in the surf zone during open and closed phases of Van Stadens and Kabeljous estuaries.

DISCUSSION

The Van Stadens and Kabeljous surf zones were found to be distinctly different habitats despite their proximity to each other and their situation within the same bay system. The pocketed nature of the substrate in the sampling areas, variable wave action and the effects of natural estuary opening events distinguished these two surf zones and their associated environmental variability. Highly significant interactions were found between temporal and spatial variables and catch using the log-linear method, indicating that suites of time-space variables rather than individual variables govern catches of early stage fishes in these surf zones.

An assessment of the influence of environmental variability indicated that temperature and turbidity appeared to have no localized effect on catches. However, seasonal trends in surf zone catches were evident (Roper 1986, Whitfield 1989b, Harris & Cyrus 1996). Reductions in catch of early stage fishes during winter were expected since most estuary-dependent fish species are spring/summer spawners with peak recruitment also occurring during this period (Whitfield 1998). Overall, catches were considerably higher in the Kabeljous surf zone than those recorded in the Van Stadens surf. This was attributed to the effects of a large natural estuary-opening event into the Kabeljous surf zone that resulted in an accumulatory or cueing response by the larvae and early juveniles of estuary-dependent fishes. This was reiterated in the finding that catches of early stage fishes showed a significant relationship with salinity in the Kabeljous surf during the estuary-opening event. The size of the opening event experienced in the Kabeljous Estuary was considerably greater than that at the Van Stadens Estuary and resulted in the flushing of estuary-resident fish species such as *Gilchristella aestuaria*. This high degree of flushing was not documented in the Van Stadens surf zone. A cueing response was, however, also observed in the Van Stadens surf during two opening events even though no measurable physical variable in this study showed any significant relationship with the increase in CPUE. This suggests that an additional aspect of estuarine water quality, other than salinity per se, may be driving the cueing process for estuary-dependent species into open estuarine nursery areas. Creutzberg (1961) and Miles (1968) found that eel elvers responded to catchment odours contained in river water used in their investigations. Very small amounts of estuary / river water input into the surf zone could also be inducing a cueing response, but if this was the case, then cueing should have also been

detected in a freshwater dam release into the marine dominated Kromme Estuary (Strydom & Whitfield 2000). In this summer study, surface salinities were reduced to between 33 and 26 ‰ in the lower and middle reaches of the Kromme Estuary but despite ebb tidal action, enhanced by river flow that would move this body of water into the surf zone, no recruitment was observed into the estuary. Based on evidence from this study and others, catchment odours may be playing a larger role than was previously thought. This could explain the early stage fish cueing response observed in the Van Stadens surf and the lack of cueing from dam water released during the Kromme Estuary project where catchment odours, receptive to early stage fishes, may be lost after water is left dammed for extensive periods.

Closed phase catches off both estuaries indicated that no seepage, in measurable terms of salinity or turbidity changes, was taking place in the surf zone. This was reiterated in the lack of variation in catches of larvae or early juveniles of estuary-dependent fishes between sites situated near the mouth and away from the mouth. At all sites, catches were however dominated by estuary-dependent species even during the closed mouth phase. This supports findings by Whitfield (1989b), Cowley *et al.* (2001) and Harris & Cyrus (1996) where the larvae of estuary-dependent species dominated the surf zone. During the open phase, site variations in catches were observed. Catches of early stage fishes were concentrated along the plume line in the Kabeljous surf zone, i.e. higher catches were made at sites 1 and 3 on the western side of the Kabeljous Estuary opening and were associated with a visible brown plume that flowed in a westerly direction.

The cueing of early stage fishes, dependent on estuarine nurseries, is an important aspect in the dynamics of the life cycles of these species. Cueing has drawn international attention (e.g. Boehlert & Mundy 1988, Grimes & Kingsford 1996, Kingsford & Suthers 1996) and further elucidation of this process is necessary. This study has further indicated that traditional factors thought to facilitate the cueing process (e.g. salinity and turbidity) may be acting as surrogates for more important aspects of estuarine/riverine water quality more directly linked to cueing, specifically, qualities responsible for odours that fish may be responding to. This needs further investigation, particularly focusing on estuary-dependent species since past investigations have mainly focused on catadromous freshwater species.

Regression relationships between dominant species and physical variables in the Van Stadens surf were only evident in isolated species, e.g. *Diplodus sargus capensis* CPUE showed a significant relationship with turbidity. The engraulid *Engraulis japonicus* showed a positive relationship with decreases in salinity. *E. japonicus* is not dependent on estuaries in any way and CPUE increases associated with decreases in salinity might be linked to increased food availability associated with estuary/river water input into the surf zone following opening events (Grindley 1982, Grimes & Kingsford 1996). Most species occurring in the Kabeljous surf zone were positively linked to salinity in regression analyses and these changes were brought about by the large opening event in March which resulted in large-scale cueing of estuary-dependent species into the surf zone.

Surf zone catches were dominated, almost exclusively, by postflexion larvae of fish species displaying a degree of estuary-dependence. This finding follows the trend found in surf zones adjacent to other intermittently open estuaries (Whitfield 1989b, Cowley *et al.* 2001) and results for catches made in surf zones associated with permanently open estuaries (Lasiak 1981, 1986, Harris & Cyrus 1996) and nearshore regions (Harris *et al.* 2001). In these studies, surf zone and nearshore catches exhibit a degree of coupling with adjacent estuarine environments. In temperate Australia a different trend emerges whereby nearshore catches vary significantly from adjacent estuarine catches (Valesini *et al.* 1997). This may be indicative of the increased dependence of coastal marine fishes on estuaries as nursery areas in Southern Africa (Potter *et al.* 1990). Most specimens caught in the present study were in a postflexion stage of development. The catadromous mugilid, *Myxus capensis* dominated the species catch in both surf zones and catches increased significantly during opening events, suggesting a heightened response to riverine waters entering the marine environment. A similar trend was observed for the sparid, *Rhabdosargus holubi* and the soleids, *Heteromycteris capensis* and *Solea bleekeri*. Kabeljous catches also displayed a significant increase in abundance of estuary-dependent species (e.g. *Psammogobius knysnaensis*, *Monodactylus falciformis* and *Ambassis dussumieri*) after an opening event.

Comparatively, the species occurring in the surf zones off the Kabeljous and Van Stadens estuaries during the present study are similar to those encountered in other surf zone studies on larval fishes in South Africa (Whitfield 1989b, Cowley *et al.* 2001, Harris & Cyrus 1996).

Species rank, however, varies significantly between these studies. This is directly attributed to geographical location of these studies, sampling duration and gear selectivity. Mugilidae dominated catches in both the present study and the surf zone study by Whitfield (1989b) off the Swartvlei Estuary. Sparidae (mainly *Rhabdosargus holubi*) dominated catches off the subtropical St Lucia Estuary (Harris & Cyrus 1996) and the temperate East Kleinemonde Estuary (Cowley *et al.* 2001). The absence on any significant numbers of mugilids encountered by Cowley *et al.* (2001) when compared to similar temperate studies (Whitfield 1989b, the present study) may be a function of gear selectivity. Catches made off the East Kleinemonde were dominated by sparids in a postflexion stage. Mugilids tend to be represented in the surf zone predominantly as late postflexion and early juvenile stage fishes that are more capable swimmers. These stages may have been able to avoid the gear used by Cowley *et al.* (2001), which sampled the smallest volume per sample out of all three temperate studies and only sampled the upper parts of the water column. Gear avoidance and small sample volume may also account for the lower number of family and species representations in this study when compared to the other temperate surf zone studies. The geographical influence is also evident in the surf catches with families and taxa declining in number from the subtropical region (Harris & Cyrus 1996) to the temperate region (Whitfield 1989b, Cowley *et al.* 2001, present study). Harris & Cyrus (1996) encountered 22 families and 43 taxa in a 24-hr study off the closed St Lucia Estuary. Cowley *et al.* (2001) identified 14 families and 21 species in the surf off the temperate East Kleinemonde Estuary. In total, 15 families and 26 taxa occurred in the surf zones off the Van Stadens and Kabeljous estuaries in the present temperate study. Whitfield (1989b) identified 16 families, 20 species and a further >5 unidentified species. Varying sampling times and gear types used make further quantitative comparisons between these studies impossible.

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CHAPTER 3

HABITAT ASSOCIATION OF EARLY STAGE FISHES IN A WARM TEMPERATE ESTUARINE CREEK

(This work has been submitted to the journal *Estuaries*)

SYNOPSIS

Early stage fishes were sampled in a tidal creek of the Swartkops Estuary using light traps. A total of 12 fish families represented by 28 species was recorded during October and November 2000. Fishes were predominantly in a larval stage of development. The distribution of fish larvae was spatially influenced rather than showing preferences for particular habitats. Estuary-dependent marine species were caught in higher numbers along the margins of the estuary. Length frequencies of both estuary-resident and estuary-dependent marine fishes showed that larger individuals were found in the littoral regions suggesting active migration of these early stages to the margins. Catches of straggler marine species were higher in the channel areas and showed no difference in size distribution between littoral and channel sites. Estuary-dependent species may be using marginal areas as a means of avoiding high flow in the channel and as a predator avoidance mechanism. The low affinity of early stage fishes for eelgrass beds may also have predator avoidance implications as these areas have higher densities of juvenile fish. Light traps were found to be a useful tool for localized studies on the early life stages of fishes in an estuary.

INTRODUCTION

Investigations into the use of varying habitat types by fishes in South African estuaries has largely been confined to eelgrass beds which are widely distributed in South African estuaries (Hanekom & Baird 1988) and sheltered bays (Whitfield *et al.* 1989). *Zostera capensis* is the only eelgrass species occurring in South Africa and is usually confined to the lower and middle reaches of permanently open estuaries (Talbot & Bate 1987, Adams *et al.* 1992). The importance and integral role that eelgrass habitats play in the nursery function of South African estuaries has been well documented (Beckley 1983, Hanekom & Baird 1984, Ter Morshuizen & Whitfield 1994). These investigations, however, have primarily focused on juvenile fishes. As more information comes to light about the use of estuarine nurseries by early developmental stages (Miskiewicz 1986, Gaughan *et al.* 1990, Warlen & Burke 1990),

it becomes imperative to reassess the importance of habitat, in particular eelgrass, for larval and early juvenile stages utilizing these nursery areas. Moreover, there are also practical problems associated with sampling larval and early juvenile fishes in shallow regions of estuaries particularly macrophyte-covered areas, by traditional seine or trawling methods.

Light traps (Doherty 1987) may provide a solution to these problems. Light traps exploit the positively phototactic behaviour exhibited by larval and juvenile fishes (Doherty 1987, Hickford & Schiel 1999). The efficiency of light traps has been extensively reviewed (e.g. Choat *et al.* 1993, Hickford & Schiel 1999) and successful applications have been made in habitats ranging from freshwater streams (Peterson & VanderKooy 1995) and lakes (Conrow *et al.* 1990, Dewey & Jennings 1992) to coral reefs and lagoons (Thorrold 1992, 1993, Doherty *et al.* 1994).

The aim of this study was to assess the habitat preferences of larval fishes in the lower reaches of the Swartkops Estuary. To ascertain whether fish larvae show similar preferences for eelgrass (*Zostera capensis*) covered areas, vegetated and non-vegetated areas were sampled in a tidal creek of the Swartkops Estuary. The habitat preferences of fish larvae were also assessed relative to the proximity of the vegetated and non-vegetated areas within the creek, i.e. whether situated littorally or in the main channel of the creek. Collections of fishes were made using light traps modified for use in shallow habitats. The effectiveness of this technique for use in estuaries is discussed relative to plankton net catches of larval fishes in the same estuary (Melville-Smith & Baird 1980, Beckley 1985).

MATERIAL AND METHODS

Study area

The permanently open Swartkops Estuary (33°52'S, 25°38'E) (Fig. 1) is situated on the warm temperate coast of South Africa. The estuary is approximately 16 km long and varies in width from 90 m in the upper reaches to 350 m in the lower reaches. Depth varies from approximately 3.5 m in the upper reaches to 2 m in the lower reaches (Baird *et al.* 1986). The estuary is subject to altered flow from the Swartkops River. The river is dammed on the main course as well as in the tributaries but these obstructions together with bridges and causeways

have a minimal effect on river flow and dam capacity does not exceed the mean annual runoff of $75\text{--}84 \times 10^6 \text{ m}^3$ (Baird *et al.* 1986). The lower reaches of the estuary are characterised by extensive intertidal mud flats, islands and saltmarshes (Baird *et al.* 1986). *Zostera capensis* beds cover approximately 14 ha in the lower reaches of the estuary. Most of this cover (59 %) is confined to Tippers Creek, a major side arm of the lower estuary (Baird *et al.* 1986).

Field sampling and laboratory analyses

All early stage fishes were sampled using two battery operated light traps based on a design by Beckley & Naidoo (submitted, *African Zoology*). The light trap was slightly modified (500 % 500 % 460 mm) to allow ease of use in shallow habitats. The modified perspex trap consisted of two compartments (Plate 1). The upper compartment included four sub surface entrance slits (15 % 200 mm), an internal concentration area for fishes, fluorescent tube housing and watertight battery box. The removable collection box, with four 500 μm mesh-covered draining windows formed the lower compartment. An 8-Watt fluorescent tube is powered by a 12 V, 12-amp/h rechargeable battery. The battery was switched on manually and the battery box resealed prior to use.

Sampling was conducted on eight occasions over a two-month period in October and November 2000, coinciding with the first and last quarter moon phases of each month. These lunar periods were selected to reduce any possible influence of lunar intensity associated with new and full moon phase on catches (Rooker *et al.* 1996, Strydom 1998). Each moon phase was sampled for two consecutive nights around the neap high tide. Sampling was confined to the turn of the tide to reduce current variation between samples. Light traps were deployed at 4 sites in a side arm of Tippers Creek, in the lower reaches of the Swartkops Estuary (Fig. 1). These sites represented vegetated and non-vegetated areas associated with littoral and channel areas. Anchored traps were deployed for 15 minutes at a time and four samples were collected at each site on each sampling trip. Trap emptying and resetting took approximately five minutes to complete. A total of 128 samples was collected during this study. Catch is expressed as catch per unit effort (CPUE) and is defined as the number of early stage fishes per 15 minutes of light trapping. Littoral sites were sampled simultaneously after which channel sites were sampled simultaneously. Littoral sampling depth ranged 0.6 – 1.0m and

channel sampling depth ranged 1.0 – 1.5m. Early stage fishes were removed from the trap and preserved on site with 5 % buffered formaldehyde.

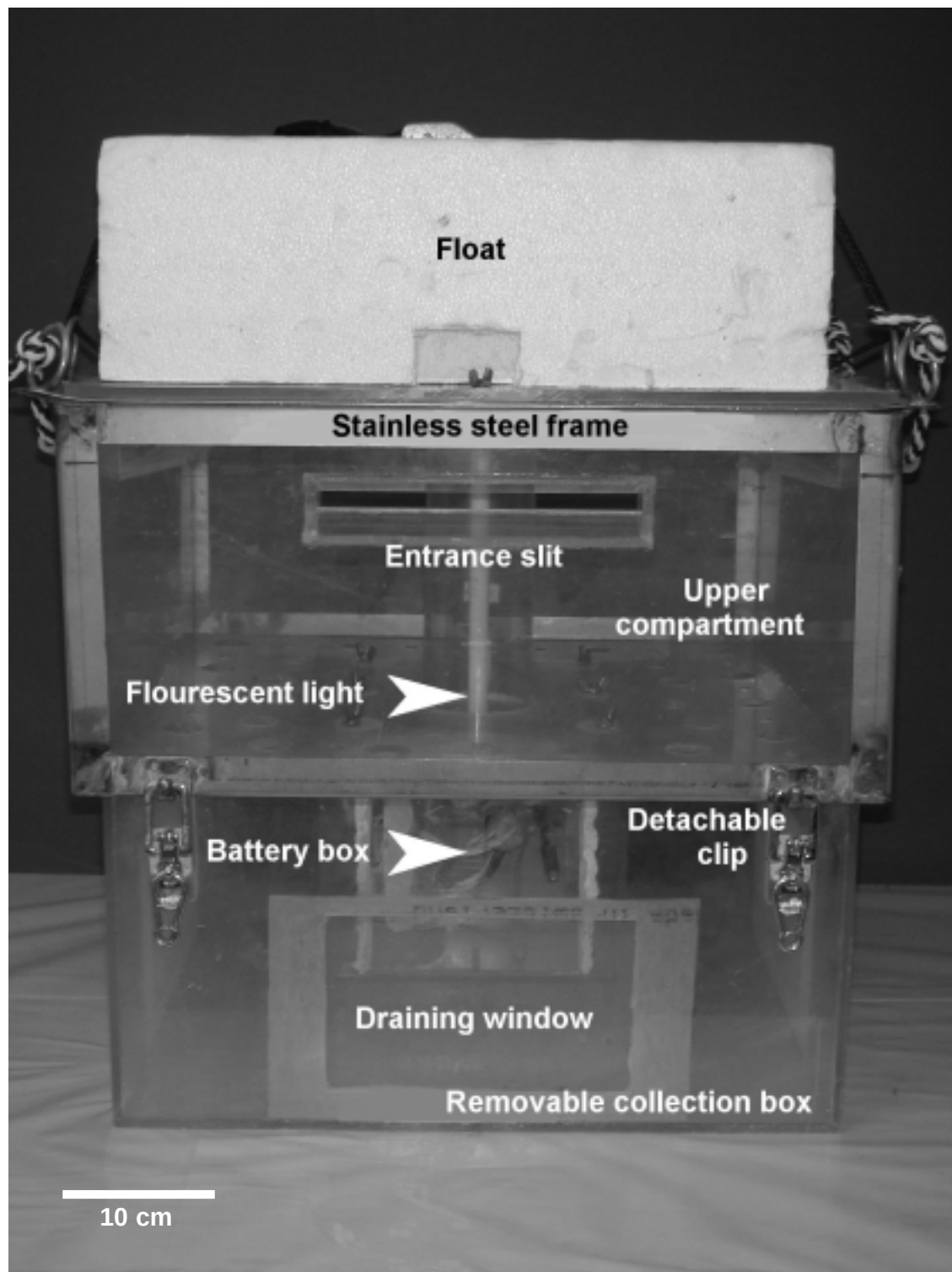


Plate 1. Modified light trap used for catching early stage fishes in Tippers Creek.

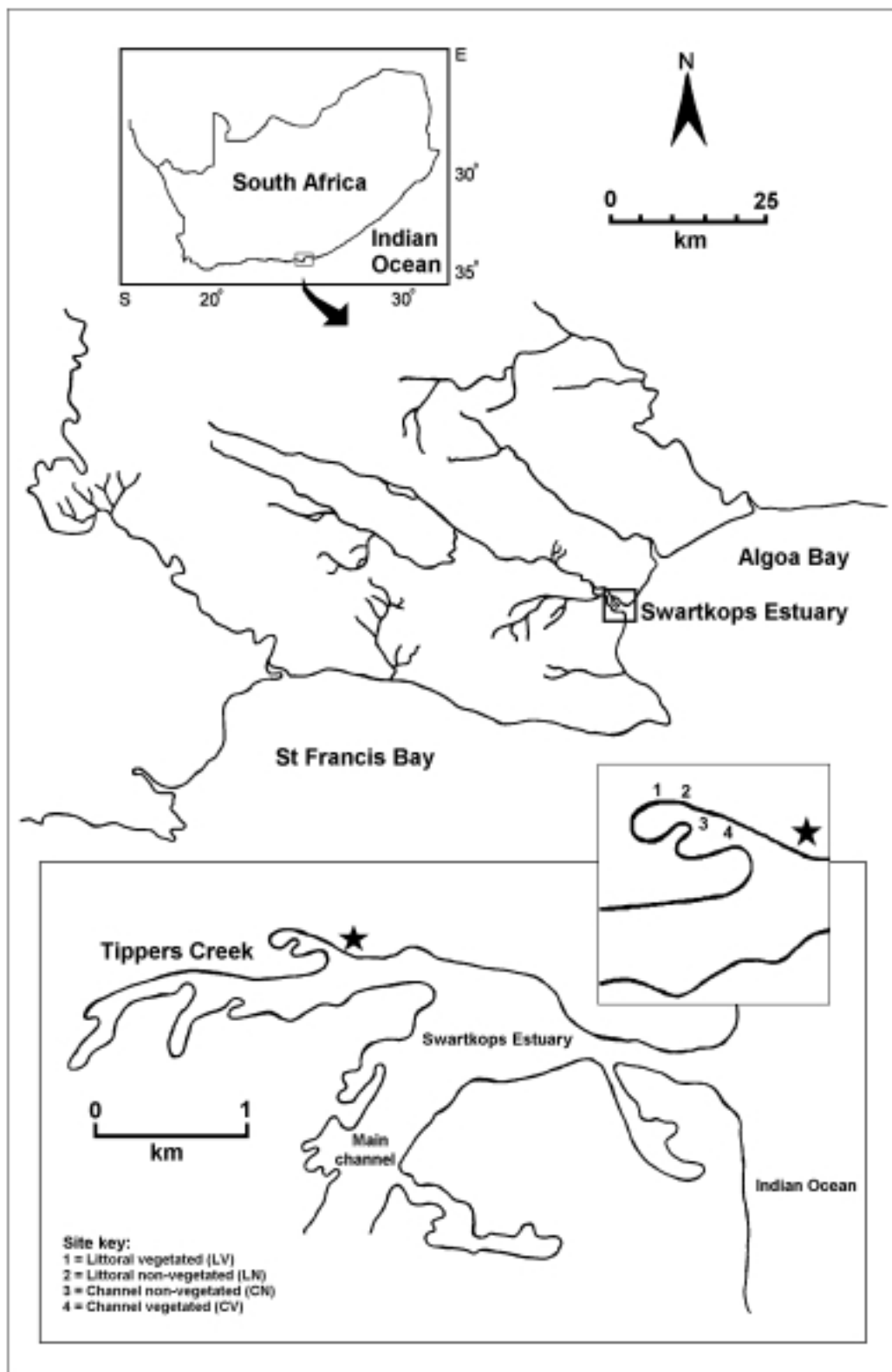


Figure 1. Geographical position of the Swartkops Estuary showing the location of sampling sites in Tippers Creek.

Samples were processed in the laboratory and larval fish were identified to the lowest possible taxon according to Van der Elst & Wallace (1975), Brownell (1979), Moser *et al.* (1984), Leis & Trnski (1989), Olivar & Fortuño (1991), Smith & Heemstra (1995) and Neira *et al.* 1998. All terminology pertaining to larval fish follows that of Kendall *et al.* (1984). The term “early stage fishes” is used to collectively designate all larval, transforming and early juvenile (settlement) stages, with distinction made where necessary to the relevant developmental stages. Early stage fishes were measured to the nearest 0.1 mm body length (BL), which represents notochord length in preflexion and flexion stage larvae, and standard length in postflexion larvae and early juveniles. Measurements were made using an eyepiece micrometer for larvae <10 mm and Vernier calipers for larger specimens. At each site on each occasion, sub-surface (>300 mm) temperature, salinity and turbidity measurements were taken. Temperature (°C) was measured on site with a standard mercury thermometer. Salinity (‰), pH and turbidity (Formazin Attenuation Units or FAU) were measured in the laboratory using a WTW Multiline P4 Meter and Hach DR/890 Colorimeter, respectively.

Data analyses

All physical data were log-transformed ($\log_{10}$) and tested for differences between sites using analysis of variance (ANOVA). Biological data did not comply with parametric assumptions of normality and homogeneity of variance, and non-parametric tests were used for all biological analyses. The Kruskal-Wallis ANOVA by ranks test was used to assess differences in CPUE of all taxa, dominant species (occurring in numbers μ 10) and estuary-dependent species between sites. The Mann-Whitney U-test was used to assess differences between vegetated and non-vegetated areas and littoral and channel sites in terms of CPUE and body length. Multiple linear stepwise regression (MLR) was used to test whether environmental variables displayed any significant relationships with total CPUE or individual dominant species CPUE. Diversity indices (Margalef's species richness and Shannon-Wiener diversity) were calculated using PRIMER statistical software (Clarke & Warwick 1994).

Non-parametric multivariate community analysis was conducted using PRIMER statistical software. All density data were square-root-transformed or tested based on species presence

or absence prior to analyses. A Bray-Curtis similarity matrix was generated for creek sites. Clusters in a dendrogram format were assessed using group average hierarchical sorting.

ANOSIM was used to detect differences between groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity or differences between groups. Only the top 50 % of species contributors to each group tested were used in the analysis.

RESULTS

Environmental variability

No differences ($P > 0.05$) in salinity, temperature or turbidity were observed between sites during the study period. Mean salinity, temperature and turbidity recordings are shown in Figure 2. Multiple linear regression analyses showed that environmental variability played a significant role in total CPUE of early stage fishes and more specifically in selected dominant species. Salinity showed a significant ($P < 0.001$) positive relationship with total catch in Tippers Creek. Environmental variables affecting dominant species CPUE are shown in Table 1.

Species composition and estuary association

Catches of early stage fishes comprised 1627 individuals, incorporating 12 fish families and 28 representative species. These taxa were caught during 32 trapping hours, averaging 51 individuals per hour. Dominant families were the Blenniidae (45 %), Atherinidae (22.4 %), Mugilidae (11.6 %), Gobiidae (9.8 %) and Clupeidae (6 %). Dominant species represented were *Omobranchus woodi* (22 individuals per trapping hour), *Atherina breviceps* (11 / hr), *Myxus capensis* (5 / hr), *Caffrogobius gilchristi* (2 / hr), *Etrumeus whiteheadi* (2 / hr) and *Sardinops sagax* (1 / hr). Positively identified species (22) were grouped into estuary-dependence categories (Whitfield 1998). Most species recorded were marine estuary-dependent (Category II) species (40.9 %) with estuary-resident (category I) species (27.3 %), marine straggler (category III) species (22.7 %) and catadromous species (9.1 %) making smaller contributions to the catch.

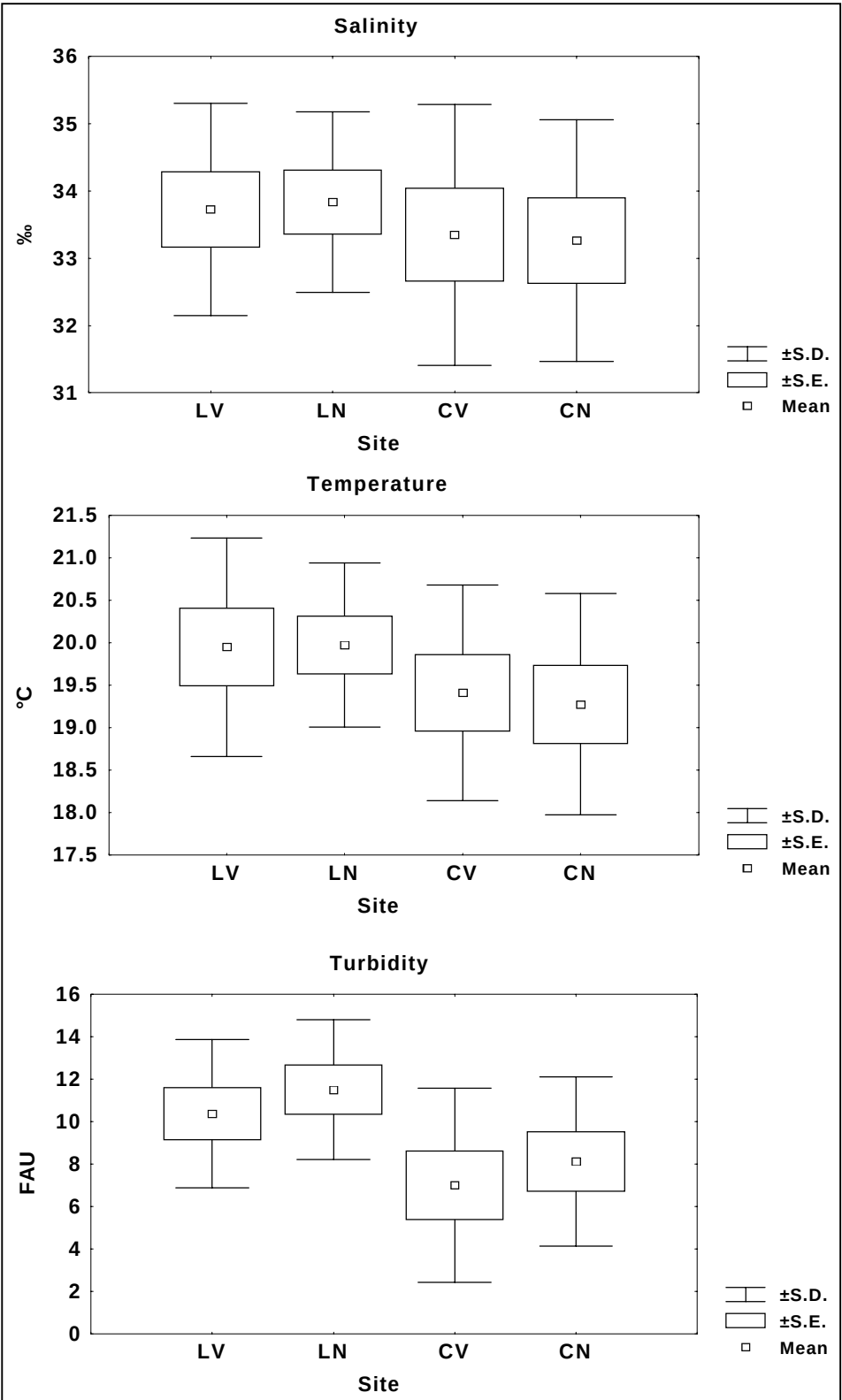


Figure 2. Mean salinity, temperature and turbidity recorded at four sites in Tippers Creek, Swartkops Estuary. LV = Littoral vegetated, LN = Littoral non-vegetated, CV= Channel vegetated, CN = Channel non-vegetated.

Table 1. Stepwise multiple linear regression statistics relating CPUE of early stage fishes and environmental variables for all taxa and dominant species recorded in Tippers Creek, Swartkops Estuary. Only species with statistically significant results are shown. $\text{adj}R^2$ = adjusted coefficient of determination; R = Correlation coefficient; F = F-statistic; sa = Salinity; te = Temperature; tu = Turbidity; Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

	$\text{adj}R^2$	R	F	Significant variable
All taxa	0.27	0.54	16.79	sa***
Dominant species				
<i>Atherina breviceps</i>	0.06	0.29	3.84	sa*
<i>Omobranchus woodi</i>	0.20	0.46	11.37	sa***
<i>Parablennius cornutus</i>	0.05	0.26	3.03	-
<i>Clinus superciliosus</i>	0.06	0.29	3.73	sa**
<i>Etrumeus whiteheadi</i>	0.21	0.47	11.95	sa**te*tu***
<i>Sardinops sagax</i>	0.16	0.424	8.91	sa*tu**
Gobiid 2	0.05	0.28	3.41	te**
<i>Heteromycteris capensis</i>	0.22	0.48	13.00	sa***

Table 2. Species composition, total catch, length, estuary association (after Whitfield 1998) and developmental stages for fishes caught in Tippers Creek by means of light trapping (Ys = yolk sac, Pr = preflexion, F = flexion, Po = postflexion, Ju = juvenile, El = elver).

Family	Species	Total Catch		Body length (mm)		Developmental stage	Estuary association
		No.	%	Mean	Range		
Anguillidae	<i>Anguilla mossambica</i>	2	< 1	48.0	47.5 – 48.5	El	Va
Ariidae	<i>Galeichthys feliceps</i>	1	< 1	74.7	74.7	Ju	IIb
Atherinidae	<i>Atherina breviceps</i>	365	22.4	9.6	5.3 – 24.9	Ys, Pr, F, Po	Ib
Blenniidae	<i>Omobranchus woodi</i>	709	43.5	3.6	2.9 – 4.4	Ys	Ia
	<i>Parablennius cornutus</i>	17	1	11.7	3.2 – 17.3	Pr, F, Po	III
	Blenniid 5	7	< 1	3.2	2.9 – 3.4	Ys, Pr	?
Clinidae	<i>Clinus superciliosus</i>	25	1.5	18.4	11.7 – 21.2	Po	Ib
	Clinid 5	1	< 1	9.9	9.9	Po	?
Clupeidae	<i>Gilchristella aestuaria</i>	2	< 1	8.0	7.3 – 8.7	F, Po	Ia
	<i>Etrumeus whiteheadi</i>	56	3.4	24.4	17.7 – 35.3	Po, Ju	III
	<i>Sardinops sagax</i>	40	2.5	26.6	16.7 – 34.0	Po, Ju	III
Engraulidae	<i>Stolephorus holodon</i>	5	< 1	20.7	19.2 – 24.0	Po	IIc
	<i>Engraulis japonicus</i>	1	< 1	25.4	25.4	Po	III
Gobiidae	<i>Caffrogobius gilchristi</i>	73	4.5	2.9	2.4 – 9.9	Pr, Po	Ib
	<i>Caffrogobius</i> sp 1	8	< 1	6.2	2.4 – 9.7	Pr, Po	?
	<i>Caffrogobius</i> sp 2	2	< 1	9.5	9.4 – 9.7	Po	?
	<i>Psammogobius knysnaensis</i>	3	< 1	7.8	2.6 – 16.7	Pr, Po	Ib
	Gobiid 2	76	4.7	3.5	2.9 – 11.1	Pr, Po	?
	Gobiid 7	1	< 1	12.75	12.75	Po	?
Mugilidae	<i>Liza dumerilii</i>	8	< 1	16.0	12.1 – 22.8	Po, Ju	IIb
	<i>Liza macrolepis</i>	5	< 1	19.8	14.5 – 29.3	Po, Ju	IIa
	<i>Liza richardsonii</i>	6	< 1	15.3	13.3 – 18.9	Po, Ju	IIc
	<i>Mugil cephalus</i>	1	< 1	17.3	17.3	Po	IIa
	<i>Myxus capensis</i>	169	10.4	15.7	10.2 – 30.6	Po, Ju	Vb
Soleidae	<i>Heteromycteris capensis</i>	35	2.1	7.3	6.3 – 8.5	Po	IIb
Sparidae	<i>Diplodus sargus capensis</i>	2	< 1	9.4	9.0 – 9.7	Po	IIc
	<i>Rhabdosargus holubi</i>	3	< 1	11.5	11.4 – 11.6	Po	IIa
Tetraodontidae	<i>Amblyrhynchotes honckenii</i>	3	< 1	5.4	3.6 – 7.0	Pr, F	III

Temporal and spatial trends in CPUE

No difference ($P > 0.05$) in the CPUE of early stage fishes was observed between first and last quarter moon phases. CPUE differed between sites for all taxa ($P < 0.05$). This result was species specific. Larval catches of *Atherina breviceps*, *Omobranchus woodi*, *Myxus capensis*, *Etrumeus whiteheadi*, *Sardinops sagax* and gobiid 2 showed significant ($P < 0.01$) differences in CPUE between sites. Individual species generally showed preferences related to spatial proximity (littoral vs. channel) rather than macrophyte cover. Highly significant differences ($P < 0.001$) were found between littoral and channel CPUE of postflexion *Atherina breviceps*, *Myxus capensis*, *Etrumeus whiteheadi*, gobiid 2 and *Omobranchus woodi* ($P < 0.05$). An isolated species, *Omobranchus woodi*, showed a difference ($P < 0.05$) in CPUE between vegetated and non-vegetated areas. Individual species contributions to total catch at these sites are shown Fig. 3. Species occurring in numbers greater than five are included to show the distribution of some non-dominant species that were not included in statistical analyses because they occurred in numbers less than 10.

Species were also divided into broad estuary-dependence categories namely resident, dependent and straggler species. Estuary-dependent and straggler species showed significant differences in CPUE between sites ($P < 0.001$), whereas resident species were more evenly distributed. Estuary-dependent and marine stragglers had significantly different ($P < 0.01$) CPUE between littoral and channel sites. No difference ($P > 0.05$) in CPUE between vegetated and non-vegetated sites was observed for these species.

Figure 4 shows the total catch of species representing estuary-residents, dependents and stragglers in the different habitat types sampled. Estuary-dependent species mainly occupied the littoral sites whereas the marine straggler species were predominantly found in the channel. In contrast, estuary-resident species CPUE was not significantly different between littoral and channel regions but was significantly different ($P < 0.05$) between vegetated and non-vegetated regions and this is reflected in the total catch of these species shown in Figure 4.

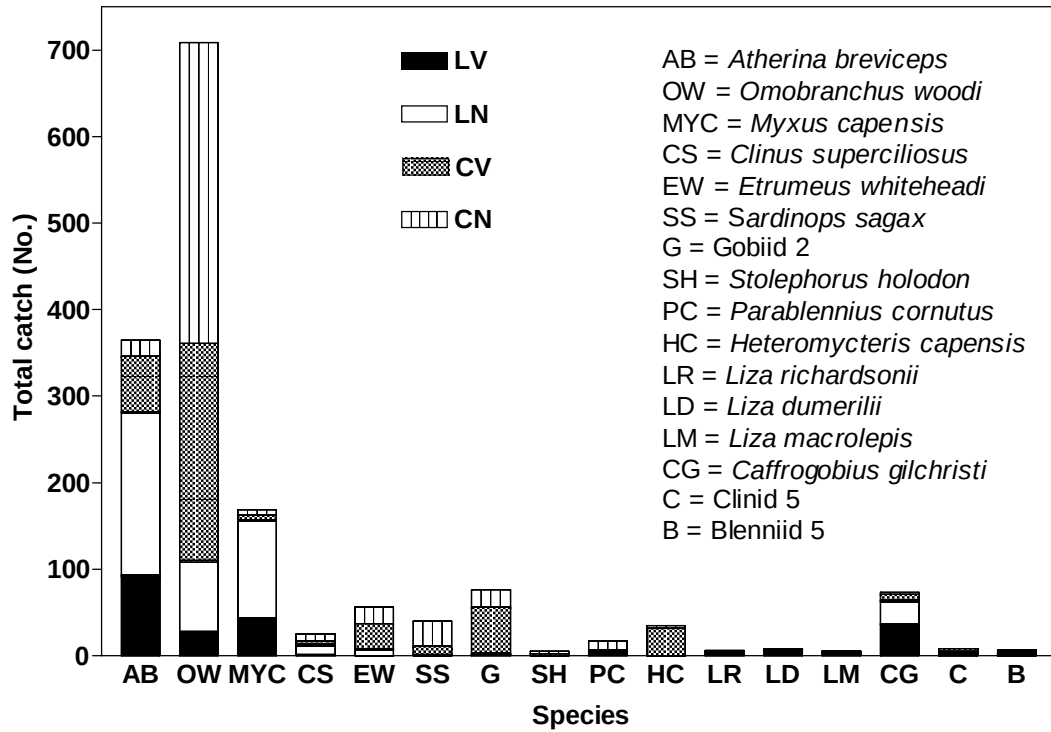


Figure 3. Individual species contributions (μ 5 individual only) to the various habitat types sampled in Tippers Creek (LV = littoral vegetated, LN = littoral non-vegetated, CV= channel vegetated, CN = channel non-vegetated).

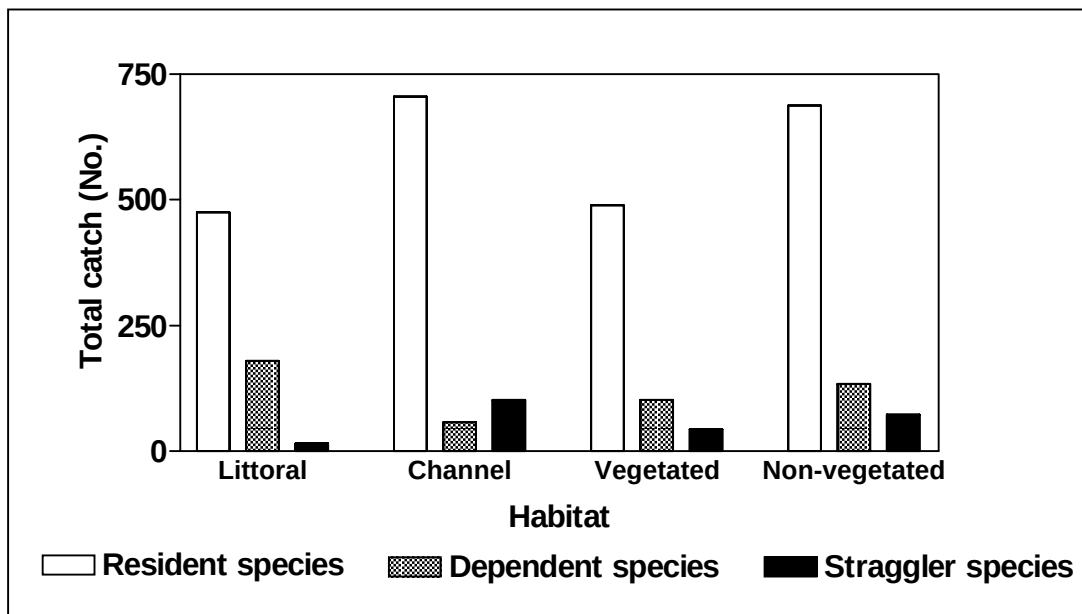


Figure 4. Total catch of early stage fishes in different habitat types in Tippers Creek.

Length frequency

Length comparisons indicated that both estuary resident and estuary-dependent marine fishes showed a significant difference ($P < 0.001$) in size range between channel and littoral sites (Fig. 5). In both cases, larger sizes of larvae and early juveniles were associated with the margins of the creek. Mean lengths for littoral catches were 7.1 and 16.3 mm for resident and dependent marine species, respectively. Mean length for resident and dependent marine species in the channel was 4.6 and 11.7 mm respectively. Marine stragglers showed no difference ($P > 0.05$) in mean length between channel and littoral sites. Larger sizes of resident (mean = 5.9 mm) and dependent marine species (mean = 16.0 mm) were also associated with non-vegetated areas. Marine straggler species showed no difference ($P > 0.05$) in mean body length between vegetated and non-vegetated areas.

Species richness and diversity

Peak species richness ($d = 2.93$) was recorded in the channel at the mouth end of the sampling area at site CV. Highest species diversity ($H' = 1.75$) was recorded in the littoral vegetated site and lowest index value ($H' = 1.18$) in the channel non-vegetated site.

Table 3. Species diversity indices for early stage fishes associated with different habitat types in Tippers Creek.

Site	Habitat	Species No.	Species richness (d)	Species diversity (H')
LV	Littoral vegetated	16	2.76	1.75
LN	Littoral non-vegetated	18	2.78	1.60
CV	Channel vegetated	19	2.93	1.63
CN	Channel non-vegetated	16	2.43	1.18

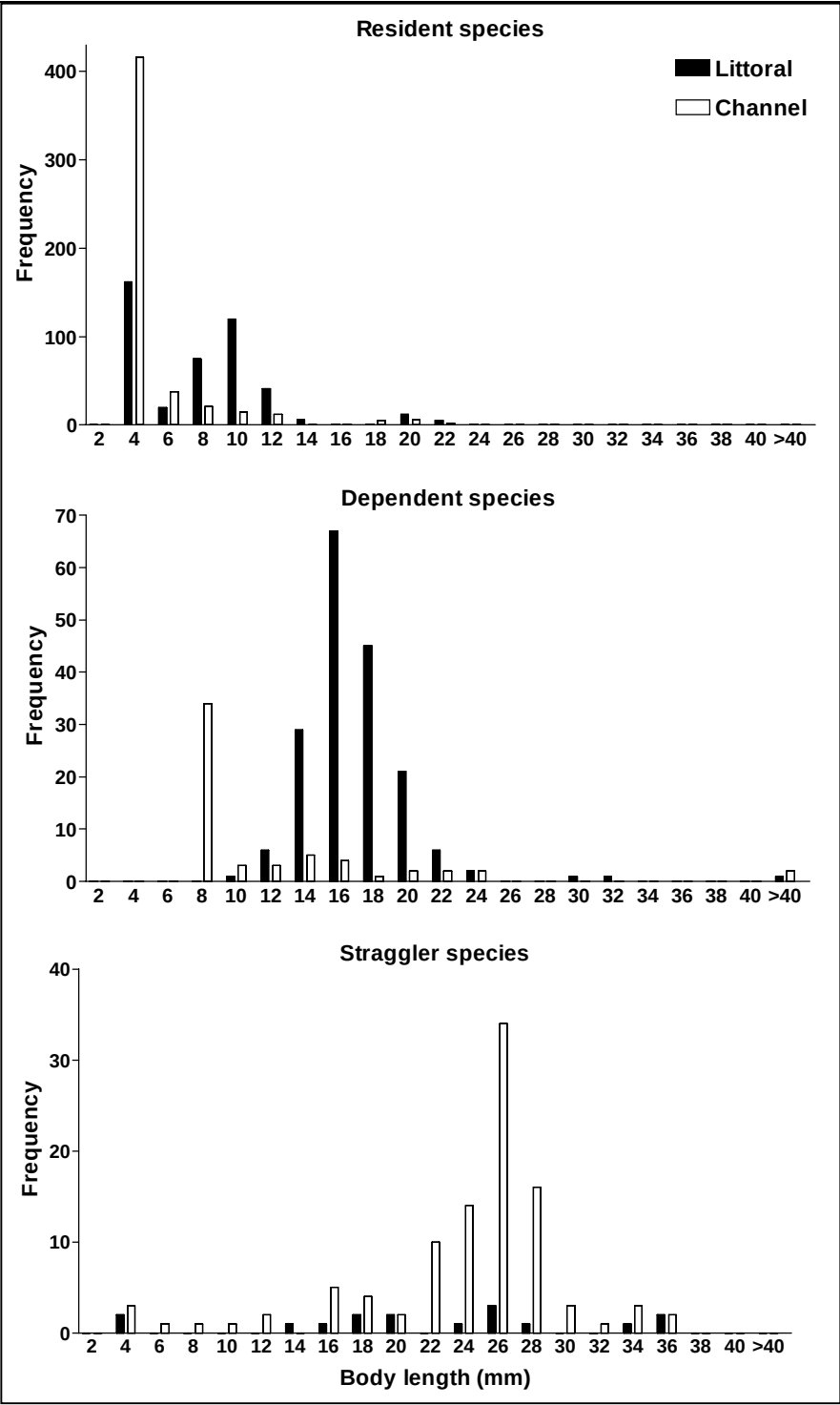


Figure 5. Length frequency range for resident, dependent and straggler species caught using light traps in Tippers Creek.

Community analysis

Multivariate community analysis was used to differentiate between sites and habitat types using CPUE and presence/absence of species in Tippers Creek. Overall, groupings were not significantly separated (ANOSIM). CPUE at littoral sites (LV and LN) was separated at the 66 % similarity level from channel sites (sites CV and CN) (Fig. 6). This separation was attributed (SIMPER) primarily to higher catches of postflexion *Myxus capensis* and *Atherina breviceps* along the margins of Tippers Creek. Yolk sac stage *Omobranchus woodi* and preflexion gobiid 2 in the channel sites further contributed to the separation from littoral sites.

The species presence or absence dendrogram (Fig 6.) shows a separation of vegetated littoral site LV from other sites. This separation, although not significant (ANOSIM), was driven primarily by the exclusive presence of *Galeichthys feliceps*, *Gilchristella aestuaria* and the mugilids *Liza richardsonii* and *L. macrolepis* in this habitat (SIMPER). *Etrumeus whiteheadi* and *Sardinops sagax* were found almost exclusively in the channel areas. Non-vegetated littoral site LN was separated from the channel sites by the presence of gobiid 7 and *Caffrogobius* sp. 2 (SIMPER). Channel sites were characterized by the presence of *Stolephorus holodon* and postflexion *Heteromycteris capensis*.

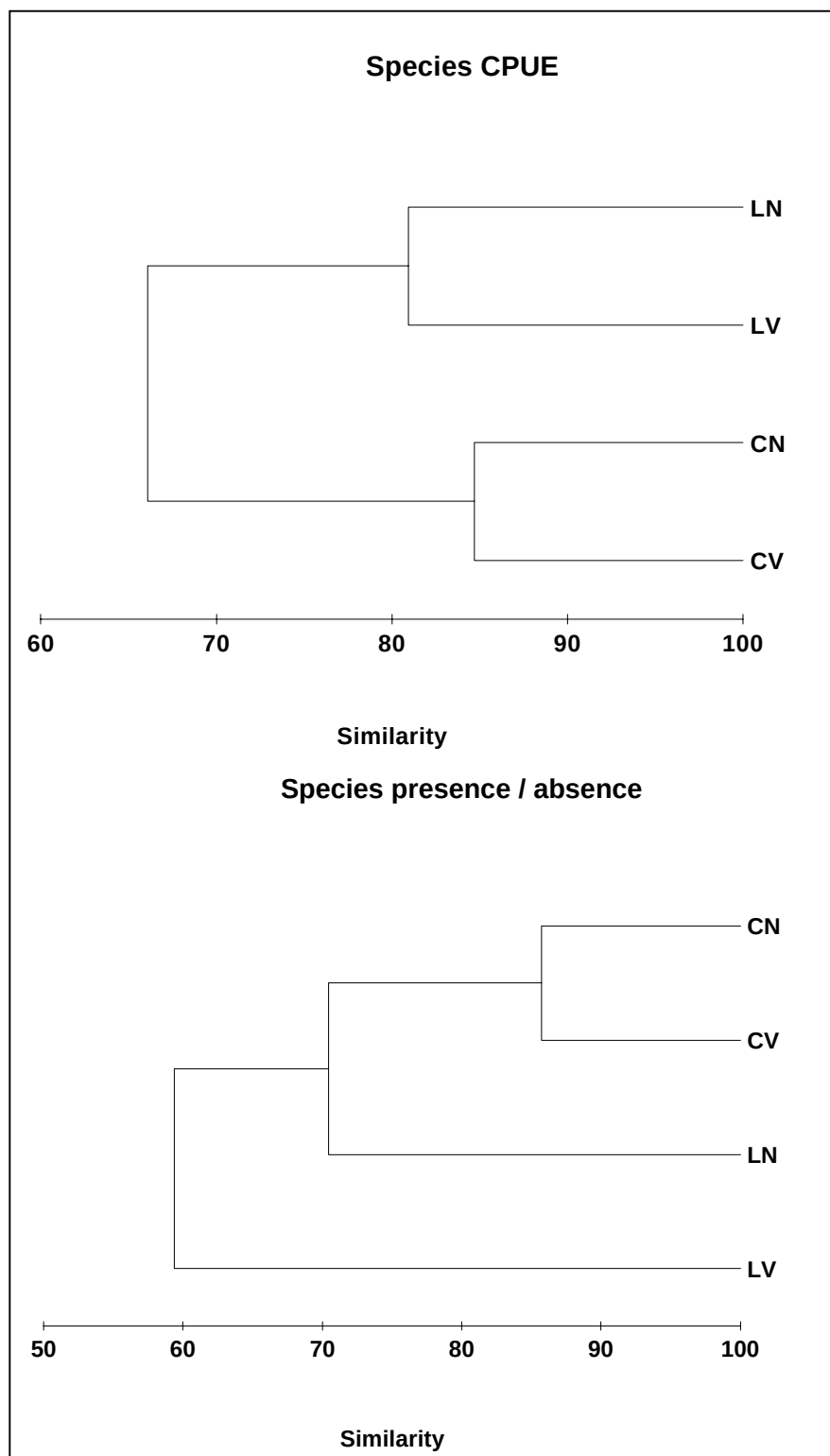


Figure 6. Bray-Curtis similarity dendrogram showing classification of various habitat types sampled by light trap in Tippers Creek (LV = littoral vegetated, LN = littoral non-vegetated, CV= channel vegetated, CN = channel non-vegetated).

DISCUSSION

Early stage fishes in Tippers Creek showed laterally influenced distribution patterns rather than preferences for submerged aquatic vegetation. Submerged aquatic vegetation plays a significant role as a refuge area for juvenile fishes in a variety of habitats (Beckley 1983, Hanekom & Baird 1984, Connolly 1994, Ter Morshuizen & Whitfield 1994) but this high affinity for vegetated areas was not observed in light trap catches of the earlier developmental stages of these fishes. Estuary-dependent marine species were distributed mainly along the margins of the sampling area and conversely, straggler marine species were found in the channel region. Estuary-resident species were evenly distributed between littoral and channel areas. Length frequency analyses also indicated that larger sizes of both estuary-resident and estuary-dependent marine fishes were found along the marginal areas of the creek. This phenomenon exhibited by postflexion larvae has been attributed by Beckley (1985) as possibly an active migration to the margins as an ebb tide avoidance mechanism. Fishes thereby maintain their position within the estuary and avoid strong currents as a result of lateral migration. Concentration of young fishes in shallow water also serves as a predator avoidance mechanism as larger piscivorous fishes are excluded at these depths (Copp 1990, Bryan & Scarnecchia 1992).

A lower affinity for vegetated areas by early developmental stages has been observed by Hannan & Williams (1998) in a temperate Australian estuary. Early developmental stages of marine species that rely on estuaries as nursery areas will enter estuaries and initially concentrate in the lower reaches of these systems (Loneragen *et al.* 1986, Whitfield 1994). Hannan & Williams (1998) suggest that these estuary-dependent fishes use the shallow littoral regions of the estuary to make their way towards more suitable settlement habitat within the system. Recruitment to vegetated areas only occurs later in their development, accompanied by dispersion of fish within the nursery habitat. This mechanism may explain the results obtained in the present study and possibly be an adaptive response by the larvae of estuary dependent marine fishes to dynamic tidal environments where position maintenance in the initial stages of recruitment is imperative to the success of this process. In habitats where strong currents are not prevalent (e.g. lakes), larval fishes have been shown to associate with vegetation beds and floating mats of algae from early developmental stages (Conrow *et al.* 1990, Bryan & Scarnecchia 1992). The lower affinity for vegetated areas

displayed by early developmental stage fishes in the present study may have a further advantage in lowering the predation risk from juvenile fish already associated with vegetated areas of the estuary. Diversity of fishes however appeared highest in the vegetated littoral site and this is attributed to the prevalence of low numbers of juvenile mugilids, namely *Liza richardsonii* and *L. macrolepis*, in this area. Species richness was highest in the vegetated channel site and this was attributed to the higher incidence of marine stragglers in the channel area.

Although quantitative comparisons of early stage fishes cannot be made between plankton tows (Melville-Smith & Baird 1980, Beckley 1985) and light traps (present study), tentative qualitative comparisons of larval fish species composition and diversity can be made between these gear types in the Swartkops Estuary. Melville-Smith & Baird (1980) encountered a total of 15 families and 17 identified species of larval fish over 14 plankton towed stations throughout the Swartkops Estuary. Beckley (1985) identified a total of 17 species in the mouth region of the Swartkops Estuary, below Tippers Creek. Light traps used in present study compared favourably with a yield of 12 families and 28 species. Most species encountered in the plankton net studies were also represented in light trap catches, contrary to findings by Hickford & Schiel (1999). Species rank however, did vary greatly between plankton net and light trap catches. Plankton towed catches in the Swartkops Estuary were dominated by Gobiidae and Clupeidae, mainly represented by the estuarine roundherring, *Gilchristella aestuaria*. This common species was poorly represented in light trap catches as breeding and early life history usually takes place in the upper reaches of Eastern Cape estuaries (Melville-Smith *et al.* 1981), an area not sampled during the present study. Light trap dominance was confined to Blenniidae and Atherinidae. Many early stage gobiids were trapped but these do not compare with the high numbers towed by Melville-Smith & Baird (1980) and Beckley (1985) in the channel waters of the estuary. Sparidae and Monodactylidae were poorly represented in light trap catches when compared to trawled catches. Experimental trials with the light trap in the study area prior to commencement of sampling did however yield high numbers of *Diplodus sargus capensis* and *Rhabdosargus holubi* and investigations by Naidoo (1998) resulted in the trapping of Sparidae and Monodactylidae off KwaZulu-Natal. It is assumed that the low numbers or absence of these families in light trap catches were not as a result of the inability of the trap to attract these

fish but rather that these species were not in the water column during sampling. Peak recruitment of Sparidae and Monodactylidae into estuaries of the Eastern Cape occurs during the spring and summer months (Whitfield 1998) indicating that these species should have been recorded if they were present at the sampling sites. Light traps tend to select larger individuals (Thorrold 1992) but yolk sac and preflexion larvae were represented in the catch in the present light trap study. Large numbers of yolk-sac larvae of the estuary-resident fish, *Omobranchus woodi*, were recorded in the water column. Plankton nets generally trap smaller individuals (Hickford & Schiel 1999), which accounts for the high numbers of small Gobiidae sampled by Melville-Smith & Baird (1980) and Beckley (1985).

Light trap use for catching early stage fishes is a relatively new technique in South Africa. Beckley & Naidoo (submitted) conducted the first light trap study on larval fishes near the Durban Harbour on the KwaZulu-Natal coast. The present study is the second such investigation and the first to use light traps in a South African estuary. The technique proved to be a useful means of answering questions about localized distribution of early stage fishes in an estuary. Although rigorous quantification is not possible with light traps, relative CPUE comparisons can be made, particularly when the same species are compared (Meekan *et al.* 2000). Trapping success is also related to the turbidity of the water and the presence or absence of currents (Doherty 1987). The use of light traps in estuaries should be limited to areas with similar turbidities. In the present study, sampling was localized in a small creek, off the main channel, where variations in turbidity were minimal and current velocity was reduced. Total catch was not significantly different between littoral (681 individuals) and channel sites (946 individuals). Although not shown to be a criterion in the present study, high velocities of water may also exclude larvae from the trap due to their inability to access the trap against fast flowing water (Thorrold 1992). A solution to working in high flow regions may be to use drifting traps where fish and trap move at the same speed thereby facilitating the entry of fishes (Thorrold 1992).

All sampling methods have their advantages and disadvantages. It is well known that light traps are species- and size-selective (Doherty 1987, Thorrold 1992, Choat *et al.* 1993). Despite this, light traps can be useful devices for catching early stage fishes because they sample larger sizes of fish usually excluded from conventional netting techniques and fishes

are merely trapped, not killed, so they can be removed for controlled grow-out to confirm identification (Doherty 1994, Doherty *et al.* 1994). The trapping of larger individuals also allows easier larval series construction to aid problematic identifications. Furthermore, light trap catches do not exhibit the structural damage of fishes often observed in plankton towed catches (Doherty 1987, Conrow *et al.* 1990). Traps can also be deployed in a range of habitat types and depths (Gregory & Powles 1988, Zigler & Dewey 1995) and samples can be simultaneously replicated with less inter-replicative variation (Hickford & Schiel 1999). The spectral distribution of the light source can also be matched to the spectral response of the target fishes (Gehrke 1994). Gregory & Powles (1988) suggest that a mixed-method approach to sampling ichthyoplankton will provide a more accurate evaluation of numerical and size composition. Light traps may mitigate the deficiency of towed nets in their representation of smaller size ranges and towed nets can provide quantitative data not obtainable from light traps. Mixed-method sampling will also supplement species exclusion by any particular method (Hernandez & Lindquist 1999).

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CHAPTER 4

THE ROLE OF ESTUARINE TYPE IN CHARACTERISING EARLY STAGE FISH ASSEMBLAGES IN WARM TEMPERATE ESTUARIES, SOUTH AFRICA

(This work has been submitted to the journal *African Zoology*)

SYNOPSIS

Early stage fish assemblages were investigated and compared in seven permanently open and five intermittently open estuarine systems on the warm temperate Eastern Cape coast of South Africa. Estuarine type, by virtue of mouth state and prevailing physico-chemical conditions, was found to play a defining role in the structure of assemblages occupying these systems. Clupeidae and Gobiidae were the dominant fish families in both estuarine types. Permanently open estuaries were dominated by the larvae and early juveniles of estuary-dependent marine fish species while estuary-resident fishes dominated intermittently open estuaries. Seasonal changes were observed in species density and diversity in both estuarine types. Species richness and diversity were highest in an open estuary with large nursery habitat availability. Diversity was also high in estuaries with a high freshwater input and in systems dominated by marine species because of a lack of freshwater supply. Salinity zones appeared to play a significant role in both species density and the presence or absence of species in both estuarine types. Mesohaline zones were found to be the most productive in terms of accumulator regions for larval fishes.

INTRODUCTION

Studies assessing the role of estuarine type in the nursery function of estuaries for larval fishes are generally lacking in South Africa. Estuarine larval fish studies have been confined to specific focus areas targeted at single estuarine systems. Past investigations have largely focused on defining the assemblage in a particular estuarine system (Melville-Smith & Baird 1980, Melville-Smith 1981, Whitfield 1989a, Harrison & Whitfield 1990, Harris & Cyrus 1995, Harris *et al.* 1995) or have assessed dynamic aspects associated with these single-estuary assemblages such as tidal exchange (Beckley 1985, Whitfield 1989b, Strydom 1998), tidal current use by a larval fish species (Melville-Smith *et al.* 1981), recruitment (Harris & Cyrus 1996), ocean-estuary coupling (Harris *et al.* 2001) and natural and artificial flushing effects (Strydom & Whitfield 2000, Strydom *et al.* 2002). Varying sampling methods and

time duration, climatic regions and varying terminology relating to early stage fishes make comparisons between past studies difficult and often impossible.

Multi-estuary approaches to understand the composition and dynamics of early stage fish assemblages in different types of estuaries are lacking in South Africa and worldwide. Locally, these are limited to isolated studies by Whitfield (1994a) and Harris & Cyrus (2000) where three estuaries are compared in each study. Generally, there is a paucity of research adopting a holistic approach to defining early stage fish assemblages utilizing estuarine nurseries. Moreover, very little work has been conducted in intermittently open estuarine systems in South Africa. Dundas (1994) compared larval fishes in three intermittently open estuaries but generally these systems have been largely overlooked and comparisons with permanently open systems, as yet, not made.

The aim of this study was primarily to define the species composition, estuarine association and species diversity of early stage fishes occupying seven permanently open and five intermittently open estuaries characterized by varying physico-chemical and hydrodynamic features. Furthermore, this study aimed to investigate the physical, temporal and spatial factors governing these early stage fish assemblages and to define and interpret the communities and key species contributing to the differences between systems.

MATERIAL AND METHODS

Study area

Larval fishes were collected from 12 estuaries along the Eastern Cape coast of South Africa. Large permanently open systems included, from west to east, the Kromme, Gamtoos, Swartkops, Sundays, Kariega, Great Fish and Keiskamma estuaries (Fig. 1). Intermittently open systems included, from west to east, the Kabeljous, Van Stadens, East Kleinemonde, Old Womans and Gqutywa estuaries (Fig. 1). Climate in the region is classified as warm temperate and rainfall is bimodal in nature with peaks generally occurring in winter and spring (Lubke & de Moor 1998). Permanently open estuaries are subjected to a semi-diurnal tidal pattern with a tidal range of approximately 1.6 m. A summary of the physical characteristics defining these systems is given in Table 1 and further information can be found in Whitfield (2000).

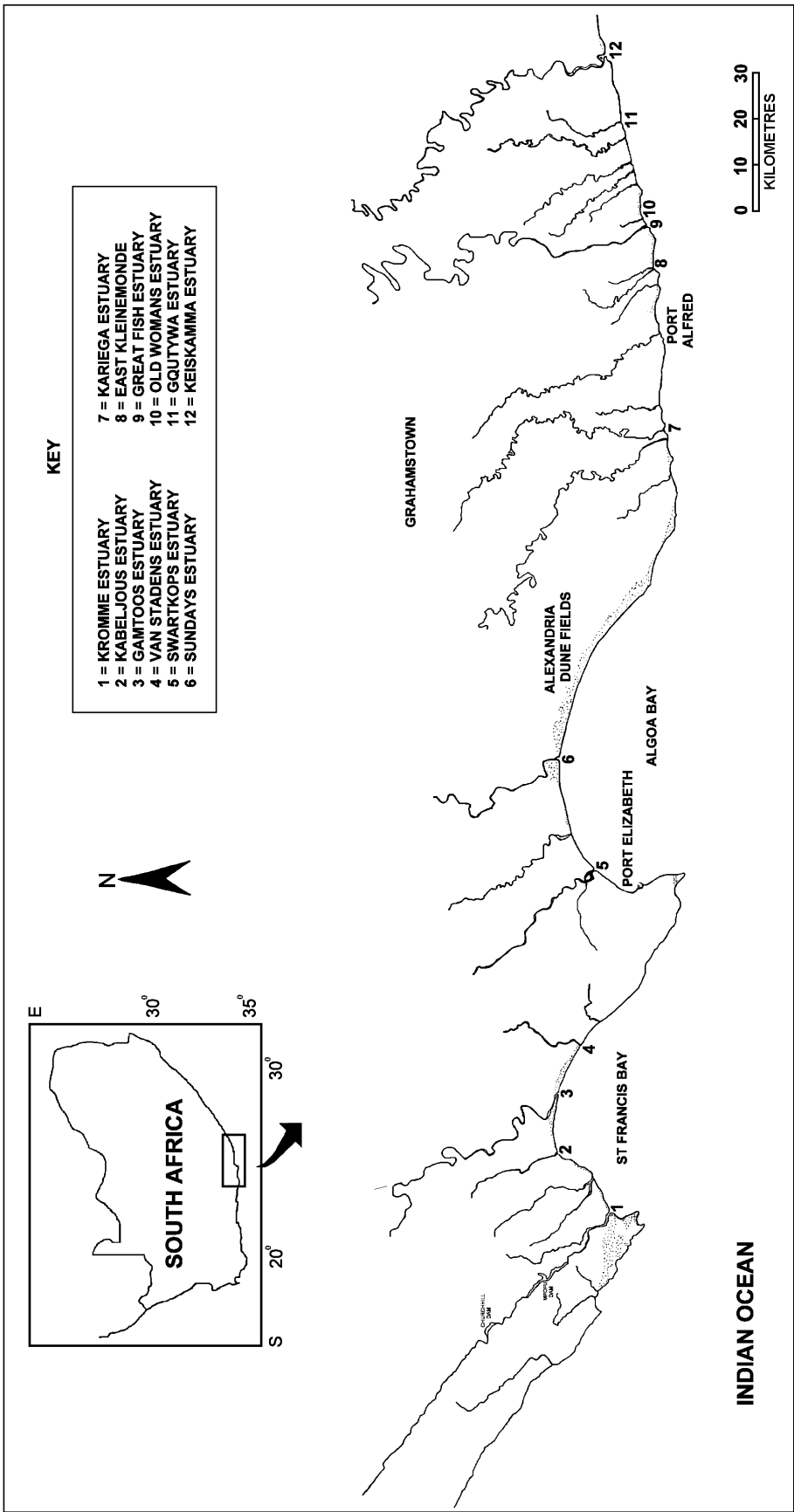


Figure 1. Geographical position of the study area showing location of warm temperate Eastern Cape estuaries sampled.

Table 1. Physical characteristics of 12 Eastern Cape estuaries sampled during the present study. (MAR = mean annual runoff).

Estuary	Co-ordinates at mouth	Length sampled (km)	Width (m)	Channel depth (m)	Catchment (km ²)	MAR (m ³)	Sites sampled	Reference
Permanently open								
Kromme	34°08'S 24°51'E	14	80 - 175	1 - 5	1 125	105 % 10 ⁶	7	Bickerton & Pierce (1988)
Gamtoos	33°58'S 25°04'E	18	30 - 80	1.5 - 4	34 438	485 % 10 ⁶	8	Heinecken (1981)
Swartkops	33°52'S 25°38'E	15	90 - 350	2 - 4	1 354	84 % 10 ⁶	7	Baird <i>et al.</i> (1986)
Sundays	33°43'S 25°51'E	19	20 - 80	1 - 4	22 063	29 % 10 ⁶	9	MacKay & Schumann (1990)
Kariega	33°41'S 26°44'E	17	20 - 200	1 - 5	688	15 % 10 ⁶	9	Watling & Watling (1983)
Great Fish	33°30'S 27°08'E	14	15 - 120	1.5 - 2.5	29 284	526 % 10 ⁶	6	Watling & Watling (1983)
Keiskamma	33°17'S 27°29'E	20	20 - 80	1 - 3	2 745	143 % 10 ⁶	9	Read (1983)
Intermittently open								
Kabeljous	34°00'S 24°56'E	1.7	10 - 100	0.5 - 1.6	312	27 % 10 ⁶	3	Bickerton & Pierce (1988)
Van Stadens	33°58'S 25°13'E	1.5	10 - 30	1 - 2	271	21 % 10 ⁶	3	Crowther (1987)
East Kleinemonde	33°32'S 27°03'E	2.5	20 - 62	1 - 1.5	46	2 % 10 ⁶	5	Badenhorst (1988)
Old Womans	33°30'S	0.8	10 - 20	0.75 - 1.5	24	1.2 % 10 ⁶	2	NRIO (1987)

Gqutywa	27°09'E 33°22'S 27°22'E	2	40 - 70	0.5 - 1.5	85	6 % 10 ⁶	3	NRIO (1987)
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Field sampling and laboratory analyses

Plankton towing was conducted at approximately equidistant sites (Table 1) spanning the traversable length of each estuary using two slightly modified WP2 plankton nets (570 mm mouth diameter and 0.2 mm mesh aperture size) fitted with Kahlsico 005 WA 130 flow meters. Nets were simultaneously lowered from two short booms (1.5 m length) fixed on either side of the bow of a 4.5 m twin-hull boat in permanently open estuaries. A smaller 2.5 m single hull boat was used in intermittently open estuaries. Two sub-surface samples were collected (replicates) per site, per estuary, during all four seasons for a period of one year between July 1998 and July 1999. Towing was done obliquely through each site at a speed ranging between 1 and 2 knots. Each tow lasted for 3 min and was conducted in complete darkness. The average water volume filtered by the nets was 16.30 m³ (SE ! 0.54). Samples were preserved on site with 5 % buffered formaldehyde.

Samples were processed in the laboratory and all larval and early juvenile fish removed. Fish were identified to the lowest possible taxon according to Brownell (1979), Leis & Trnski (1989), Moser *et al.* (1984), Olivar & Fortuño (1991), Smith & Heemstra (1995) and Neira *et al.* (1998). All terminology pertaining to larval fish follows that of Kendall *et al.* (1984). The term “early stage fishes” is used to collectively designate all larval, transforming and early juvenile (settlement) stages, with distinction made where necessary to the relevant developmental stages. Early stage fishes were measured to the nearest 0.1 mm body length (BL), which represents notochord length in preflexion and flexion larvae, and standard length in postflexion larvae and early juveniles. Measurements were made using an eyepiece micrometer for larvae <10 mm and Vernier calipers for larger specimens. Larval fish density is expressed as number of larvae per 100 m³ of water. Density was calculated using a formula based on a predetermined calibration value for each flow meter used:

$$\text{Larval density} = \frac{\text{Number of larvae per haul}}{(\text{Flow meter revolutions} + \text{calibration value in m}^3)} \times 100$$

Temperature (°C) and salinity (‰) profiles were obtained at each site using a Valeport CTD instrument. Recordings were made at intervals of 0.5 m between the surface and bottom of the water column. Water transparency measurements were also taken at all sites using a Secchi disc. All Secchi disc depth recordings were converted into an extinction coefficient (*k*) using methods described by Dawes (1981) where $k = 1.7 / D$ (Secchi depth in cm).

Data analyses

For statistical purposes, sites in each estuary were divided into regions based on the salinity environment at that site. The salinity environment at each site was defined by averaging the water column salinity obtained from depth profiling and categorizing these values according to an adaptation of the Venice system (Whitfield 1998), used to describe salinity zones (Table 2). An additional “fresh” category was added and the hypersaline category was adjusted to suit estuaries within the region and take into account the average salinity of seawater (≥ 35.2) in the Eastern Cape region (Schumann 1998).

Table 2. Adaptation of the Venice System for classification of salinity zones for use in Eastern Cape estuaries.

Salinity Zone	Salinity Range (‰)
Fresh	0 – 0.49
Oligohaline	0.5 – 4.9
Mesohaline	5.0 – 17.9
Polyhaline	18.0 – 29.9
Euhaline	30.0 – 35.9
Hypersaline	μ 36

Parametric test assumptions (normality and homogeneity of variance) were not met and non-parametric tests were therefore used for all analyses. Heterogeneity of variance between samples was attributed to variation in sampling sites between estuaries and variations in catches between estuaries. The Kruskal-Wallis ANOVA by ranks test was used to assess differences in fish density and physical data between seasons, sites and zones between and within each estuary. In all analyses, actual replicate values of fish density per site were used, i.e. no data were averaged prior to statistical tests. Multiple linear stepwise regression (MLR) was used to ascertain whether environmental variables displayed any significant relationship with fish density or individual species density. These analyses were conducted using total fish density per site and individual species density. Only species occurring in numbers μ 10 were considered for these analyses.

Diversity indices (Margalef's species richness and Shannon-Wiener diversity) were calculated using PRIMER statistical software (Clarke & Warwick 1994). These indices were compared using the Kruskal Wallis ANOVA by ranks to test for differences between season, sites and zones (Table 2) for each estuary. Diversity indices were also used in a multiple linear regression with physical variables to assess any relationship with these variables.

Non-parametric multivariate community analysis was conducted using PRIMER statistical software. All density data were square-root-transformed or transformed based on species presence or absence prior to analyses. A Bray-Curtis similarity matrix was generated for estuaries, seasons and zones. Clusters in a dendrogram format were assessed using group average hierarchical sorting. ANOSIM was used to detect differences between groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity or difference between estuary, season and zone groups. Only the top 50 % of species contributors to each group tested were used in the analysis.

RESULTS

Environmental variability

Salinity and water transparency varied significantly ($P < 0.05$) between estuaries, both within permanently open and intermittently open estuaries. Hypersaline/marine dominated estuaries included the Kariega, Kromme, Kabeljous and Gqutywa systems. Freshwater dominated estuaries included the Keiskamma, Great Fish, Sundays, Van Stadens and Gamtoos systems. Systems displaying very high turbidities were the Keiskamma and Great Fish estuaries and those characterized by very low turbidities were the Kariega, Great Fish and Van Stadens estuaries. No significant difference in temperature was found between estuaries. Salinity, temperature and water transparency mean, median and range are shown for permanently open and intermittently open estuaries in Table 3.

The relationship between environmental variables and total density of early stage fishes per site was not significant in open systems ($P > 0.05$) but highly significant in intermittently open systems where salinity ($P < 0.001$) and water transparency ($P < 0.001$) played a role in larval fish density. Regression statistics are shown for all species displaying significant

Table 3. Salinity (‰), temperature (°C) and water transparency (k) measurements taken in selected Eastern Cape Province estuaries during the entire study period.

Permanently open estuaries	Physico-chemical variables	Mean	Median	Range
<i>Kariega</i>	Salinity	32.75	34.18	25.45 - 35.74
	Temperature	19.45	20.28	9.01 - 27.92
	Water transparency	0.02	0.02	0.01 - 0.03
<i>Great Fish</i>	Salinity	14.03	9.69	0.00 - 35.26
	Temperature	20.33	20.13	15.09 - 26.43
	Water transparency	0.34	0.09	0.01 - 1.70
<i>Keiskamma</i>	Salinity	12.67	10.19	0.00 - 34.70
	Temperature	20.94	20.76	15.71 - 26.38
	Water transparency	0.36	0.07	0.02 - 1.70
<i>Sundays</i>	Salinity	14.80	14.43	1.94 - 33.31
	Temperature	20.40	18.82	12.60 - 28.49
	Water transparency	0.04	0.03	0.01 - 0.09
<i>Swartkops</i>	Salinity	28.75	29.60	19.10 - 35.39
	Temperature	20.08	18.11	14.89 - 26.52
	Water transparency	0.01	0.01	0.01 - 0.03
<i>Gamtoos</i>	Salinity	22.83	26.31	0.60 - 34.68
	Temperature	19.52	19.37	11.13 - 25.77
	Water transparency	0.02	0.02	0.01 - 0.03
<i>Kromme</i>	Salinity	34.62	34.93	32.32 - 36.68
	Temperature	18.70	17.14	13.00 - 25.29
	Water transparency	0.02	0.02	0.01 - 0.03
Intermittently open estuaries	Physico-chemical variables	Mean	Median	Range
<i>East Kleinemonde</i>	Salinity	16.93	14.60	10.69 - 23.71
	Temperature	21.06	23.14	13.28 - 26.02
	Water transparency	0.02	0.02	0.01 - 0.03
<i>Old Womans</i>	Salinity	30.72	31.65	16.91 - 36.28
	Temperature	20.29	21.55	13.27 - 27.20
	Water transparency	0.01	0.01	0.01 - 0.02
<i>Gqutywa</i>	Salinity	39.82	39.87	35.66 - 43.19
	Temperature	21.92	22.79	15.11 - 28.01
	Water transparency	0.03	0.03	0.02 - 0.04
<i>Van Stadens</i>	Salinity	13.02	13.27	2.69 - 18.94
	Temperature	20.10	20.60	11.99 - 28.64
	Water transparency	0.01	0.01	0.01 - 0.02
<i>Kabeljous</i>	Salinity	32.76	34.33	19.79 - 40.57
	Temperature	20.16	20.07	14.33 - 26.43
	Water transparency	0.02	0.02	0.01 - 0.04

relationships between abundance and environmental variables in Table 4. MLR analyses of individual estuaries and environmental variables indicated salinity had a significant effect ($P < 0.05$) on fish density in the Kariëga, Gqutywa, East Kleinemonde and Swartkops estuaries. Temperature also had a significant ($P < 0.05$) effect on catches in the Keiskamma, Great Fish, East Kleinemonde, Sundays, Swartkops and Kabeljous estuaries. Water transparency affected catches ($P < 0.05$) in the Keiskamma, Van Stadens and Kromme estuaries. Species diversity was tested for relationships with environmental variables. Temperature was found to significantly ($P < 0.01$) influence species diversity in open estuaries.

Species composition and estuary association

A total of 43 301 early stage fishes was caught in this study. The permanently open estuary catch comprised 29 557 individuals, 23 fish families and 67 species. Intermittently open systems yielded 13 744 individuals, 6 families and 13 species. Clupeidae were the dominant fish family in permanently open and intermittently open systems, predominantly represented by a single species (*Gilchristella aestuaria*) that comprised 76.7 and 61.4 % of the total catch, respectively. The family Gobiidae made the second largest contribution of 18.6 and 37.8 % in permanently open and intermittently open estuaries respectively. The third most abundant family, the Sparidae, made a much smaller contribution in open systems (1.2 %) and an even smaller contribution (< 1 %) in intermittently open systems. All other fish family contributions were considerably less than 1 % of the total catch in both estuary types (Table 5).

Early stage fishes that were positively identified (38 species) were categorized according to the degree to which the species is dependent on South African estuaries. All taxa were grouped into categories defined by Whitfield (1998). Specific category allocation for each species is shown in Table 5. Estuary-dependent marine species (category II) were dominant in open estuaries and comprised 47 % of the catch. Estuary-resident species (category I) comprised 50 % of the intermittently open estuary catch. Unidentified species occurred in low numbers and did not contribute significantly to the catches. It is assumed that most of these species were marine stragglers (category III) and were entering estuaries incidentally via tidal exchange.

Table 4. Stepwise multiple linear regression statistics for early stage fish density versus environmental variables for all taxa and dominant species recorded in selected Eastern Cape estuaries. Only species with statistically significant results are shown. $\text{adj}R^2$ = adjusted coefficient of determination (goodness of fit); R = correlation coefficient; F = F-statistic; sa = salinity; te = temperature; tr = water transparency; Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant

	PERMANENTLY OPEN				INTERMITTENTLY OPEN			
	$\text{adj}R^2$	R	F	Significant variable	$\text{adj}R^2$	R	F	Significant variable
All taxa	0.01	0.11	1.77	ns	0.15	0.41	8.28	sa****tr***
Dominant species								
<i>Ambassis dussumieri</i>	0.06	0.25	9.48	sa*te***	-	-	-	-
<i>Atherina breviceps</i>	0.02	0.16	3.66	te**	0.05	0.27	3.17	none
<i>Omobranchus woodi</i>	0.03	0.18	5.03	te**	0.36	0.11	6.16	te**
<i>Gilchristella aestuaria</i>	-	-	-	ns	0.18	0.45	10.24	sa****tr**
Blenniid 2	0.01	0.14	3.03	tr*	-	-	-	-
<i>Labeo</i> sp.	0.05	0.24	8.69	te*tr**	-	-	-	-
<i>Elops machnata</i>	0.09	0.31	15.67	sa****te*	-	-	-	-
<i>Caffrogobius gilchristi</i>	0.02	0.15	3.19	sa*	0.05	0.28	3.40	sa**te*tr*
<i>Caffrogobius</i> sp 1	-	-	-	ns	0.07	0.31	4.37	sa**te***tr**
<i>Caffrogobius</i> sp 3	-	-	-	ns	0.07	0.31	4.40	sa**te***tr**
<i>Glossogobius callidus</i>	0.10	0.33	17.31	sa****te***	-	-	-	-
<i>Psammogobius knysnaensis</i>	0.04	0.22	7.40	te*tr*	-	-	-	-
<i>Redigobius dewaali</i>	0.06	0.25	9.45	sa**te*	-	-	-	-
Gobiid 2	0.01	0.14	2.74	tr*	-	-	-	-
Gobiid 10	0.05	0.23	8.27	sa**	-	-	-	-
Gobiid 11	0.02	0.17	4.21	sa**	-	-	-	-
Gobiid 13	0.02	0.17	4.07	tr**	-	-	-	-
<i>Pomadasys commersonnii</i>	0.01	0.13	2.63	tr*	-	-	-	-
<i>Liza dumerilii</i>	0.03	0.18	5.05	te*	-	-	-	-
<i>Liza richardsonii</i>	0.04	0.22	7.28	sa****	-	-	-	-
<i>Myxus capensis</i>	0.07	0.27	11.22	sa****	-	-	-	-
<i>Rhabdosargus holubi</i>	0.06	0.25	9.45	te*tr*	-	-	-	-
<i>Syngnathus acus</i>	0.03	0.20	6.04	tr****	-	-	-	-

Table 5. Species composition, total catch, length, estuary association (after Whitfield 1998) and developmental stage of fishes caught in a 12-estuary study of early stage fishes in the Eastern Cape. Ys = yolk sac, Pr = (preflexion), F = flexion, Po = postflexion, Ju = early juvenile, Ge = glass eel.

Family	Species	Permanently open	Intermittently open	Total catch	Body length (mm)		Developmental stage	Estuary association
		No.	No.	%	Mean	Range		
Ambassidae	<i>Ambassis dussumieri</i>	20	-	< 1	18.5	10.4 – 27.7	Po, Ju	Ib?
Anguillidae	<i>Anguilla mossambica</i>	1	-	< 1	46.7	-	Ge	Va
Atherinidae	<i>Atherina breviceps</i>	20	-	< 1	8.17	3.9 – 22.2	Ys,Pr,Po	Ib
Blenniidae	<i>Omobranchus woodi</i>	70	15	< 1	3.7	2.7 – 13.6	Ys,Pr,Po	Ia
	Blenniid 1	29	-	< 1	3.6	2.9 – 14.6	Pr,Po	-
	Blenniid 2	47	-	< 1	2.3	2.0 – 4.8	Ys,Pr	-
Clinidae	<i>Clinus superciliosus</i>	1	-	< 1	19.2	-	Po	Ib
	Clinid 1	3	-	< 1	15.6	12.8 – 18.8	Po	-
	Clinid 2	2	-	< 1	22.4	22.4	Po	-
	Clinid 3	1	-	< 1	10.3	-	Po	-
	Clinid 4	3	-	< 1	19.0	18.8 – 19.2	Po	-
	Clinid 5	5	-	< 1	11.9	9.3 – 14.8	Po	-
Clupeidae	<i>Gilchristella aestuaria</i>	22667	8437	71.8	13.3	2.2 – 31.8	Pr,F,Po, Ju	Ia
	<i>Etrumeus whiteheadi</i>	15	1	< 1	19.3	10.9 – 23.3	Po	III
	Clupeid 1	1	-	< 1	22.0	-	Po	-
Cynoglossidae	<i>Cynoglossus capensis</i>	2	-	< 1	2.2	2.2	Ys	III
Cyprinidae	<i>Labeo</i> sp.	111	-	< 1	6.7	4.8 – 13.9	Ys,F,Po	IV
Eleotridae	<i>Eleotris</i> sp.	247	-	< 1	13.8	4.8 – 18.2	Pr,F,Po	IV
Elopidae	<i>Elops machnata</i>	59	-	< 1	25.3	10.9 – 36.0	Le,Ju	Ila
Engraulidae	<i>Stolephorus holodon</i>	21	-	< 1	14.7	7.7 – 19.5	F,Po	Ilc
Gobiidae	<i>Caffrogobius gilchristi</i>	218	574	1.8	3.5	2.2 – 10.4	Pr,Po	Ib

Table 5. continued...

Family	Species	Permanently open	Intermittently open	Total catch	Body length (mm)		Developmental stage	Estuary association
		No.	No.	%	Mean	Range		
	<i>Caffrogobius</i> sp. 1	179	3505	8.5	3.8	2.0 – 17.2	Ys,Pr,Po	-
	<i>Caffrogobius</i> sp. 2	86	707	1.8	3.2	2.0 – 3.7	Ys,Pr	-
	<i>Glossogobius callidus</i>	186	336	1.2	6.7	2.2 – 22.9	Ys,Pr,F,Po	Ib
	<i>Psammogobius knysnaensis</i>	302	74	< 1	2.9	1.7 – 15.5	Ys,Pre,Po	Ib
	<i>Redigobius dewaali</i>	3872	-	8.9	3.5	2.0 – 18.7	Ys,Pr,Po	Ib
	Gobiid 1	26	-	< 1	3.8	3.4 – 4.6	Pre	-
	Gobiid 2	115	2	< 1	2.9	2.6 – 4.8	Ys,Pre	-
	Gobiid 3	8	-	< 1	2.7	2.4 – 2.9	Pre	-
	Gobiid 4	4	-	< 1	3.4	2.4 – 3.9	Pre,Po	-
	Gobiid 6	12	2	< 1	3.3	1.9 – 4.4	Pre	-
	Gobiid 7	4	-	< 1	13.9	6.3– 30.6	Po, Ju	-
	Gobiid 8	1	-	< 1	12.2	-	Po	-
	Gobiid 10	234	-	< 1	2.4	2.0 – 4.4	Ys,Pre	-
	Gobiid 11	54	-	< 1	2.2	2.0 – 2.4	Pre	-
	Gobiid 12	11	-	< 1	2.3	2.2 – 2.6	Po	-
	Gobiid 13	184	-	< 1	3.0	2.6 – 3.4	Ys,Pre	-
Gobiesocidae	Gobiesocid 1	3	-	< 1	5.0	4.3 – 6.0	Pre,Po	-
	Gobiesocid 2	10	-	< 1	4.7	3.4 – 6.6	Pre,F	-
	Gobiesocid 3	3	-	< 1	6.1	6.0 – 6.3	Po	-
Haemulidae	<i>Pomadasys commersonnii</i>	92	-	< 1	15.2	7.3 – 26.4	Po, Ju	IIa
	<i>Pomadasys olivaceum</i>	2	-	< 1	37.2	37.2	Ju	III
Hemiramphidae	<i>Hemiramphus far</i>	1	-	< 1	3.4	-	Pre	IIc
Megalopidae	<i>Megalops cyprinoides</i>	1	-	< 1	31.8	-	Ju	Vb
Monodactylidae	<i>Monodactylus falciformis</i>	51	-	< 1	7.7	4.9 – 20.9	Po,Ju	IIa

Table 5. continued...

Family	Species	Permanently open	Intermittently open	Total catch	Body length (mm)		Developmental stage	Estuary association
		No.	No.	%	Mean	Range		
Mugilidae	<i>Liza dumerilii</i>	16	-	< 1	13.8	11.2 – 20.9	Po,Ju	I Ib
	<i>Liza richardsonii</i>	20	-	< 1	14.4	10.2– 21.2	Po,Ju	I Ic
	<i>Mugil cephalus</i>	9	-	< 1	18.9	17.2 – 19.8	Po,Ju	I Ia
	<i>Myxus capensis</i>	162	-	< 1	13.8	7.3 – 24.2	Po,Ju	Vb
Sciaenidae	<i>Argyrosomus japonicus</i>	4	-	< 1	13.7	5.3 – 17.8	F,Po	I Ia
Soleidae	<i>Heteromycteris capensis</i>	27	-	< 1	7.0	1.9 – 11.1	Po	I Ib
	<i>Solea bleekeri</i>	5	-	< 1	7.9	4.1 – 14.8	Po	I Ib
Sparidae	<i>Acanthopagrus berda</i>	1	-	< 1	11.1	-	Po	I Ia
	<i>Diplodus sargus capensis</i>	45	-	< 1	9.6	7.5 – 13.6	Po	I Ic
	<i>Lithognathus lithognathus</i>	2	-	< 1	13.6	13.6	Po	I Ia
	<i>Rhabdosargus globiceps</i>	12	-	< 1	12.3	9.6 – 16.2	Po	I Ic
	<i>Rhabdosargus holubi</i>	284	2	< 1	11.4	8.8 – 17.9	Po	I Ia
	<i>Rhabdosargus sarba</i>	6	-	< 1	12.5	11.7 – 13.3	Po	I Ib
	<i>Sarpa salpa</i>	1	-	< 1	21.8	-	Po	I Ic
	<i>Spondyllosoma emarginatum</i>	8	-	< 1	9.5	8.3 – 10.2	Po	III
	Sparid 1	1	-	< 1	10.6	-	Po	-
Syngnathidae	<i>Syngnathus acus</i>	13	1	< 1	13.3	9.7 – 21.5	Po,Ju	Ib
Tetraodontidae	<i>Amblyrhynchotes honckenii</i>	5	-	< 1	3.0	2.0 – 4.3	F,Po	III
Unidentified	Unidentified species 2	1	-	< 1	3.4	-	Pr	-
	Unidentified species 3	2	-	< 1	12.24	12.24	Po	-
	Unidentified species 4	1	-	< 1	1.7	-	Ys	-
	Unidentified species 5	1	-	< 1	8.0	-	Po	-

Temporal and spatial trends in fish density

Densities of larval fishes in both open estuaries ($P < 0.001$) and intermittently open estuaries ($P < 0.001$) varied significantly during the study period. Seasonal differences were highly significant ($P < 0.001$) in a comparison of intermittently open and permanently open systems. Summer densities were significantly higher ($P < 0.01$) than other seasons sampled in both intermittently open and permanently open estuaries. Individual analysis of each estuary indicated that there was no difference in larval density between seasons in the permanently open Keiskamma Estuary and in the intermittently open Kabeljous Estuary. Site variations in estuaries were less pronounced with only the permanently open Keiskamma, Sundays and Swartkops estuaries showing significant ($P < 0.05$) variation between sampling sites. Intermittently open estuaries showed no significant differences in density per site within each estuary (Table 6).

Zonal differences in density of fishes were however highly significant in both a multi-estuary analysis ($P < 0.001$) and in separate analyses focusing on permanently open systems ($P < 0.001$) and intermittently open systems ($P < 0.001$). Mesohaline zones had significantly higher ($P < 0.01$) densities of predominantly larval but also early juvenile fish. Individual estuaries also showed significant ($P < 0.05$) density differences between these zones. Zonal differences were not significant in the intermittently open Old Womans, Kabeljous, Van Stadens and the permanently open Gamtoos and Kromme estuaries (Table 6).

Temporal and spatial trends in species diversity

The permanently open Swartkops Estuary differed from all other systems by virtue of the high species richness and diversity of early stage fishes caught in this system. The freshwater rich Great Fish and Keiskamma estuaries and freshwater deprived Kromme and Kariega systems showed similar index trends in both species richness and diversity. Intermittently open systems were generally characterized by lower species richness and diversity. Peak species richness and diversity occurred in the Kabeljous Estuary. A summary of these indices is shown in Table 7. Species diversity was found to be significantly different ($P < 0.01$) between permanently open estuaries but showed no statistically significant difference between the intermittently open systems. No difference in species diversity was found between sites in either estuary type. Seasonal differences were however highly significant

($P < 0.001$) for both permanently open and intermittently open systems. Only open systems showed a significant difference in species diversity between salinity zones ($P < 0.05$).

Table 6. Mean seasonal and salinity zone density for early stage fishes recorded in 12 Eastern Cape estuaries.

	Density (number per 100 m ³)					
	Permanently open estuaries			Intermittently open estuaries		
	Mean	Median	Range	Mean	Median	Range
Season						
Summer	859	92	0 - 56890	1372	314	0 - 5346
Autumn	239	30	0 - 4699	65	34	0 - 313
Winter	197	5	0 - 5513	3	0	0 - 19
Spring	44	6	0 - 411	1099	26	0 - 13881
Salinity zone						
Fresh	131	68	0 - 826	-	-	
Oligohaline	436	44	0 - 4699	14	14	11 - 17
Mesohaline	1571	171	0 - 56890	1505	121	0 - 13881
Polyhaline	134	7	0 - 3297	116	6	0 - 2590
Euhaline	71	15	0 - 823	379	10	0 - 2612
Hypersaline	105	37	0 - 345	176	33	0 - 2355

Table 7. Species richness and diversity indices for early stage fish assemblages in 12 Eastern Cape estuaries.

Estuary	No. of species	Species richness (d)	Species diversity (H')
Permanently open			
Kromme	25	5.72	1.91
Gamtoos	28	3.89	0.30
Swartkops	28	8.70	2.74
Sundays	21	3.85	0.51
Kariega	24	4.91	0.78
Great Fish	32	5.22	0.86
Keiskamma	37	5.94	1.1
Intermittently open			
Kabeljous	9	2.63	1.22
Van Stadens	4	0.78	0.40
East Kleinemonde	10	1.21	1.08
Old Womans	5	0.67	0.93
Gqutywa	4	0.51	0.19

Community analysis

A cluster analysis of estuaries based on early stage fish density showed no separation between permanently open and intermittently open systems. The cluster analysis was repeated based on fish species presence or absence (Fig. 2) and this showed a significant separation ($P < 0.001$) between permanently open and intermittently open estuaries (ANOSIM). The intermittently open Old Womans, Gqutywa, East Kleinemonde and Kabeljous estuaries separated from permanently open systems at the 33 % similarity level ($P < 0.01$). Estuary-dependent marine species and the gobiid *Redigobius dewaali* were mainly responsible for this separation (SIMPER). The Van Stadens Estuary appeared to be an outlier system in this analysis and was separated at the 17 % similarity level. This was attributed to the lack of the common estuary-resident, *Gilchristella aestuaria*, and the gobiid *Caffrogobius gilchristi* (SIMPER).

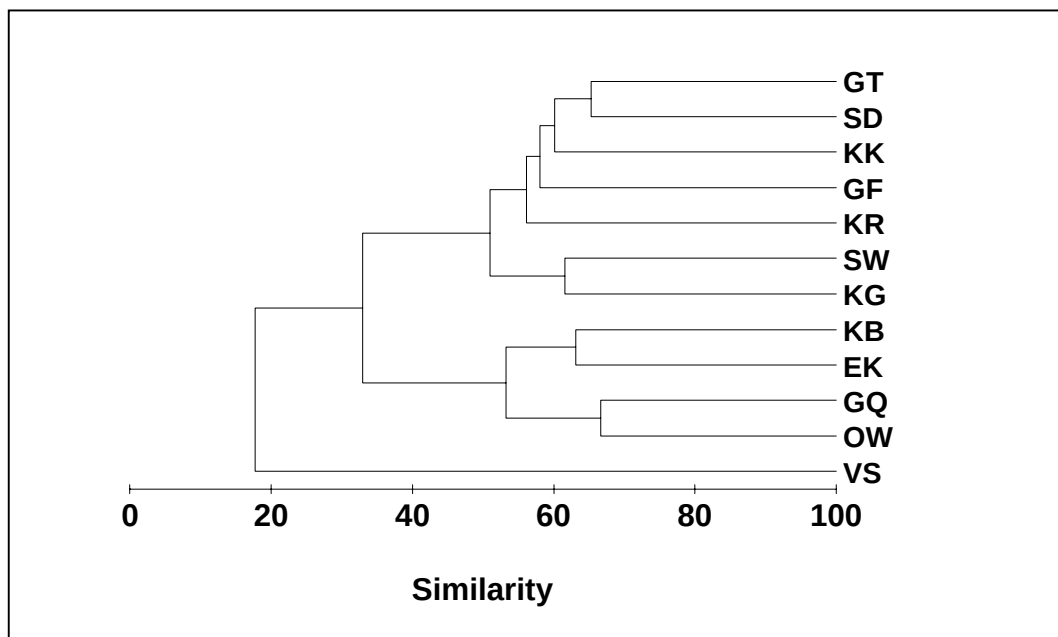


Figure 2. Bray-Curtis similarity dendrogram showing classification of selected Eastern Cape Province estuaries based on presence or absence of early stage fishes.

A community analysis approach was also used to further investigate seasonal trends using individual species density and the presence or absence of species within seasons. Although overall groupings were not significantly separated (ANOSIM), spring was separated at the 35 % similarity level (Fig. 3a) and this was mainly attributed (SIMPER) to a peak in *Caffrogobius gilchristi* and *Caffrogobius* sp. 2. Summer increases in catch were primarily accounted for by *Gilchristella aestuaria* and the gobiid *Glossogobius callidus*. Autumn and winter separations at the 50 % similarity level were mainly attributable to *Redigobius dewaali* densities peaking during this period. Species presence or absence linked summer and autumn, and separated out from winter and spring at the 83 % similarity level (Fig. 3b) but these groupings were not significantly different (ANOSIM). The separation was a result of isolated species (SIMPER) such as *Liza dumerilii*, *Labeo* sp, *Omobranchus woodi* and an unidentified gobiid being present in catches only during the summer / autumn period.

A similar approach was adopted for the estuary salinity zones based on individual species density and species presence or absence. Salinity zones were significantly separated ($P < 0.05$) (ANOSIM) based on densities of early stage fishes. Fresh and oligohaline regions clustered out at the 30 % similarity level from other zones (Fig. 4a). This separation (SIMPER) was primarily due to these fresher regions being occupied by *Redigobius dewaali*, gobiid 10 and the lack of high numbers of *Gilchristella aestuaria* larvae in these zones. *G. aestuaria* were relatively abundant in hypersaline regions and accounted for the grouping with the more truly estuarine zones. The lack of gobiid species such as *Caffrogobius gilchristi*, *Redigobius dewaali*, *Glossogobius callidus* and the unidentified *Caffrogobius* species in this region resulted in the separation at the 43 % similarity level. The separation of euhaline zones from poly- and mesohaline zones occurred as a result of species such as *G. aestuaria*, *C. gilchristi* and *R. dewaali* occurring in all three zones but in higher densities in the latter two. Mesohaline and polyhaline zones appeared more closely linked in terms of species density and separated at the 75 % similarity level (Fig. 4a).

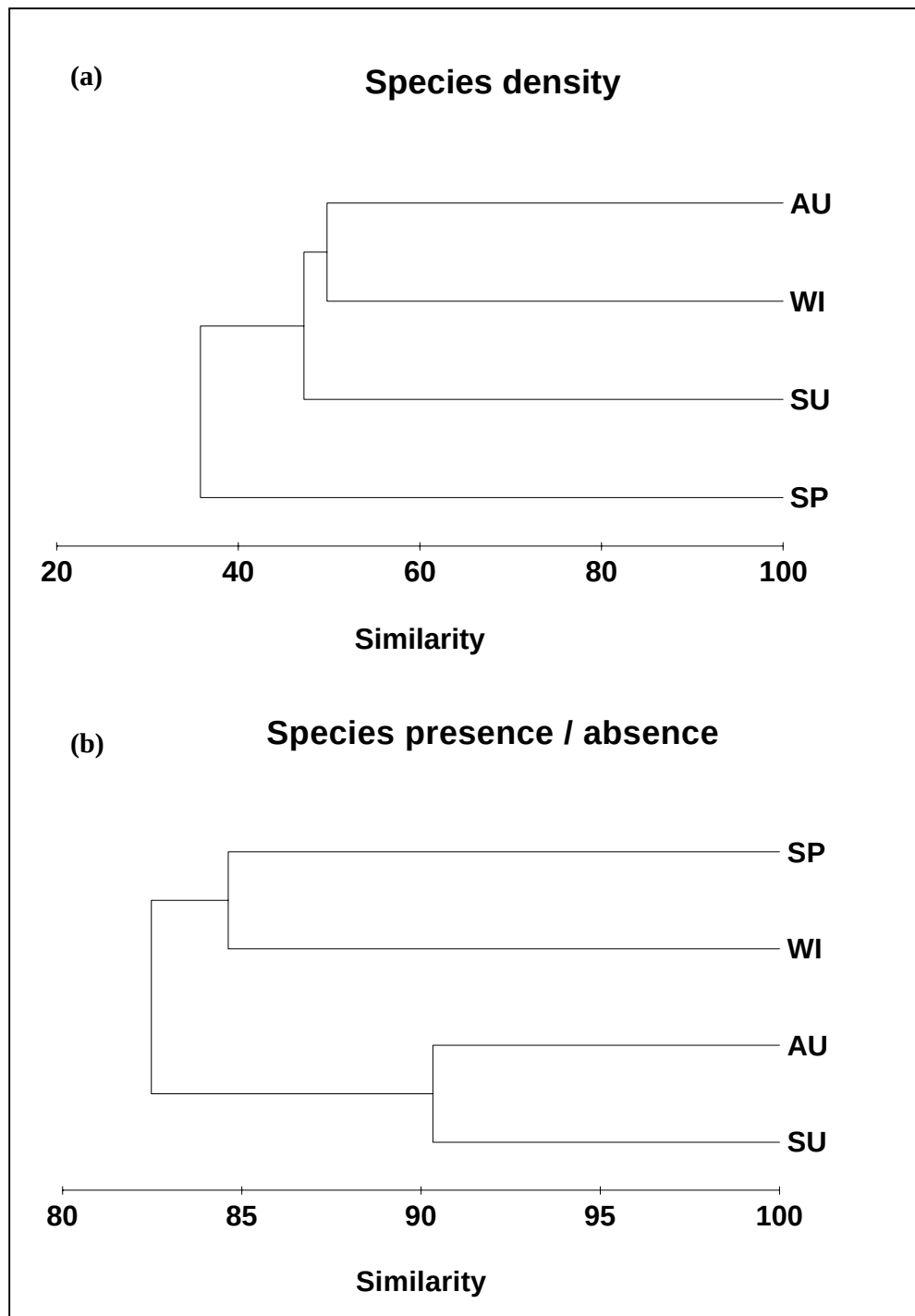


Figure 3. Bray-Curtis similarity dendrogram showing percentage similarity between seasons as measured by density (a) and presence / absence (b) of early stage fishes in selected Eastern Cape Province estuaries (SU = summer, AU = autumn, WI = winter, SP = spring).

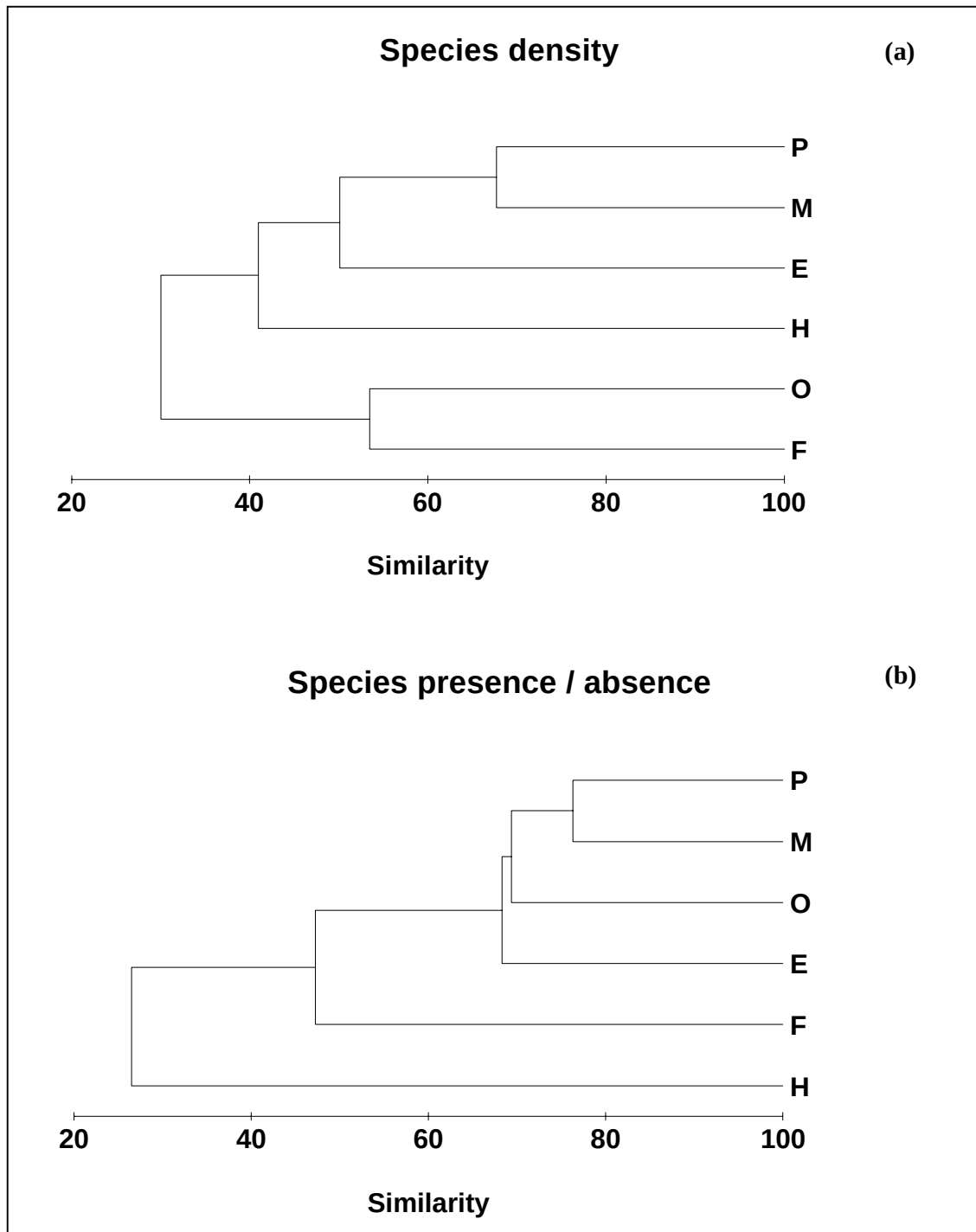


Figure 4. Bray-Curtis similarity dendrogram showing percentage similarity of salinity zones as measured by density (a) and presence / absence (b) of early stage fishes in selected Eastern Cape Province estuaries (H = hypersaline, E = euhaline, P = polyhaline, M = mesohaline, O = oligohaline, F = fresh).

Clustering of salinity zones based on species presence or absence did not show any statistically significant groupings (ANOSIM) but still resulted in distinct separations between zones, with certain species being zone specific (SIMPER). The broad distribution of species like *Gilchristella aestuaria* may be masking the significance of general zone preferences by other species. Most species were poorly represented or absent from hypersaline zones and resulted in this zone being identified as an outlier at the 25 % similarity level (Fig. 4b). Similarly, the fresh zone was further distinguished from other salinity zones characterising these estuaries at the 48 % similarity level and this separation was attributed to the lack of the more common estuary-dependent marine species (e.g. *Pomadasys commersonnii*, *Rhabdosargus holubi*) and an unidentified gobiid 3. The euhaline zone was separated at the 68 % similarity level and this zone comprised mainly unidentified marine species mainly belonging to the families Clinidae and Gobiesocidae together with unidentified gobiid 13 and *Sarpa salpa*. Mesohaline and polyhaline zones were also similarly linked as was found with species density. These zones separated from the oligohaline regions by virtue of the presence of estuary-dependent species (e.g. *Argyrosomus japonicus*, *Liza richardsonii*, *Rhabdosargus globiceps*, *Diplodus sargus capensis*) and an unidentified gobiid 1.

DISCUSSION

Results from the present study indicate that physico-chemical and hydrodynamic variability within permanently open and intermittently open estuarine systems influence the early stage fish communities residing in and utilizing these habitats as nursery areas. Although each estuarine system appears distinct from the next, driven by the physical variables governing each system, general trends emerge in spatial and temporal variability in early stage fish assemblages and community structure. Permanently open estuaries showed a distinct separation from smaller intermittently open systems in the Eastern Cape region in terms of assemblage structure. Similar trends in assemblage structure differentiating permanently open and intermittently open estuaries have been observed for juvenile and adult fishes in similar warm temperate estuaries of the Eastern Cape region (Vorwerk 2000) and in comparisons between similar estuarine types in temperate western Australia (Potter *et al.* 1990).

Water temperature was an important variable in most analyses and despite the lack of any difference in temperature between estuaries, seasonal variations in temperature were evident within most estuarine systems. A summer peak in catches in permanently open estuaries coincided with recruitment peaks for most fish species and with peaks in primary and secondary production (Whitfield & Marais 1999). The higher spring and summer catches of early stage fishes in intermittently open estuaries were mainly because of high numbers of estuary-resident *Gilchristella aestuaria* occurring in these systems, often in numbers far greater than those observed in permanently open estuaries. Species diversity was found to also fluctuate seasonally in this study. Increases in diversity during summer coincides with peaks in recruitment of many species of estuary-dependent fishes and the more incidental occurrence of early developmental stages of straggler marine species spawned over the spring/summer period (Whitfield 1998).

Salinity and water transparency relationships with catch did not feature significantly throughout all estuaries but were confined to isolated systems. Salinity zones were however highly significant in defining communities both in terms of species density and species presence or absence in different estuary types. Mesohaline zones were found to support the highest densities of early stage fishes. These mesohaline regions in estuaries have been associated with river estuary interface (REI) regions and generally become regions of high primary and secondary productivity (Wooldridge & Bailey 1982, Jerling & Wooldridge 1991, Snow *et al.* 2000). A frontal zone between fresh and saline water is formed by high concentrations of suspended particulate matter that trigger and form the basis of biological functioning in estuaries (Snow *et al.* 2000). The productivity of the REI zone will vary from system to system, largely dominated by the quality and supply pattern of river water. (Snow *et al.* 2000). In estuaries such as the Kromme and Kariega where base flow is kept to a minimum as a result of impoundments, a productive REI will not develop (Snow *et al.* 2000). A REI will also be reduced or non-existent in estuaries that are relatively uniformly distributed in terms of salinity regime, as occurred in some of the smaller estuaries during this study. Chlorophyll-a and nitrate maxima have been recorded in the Sundays (Hilmer & Bate 1990) and Gamtoos (Snow *et al.* 2000) estuaries in the oligohaline and mesohaline regions of these systems. These regions of maximum primary productivity in turn result in elevated zooplankton productivity, particularly copepods, (Wooldridge & Bailey 1982, Jerling &

Wooldridge 1991). This may have feeding implications for early stage fishes and may explain the high fish densities in the mesohaline zones of these estuaries.

In permanently open estuaries, early stage fishes belonging to the estuary-resident group were dominated by frequently recorded species namely *Gilchristella aestuaria*, *Caffrogobius gilchristi*, *Psammogobius knysnaensis* and *Omobranchus woodi* (Melville-Smith & Baird 1980, Melville-Smith 1981, Beckley 1985, Whitfield 1989a, Harrison & Whitfield 1990, Harris & Cyrus 2000). In addition to these recordings, *Redigobius dewaali* and *Glossogobius callidus* were found to make a significant contribution to catches throughout the estuaries studied, particularly in those systems receiving an adequate supply of freshwater. The dominance of larvae of estuary-resident fishes in catches in permanently open estuaries has also been observed in the KwaZulu-Natal region by Harris & Cyrus (2000). Similarly, larval assemblages in permanently open systems in temperate Australia (e.g. Neira *et al.* 1992) are also dominated by estuary-resident fish species. Dominant estuary-dependent marine species showed similar catch trends in this study when compared to past investigations in temperate South Africa. *Rhabdosargus holubi*, *Heteromycteris capensis*, *Solea bleekeri*, *L. richardsonii* and *M. falciformis* made considerable contributions to catches. In the present study, species such as *Elops machnata*, *Pomadourys commersonnii* and *Myxus capensis* also made sizable contributions to overall catches. Freshwater species also featured in the present study with *Labeo* sp. found in the Great Fish and Keiskamma systems. A new record of larval *Eleotris* sp. was also made in the Keiskamma Estuary.

Family and species representations for permanently open estuaries appear to be much higher in the present study when compared to all past permanently open estuary investigations in the warm temperate Eastern Cape region. The present study identified 23 fish families represented by 63 species, with an additional four species unidentified. Melville-Smith & Baird (1980) encountered 15 families and 17 identified species of larval fish in the Swartkops estuary. A slightly lower count occurred in the Kromme estuary (Melville-Smith 1981) where 12 families and 15 species were identified. Beckley (1985) identified 17 species in the mouth region of the Swartkops estuary. Strydom (1998) recorded 15 fish families represented by 28 species and an additional nine unidentified species in the Gamtoos Estuary. Comparatively, subtropical estuaries on the eastern shores of South Africa contain a much

greater diversity of larval fishes than temperate systems. For example, Harris *et al.* (1995) found a total of 60 families and 154 taxa in the Kosi Estuary mouth on the subtropical KwaZulu-Natal coast. Family and species representations within the study systems also appear higher than recordings made during temperate nearshore and surf zone investigations of larval fish assemblages. Beckley (1986) recorded 26 families and 32 larval fish species in Algoa Bay. Cowley *et al.* (2001) recorded 13 families represented by 18 species in the surf off the East Kleinemonde Estuary and 15 fish families and 28 species were recorded in the surf zone off the Kabeljous and Van Stadens estuaries (Chapter 2).

Studies on early stage fishes in intermittently open systems in the Eastern Cape province are limited to isolated investigations in the Kabeljous, Van Stadens and Seekoei estuaries (Dundas 1994) where two species of fish namely, *G. aestuaria* and *Atherina breviceps*, and unidentified gobies were recorded. The present study has expanded on the limited existing information on the occurrence of early stage fishes in intermittently open estuaries. The number of species occurring in these systems however, is considerably lower than the diversity of fishes in permanently open estuaries. The diversity of fishes occurring in similar intermittently open systems in temperate Australia (Neira & Potter 1992a) also appears considerably higher and this is attributed to the larger size of these estuary types in temperate Australia. The dominance of larvae of estuary-resident fishes in both temperate Australian (Neira & Potter 1992b) and South African estuaries in intermittently open systems appears similar. The presence of postflexion larvae of *Rhabdosargus holubi* and *Etrumeus whiteheadi* in the intermittently open East Kleinemonde Estuary during this study indicated that certain species are also successfully entering closed estuaries via over-wash events during high seas (Cowley *et al.* 2001).

Whitfield (1994b) characterised South African estuaries as having typically low species diversity and a dominance by relatively few species. Early stage fishes collected in the present study appeared to follow this trend with species like the resident estuarine roundherring, *G. aestuaria*, dominating catches throughout these systems. The permanently open Swartkops Estuary was differentiated from all other systems in terms of species richness and diversity. The Swartkops Estuary also has the largest lower reaches surface area dominated by extensive salt marshes and eelgrass beds (Baird *et al.* 1986). This

characteristic separates this system from the more channel like lower reaches found in other permanently open and intermittently open estuaries investigated. The greater availability of nursery habitat in this estuary may account for the distinctly higher species richness and diversity in this system. Freshwater rich and freshwater deprived systems similarly had higher richness and diversity indices. This was attributed to the increased recruitment of estuary-dependent species in the freshwater rich systems and conversely, the increased numbers of marine species with no dependence on estuaries being prevalent in the freshwater deprived estuaries. Intermittently open estuaries were characterized by low species diversity and richness and this is directly attributed to the nature of these small systems where access is limited during extended periods of closure.

Community analysis identified distinct assemblages of fishes occupying specific estuary types and salinity zones within these estuaries. Estuary-dependent marine species and the gobiid, *Redigobius dewaali*, resulted in a distinct separation of permanently open and intermittently open estuaries in this study. This gobiid species only occurred in permanently open systems. Salinity zones also appeared to be a defining factor affecting larval and early juvenile distribution in these systems and reflects the varying salinity preferences of early stage fishes utilizing estuarine nurseries. Fish density was found to be an ineffective means of defining an estuarine community as densities varied significantly between open and intermittently open systems. On occasion, densities of certain species in intermittently open estuaries were higher than catches of the same species made in permanently open systems. Species presence or absence appeared to be the most effective means of defining estuaries in terms of early stage fish use of these systems. The type of estuarine system, largely governed by river flow and associated environmental conditions, determined the composition of larval fishes utilizing the system. This influence spanned both permanently open estuaries (Whitfield 1994a, Harris & Cyrus 2000) and intermittently open systems in the present study.

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CHAPTER 5

THE EFFECTS OF A REGULATED FRESHWATER RELEASE ON LARVAL FISH RECRUITMENT INTO THE EUHALINE KROMME ESTUARY

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SYNOPSIS

In total 17 families, comprising larvae of more than 29 teleost fish species were recorded in the Kromme Estuary during the study period. In total, 16 109 specimens were collected. Dominant species included *Atherina breviceps*, *Caffrogobius gilchristi*, *Diplodus sargus capensis*, *Gilchristella aestuaria*, *Glossogobius callidus*, *Rhabdosargus holubi* and *Rhabdosargus globiceps*. The larval fish catch in the estuary indicated a marine dominance with relatively high species diversity. The introduction of a regulated freshwater pulse of $2 \times 10^6 \text{ m}^3$ into the estuary from the Mpofu Dam was monitored. Pre- and post-release collections of fish larvae were made on a weekly basis for a two-month period between October and December 1998. The regulated freshwater release into the estuary resulted in no significant changes to the fish family composition, species diversity or estuarine association of the larval fish assemblage. No significant increase in total larval fish abundance or recruitment response by estuary-dependent species was recorded. A limited breeding response by estuary-resident fish species such as *Caffrogobius gilchristi*, *Gilchristella aestuaria* and *Glossogobius callidus* was documented. The increases in larval abundance of estuarine-resident species were mainly attributed to spawning events in the Geelhoutboom Tributary. This tributary received freshwater inflow from rainfall, which coincided with the dam release. It appears that the tributary serves to supplement the Kromme Estuary ichthyoplankton with large numbers of larvae belonging to estuary resident species. Physical conditions in the estuary returned to marine dominance within two weeks of the freshwater release. It is concluded that the riverine pulse and salinity gradient induced by the release of freshwater was too short-lived and too weak to result in a cueing effect on larval fish in the marine environment. A larger amount of freshwater would be required to produce a positive recruitment response by the larvae of estuary dependent species.

INTRODUCTION

It has been well documented both in the northern and southern hemispheres that estuaries are important nursery areas for the juveniles of many species of estuarine and marine fish (Day *et al.* 1981, Dando 1984, Wallace *et al.* 1984). This is the direct result of these species being represented in estuaries predominantly by juveniles. Although some species of fish do enter estuarine nursery areas as juveniles, others enter as larvae (Beckley 1985, Whitfield 1989, Gaughan *et al.* 1990, Strydom 1998). It therefore seems probable that the nursery function of estuaries begins not only at the juvenile phase in the development of estuary dependent marine fish but starts at the postflexion larval stage in the development of some of these species. This postflexion larval stage may be very short in duration until the larva transforms into a juvenile fish but during this time the postflexion larva is already making use of the estuary as a nursery area.

The postflexion larvae (older larvae) of estuary-dependent marine fish recruit into food-rich, sheltered estuarine nurseries from marine breeding grounds. The recruitment of postflexion marine larval fishes into estuarine nurseries is also accompanied by the recruitment of postflexion larvae of certain estuary-resident species whose preflexion larvae undergo an obligatory marine phase (Whitfield, 1989). These larvae later return to the estuary as postflexion larvae or early juveniles. Estuaries are also important nursery areas for the larvae of estuarine-resident species whose life cycles are completed within the estuarine environment. The larvae of the estuarine roundherring have been recorded utilising optimal tidal stream movement in order to maintain their position within the estuarine nursery environment (Melville-Smith *et al.* 1981). In assessing the role that estuaries play in the reproductive strategies and early life histories of estuary associated species, it becomes imperative to understand the importance of cues in attracting recruitment size larval fish into estuaries. Freshwater input into estuaries has been identified as a probable cue in facilitating recruitment of larval fish into these systems (Boehlert & Mundy 1988, Whitfield 1994a).

River flow influences the salinity, temperature, turbidity and biochemical properties of estuarine waters. Fish possess a highly developed sense of smell (Stabell 1992) and estuarine water flowing into the marine environment may serve as a cue in guiding estuary-dependent larval fish species into these nursery habitats. River flow also brings nutrients and organic

material into estuarine systems. Nutrient input, via riverine base flow, has been shown to increase primary and secondary production in estuaries (Hilmer & Bate 1990, Schlacher & Wooldridge 1996), thus benefiting estuary associated fish stocks. Whitfield (1994a) found a positive correlation between estuary-dependent larval and juvenile marine fish abundance and river flow into estuaries.

Poor catchment management and freshwater deprivation have had serious impacts on many South African estuaries through their effect on biotic diversity as well as essential ecological processes (Whitfield & Wooldridge 1994). Reddering (1988) emphasised the fact that reduced river discharge due to excessive freshwater abstraction has a profound effect on the biological behaviour of estuaries. The Kromme Estuary, on the warm temperate coast of South Africa, is a typical example of a freshwater-starved estuary (Jerling & Wooldridge 1994). Impoundments within the catchment have substantially reduced freshwater inflow into the estuary and, as a result, there is an absence of a typical longitudinal salinity gradient with hypersaline conditions in the upper reaches being regularly recorded (Heymans & Baird 1995). Almost the entire runoff from the Kromme River drainage area is retained in dams. The impoundment of freshwater to meet ever-increasing human demands, together with low rainfall, has starved the Kromme Estuary of an adequate riverine supply. Whitfield & Bruton (1989) emphasised that dams or reservoirs result in the downstream flow becoming largely dependent on the operating criteria of the reservoirs. When the Mpofu Dam was built in 1982, a monthly water release program was initiated to supply the Kromme Estuary with enough freshwater to control the development of hypersaline conditions. This program failed due to unauthorised extraction of this supply by farmers upstream of the estuary. A decision was then taken by the research group to test a single-pulse freshwater release from the Mpofu Dam into the estuary and to monitor the effects on the estuarine fauna and flora.

The present study incorporated a monitoring program aimed at the larval fish community of the Kromme Estuary before and after a regulated single-pulse release of $2 \times 10^6 \text{ m}^3$ of freshwater from the Mpofu Dam situated 4 km upstream of the estuary head. The study aimed to obtain pre- and post-release information pertaining to the species composition, diversity, estuarine association and abundance of larval fish in the estuary. Special attention was given to assessing whether this amount of water produced a cueing effect on recruitable

estuary-dependent larval fish. In addition, an assessment was made whether the release was sufficient to alter a marine-dominated system into a more typically estuarine system in terms of species composition, diversity, estuarine association and abundance of the larval fish community.

MATERIALS AND METHODS

Study area

The warm temperate Kromme Estuary (Fig. 1) opens into St Francis Bay on the south-east coast of South Africa. This estuary is one of the largest in the area being 13.7 km long with an average width of approximately 80 m and an approximate surface area of 3 km². Extensive sand banks occur in the lower 3 km, resulting in water depths of < 2 m at spring low tide. Upstream, water depth averages 3 to 4 m increasing to 7 m in places (Jerling & Wooldridge 1994).

The Kromme River rises in the Tsitsikamma Mountains and is approximately 95 km long. The catchment area covers 936 km² and the virgin mean annual runoff is approximately 105.5 x 10⁶ m³ (Reddering & Esterhuizen, 1983). Two dams have been built in the catchment. These are the Churchill Dam (completed 1943) and the Mpofu Dam (completed 1982). Both dams provide water to the Port Elizabeth metropolitan area and their combined catchment area represents about 90% of the total catchment area of the Kromme system (Baird and Pereyra-Lago, 1992). The Churchill Dam has a capacity of 33.3 x 10⁶ m³ and is 36 km above the tidal reach of the estuary. The Mpofu Dam has a capacity of 100 x 10⁶ m³ and is situated only 4 km above the tidal reach. If the capacities of the two dams (133.3 x 10⁶ m³) are compared with the mean annual runoff of the Kromme (105.5 x 10⁶ m³) it is apparent that, on average, very little river discharge reaches the estuary (Adams & Talbot, 1992). This is compounded by the low mean annual rainfall, that is between 700 mm and 1 200 mm (Bickerton & Pierce 1988). During dry periods, river flow below the larger dam ceases altogether and the longitudinal salinity gradient within the estuary is often reversed (Jerling & Wooldridge 1994).

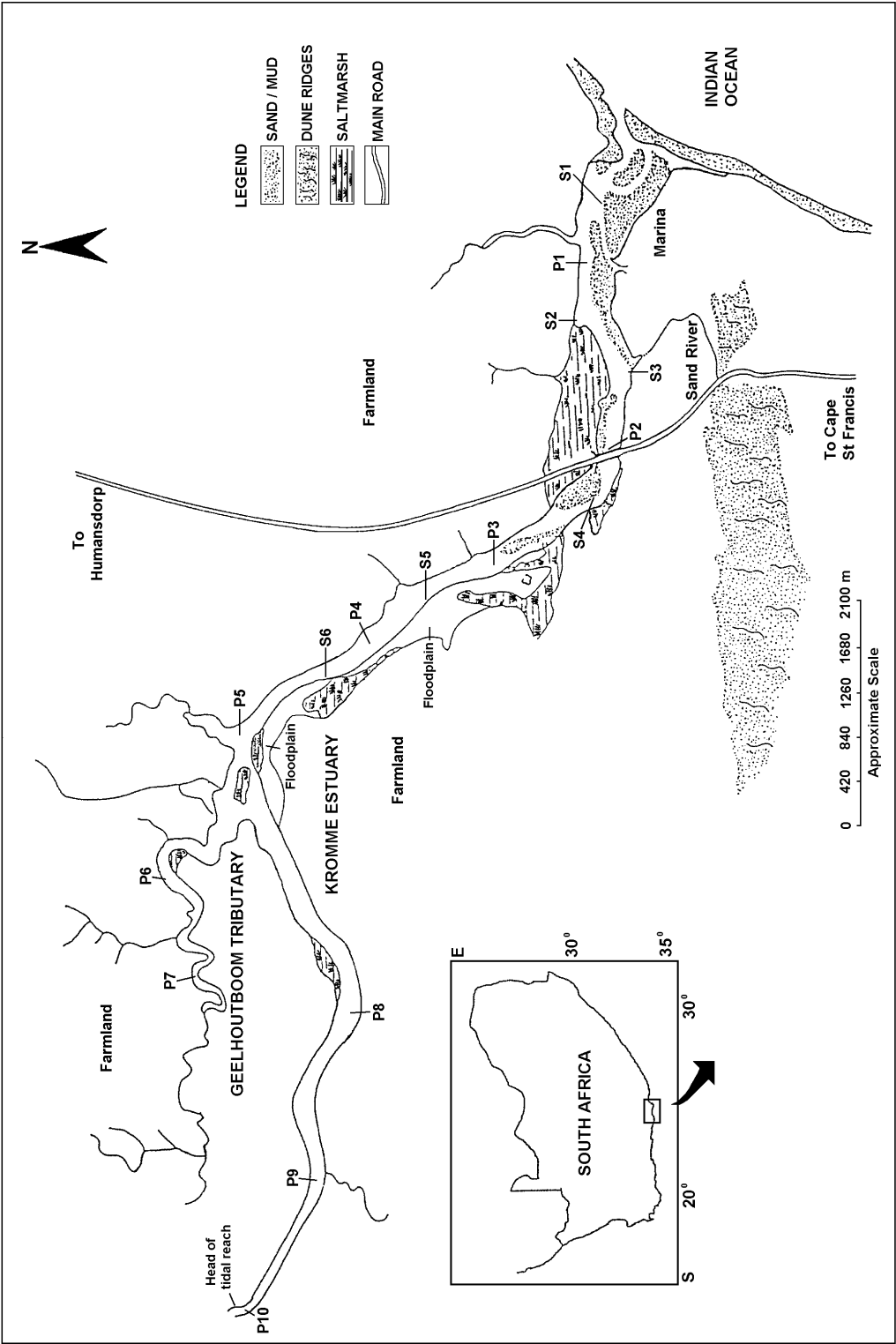


Figure 1. Geographical position of the Kromme Estuary and Geelhoutboom Tributary showing location of sampling sites.

Larval fish sampling localities are shown in Figure 1. Plankton sampling sites (P1 - P10) span the whole length of the estuary and the first 2 km of the Geelhoutboom Tributary. Beach-seine netting sites (S1 - S6) were concentrated in littoral waters in the lower reaches of the estuary to monitor any recruitment response.

Field sampling and laboratory analyses

Larval fish samples were collected during eight sessions at weekly intervals between October and December 1998. Pre-release sample collection dates occurred on 25/10, 1/11, 8/11 and 15/11. In graphical representations, these dates are numbered B1, B2, B3 and B4 respectively (B = before). Post-release sample collection dates occurred on 22/11, 29/11, 6/12 and 13/12. In graphical representations, these dates are numbered A1, A2, A3 and A4 respectively (A = after).

Samples were collected by means of a modified beach-seine net during daylight hours along the margins of the estuary (littoral waters) and boat-based mid-channel plankton netting at night. Sampling was standardised by conducting collections on neap tides in order to minimise the effects of moonlight and the cumulative effect of spring high tidal water volume on larval densities. These adjustments in sampling strategy are based on findings by Strydom (1998).

Mid-channel plankton netting was conducted at 10 sites throughout the estuary (sites P1 to P10, Figure 1), using two slightly modified WP2 plankton nets (570 mm mouth diameter and 0.2 mm mesh size) fitted with Kahlsico 005 WA 130 flowmeters. Nets were simultaneously lowered from two short booms (1.5 m length) fixed on either side of the bow of a 4.5 m twin-hull boat. A graduated pole was used to keep one of the nets just above the bottom during sampling where depth permitted bottom sample collection, otherwise two sub-surface samples were collected. On all occasions, two samples were collected per site. Towing speed ranged between 1 to 2 knots and each tow lasted for 3 min.

Littoral water sampling was conducted at six sites in the lower and middle reaches (sites S1 to S6 in Fig. 1) of the estuary by means of a 1.5 m deep x 4.5 m long modified beach-seine net with a bar mesh aperture size of 0.5 mm. This net was specifically designed for catching

larval fish and consisted of a small beach seine-net fitted with a central tapering cone (similar to a WP2 plankton net with mouth diameter of 0.6 m) that ended in a tie. The cone resulted in the concentration of larvae at the tapered end and allowed easy removal of the transparent larvae. Any larvae adhering to the sides of the beach-seine net or the cone were also easily washed down into the tapered end for removal. Each bank site was divided into four 25 m stretches and sampled by pulling the net across these distances parallel to the estuary bank. In total, 100 m comprising 4 replicates was sampled at each marginal water site.

Pre- and post-release temperature (°C) and salinity (‰) profiles were obtained at each site using a Valeport CTD instrument. Recordings were made at intervals of 0.5 m between the surface and bottom of the water column. Water transparency measurements were also taken at all sites using a Secchi disc. All Secchi disc depth recordings were converted into an extinction coefficient (k) using methods described by Dawes (1981) where $k = 1.7 / D$ (Secchi disc depth in cm).

In total 160 plankton samples and 192 seine netted samples were collected during the study period. Samples were preserved on site with 5 % formaldehyde in seawater. Whole samples were processed in the laboratory and all larval fish removed. Larval fish were identified to the lowest possible taxon according to Melville-Smith (1978), Brownell (1979), Moser *et al.* (1984), Leis & Trnski (1989), Olivar & Fortuño (1991) and Smith & Heemstra (1995).

All terminology pertaining to larval fish follows that of Kendall *et al.* (1984). The term "larva" is used to designate all stages in the early life history from hatching to the attainment of a full fin ray complement, squamation and the subsequent loss of all larval characteristics, at which stage the "larva" becomes a "juvenile". The term "larva" is further divided into yolk-sac, preflexion, flexion and postflexion larval stages. The yolk-sac stage refers to hatched larvae still in possession of yolk sac reserves. This stage is terminated by the complete absorption of the yolk. The flexion stage is characterised by rapid fin ray development, change in body shape, change in locomotive ability and feeding techniques. All specimens older than the postflexion stage were classified as juvenile. At this stage the fish resembles the adult form and these individuals were excluded from the analyses in the present study.

Data analyses

Larval fish density is expressed as number of larvae per 100 m³. Density was calculated using a formula based on a predetermined calibration value for each flow meter used:

$$\text{Larval density} = \frac{\text{Number of larvae per haul}}{(\text{Flow meter revolutions} + \text{calibration value in m}^3)} \times 100$$

Modified beach-seine net catches were expressed as catch per unit effort (CPUE) in terms of numbers. One unit of effort refers to a single seine pulled parallel to the estuary bank over a distance of 25 m in littoral waters. All data were square-root-transformed and the Student's t-test was used to compare pre- and post-release larval density and CPUE between sites and trips. Margalef's species richness, Pielou's evenness and Shannon-Wiener diversity indices were calculated using PRIMER. Diversity indices were interpreted with the aid of information provided by Magurran (1988).

RESULTS

Environmental variability

Physico-chemical recordings were taken throughout the sampling period. Pre- and post-release salinity, temperature and water transparency recordings for the Kromme Estuary and Geelhoutboom Tributary (sites P6 and P7) are shown in Fig. 2. Only surface and bottom values are shown for the salinity and temperature recordings. Salinity (Fig. 2) in the water column was well mixed with surface and bottom values ranging between 33 and 35 ‰ prior to the freshwater release. Post-release salinities (Fig. 2) ranged from 28 to 35 ‰ in the surface waters and 30 to 34 ‰ in the bottom waters. The freshwater input into the Geelhoutboom Tributary after local rainfall is clearly visible in the post-release averages for sites P6 and P7. The tributary salinity averaged 35 ‰ before the release and ranged from 27 to 30 ‰ after natural river inflow. The tributary sites no longer served as a separate control for the freshwater release into the Kromme Estuary and were therefore included in all analyses and considered an integral part of the Kromme system.

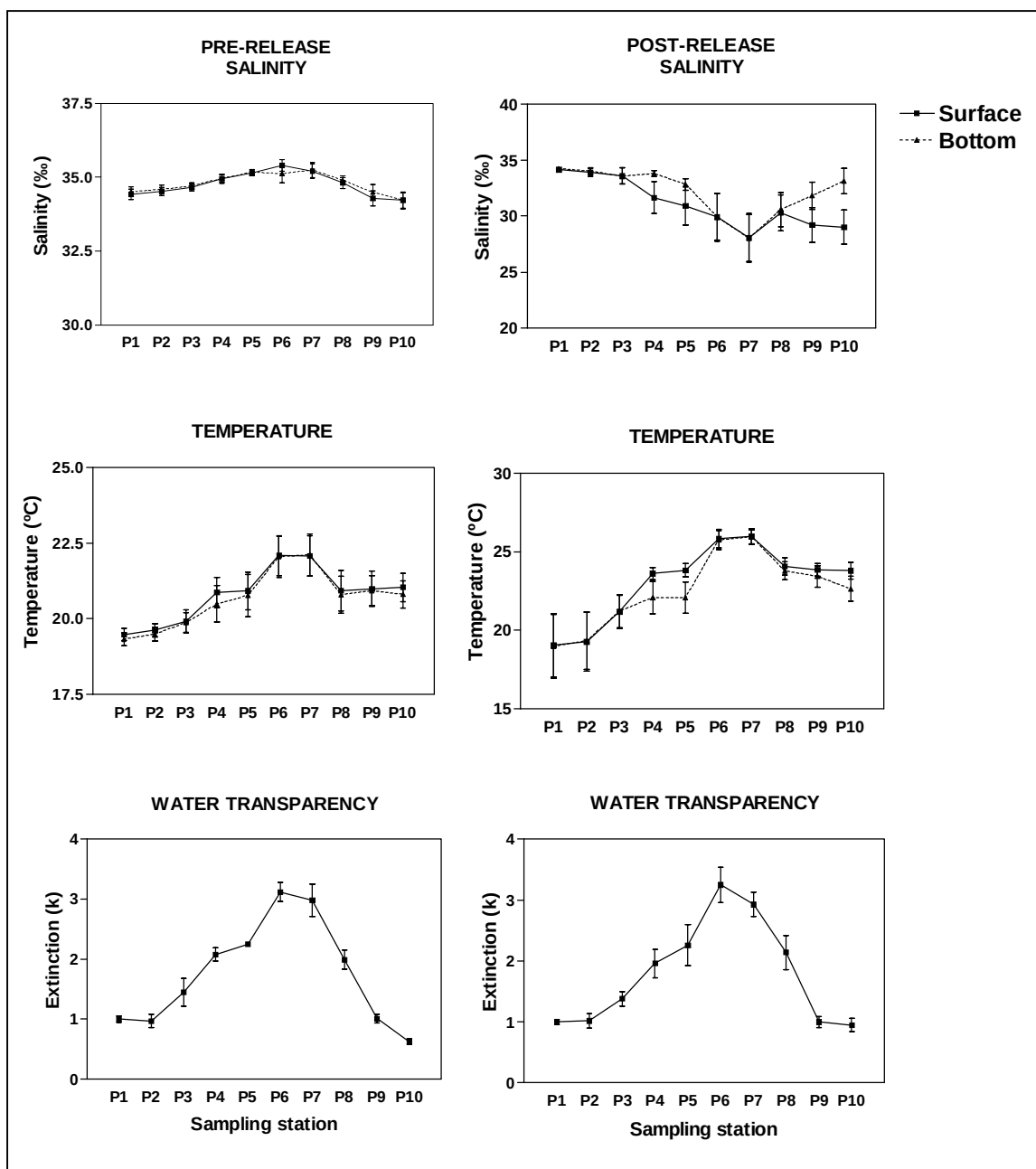


Figure 2. Pre- and post-release variations in mean ($\pm$ SE) salinity, temperature and water transparency in the Kromme Estuary and Geelhoutboom Tributary (October – December 1998).

Pre-release temperature regimes (Fig. 2) showed no stratification in the water column, which was evident from the lack of variation between surface and bottom water temperatures. Pre-release water temperatures ranged from 19 to 21 °C. Post-release water temperatures also showed little variation between surface and bottom waters with temperatures ranging from 19 to 24 °C. The lower reaches of the estuary exhibited a marine temperature influence and were generally cooler than the middle and upper reaches that were typical of summer temperatures (20 to 24 °C) in these systems. Evidence of an upwelling event in the marine inshore region was present on the third post-release sampling session. This was evident in the temperatures in the lower reaches of the estuary that dropped to 13 °C whereas in the middle and upper reaches the range was 23 to 26 °C. Upwelling events serve to introduce nutrient rich water into the marine inshore environment and this water is then flushed into the estuary through tidal action. The Geelhoutboom Tributary waters (sites P6 and P7) appeared warmer than the main estuary and this is attributed to the shallow, narrow nature of the tributary.

Pre- and post-release water transparency variations are shown in Fig. 2. Transparency is presented in terms of an extinction coefficient (k). Decreased water transparency is represented by an increase in extinction coefficient. The freshwater release did result in minor changes to the transparency of estuarine waters. The pre-release extinction coefficient (k) ranged from 0.5 to 3.2 and the post-release k was marginally higher ranging from 1 to 3.3.

Species composition, diversity and estuary association

In total, 17 families of teleost fish were recorded in the estuary and tributary. These families comprised 23 identified species and at least six species identified to family level. These taxa were represented by 16 109 specimens of which 6 329 individuals were collected by plankton nets and 9 780 individuals by seine net. The family Atherinidae, represented by a single species (*Atherina breviceps*), was numerically dominant and comprised 43 % of the total number of fish larvae caught. Other dominant families included the Gobiidae (26 %) represented by four species, the Sparidae (11 %) represented by four species and the Clupeidae (11 %) represented by two species. All other families comprised less than 10 % of the total fish caught. A summary of available species information for the entire study period is shown in Table 1.

Table 1. Family and species representations of pre-release, post-release and total catch, developmental stage and estuary association (Whitfield 1998). Pre-release and post-release catch columns: (X;Y) = (number caught by plankton net (X); number caught by seine net (Y)); Ys = yolk sac, Pr = preflexion, Fl = flexion, Po = postflexion, Ju = early juvenile.

Family	Species	Pre-release catch	Post-release catch	Total catch	Developmental stage	Estuary association
Atherinidae	<i>Atherina breviceps</i>	4729 (16;4713)	2224 (23;2201)	6 953	Pre, F, Po	Ib
Blenniidae	<i>Omobranchus woodi</i>	64 (64;0)	246 (246;0)	310	Pre, F, Po	Ia
	<i>Parablennius pilicornis</i>	0 (0;0)	1 (0;1)	1	Po	III
	Blenniid 1	13 (13;0)	0 (0;0)	13	Pre	III?
	Blenniid 2	0 (0;0)	3 (3;0)	3	Pre	III?
Clinidae	Clinid 1	1 (0;1)	0 (0;0)	1	Po	Ib?
Clupeidae	<i>Etrumeus whiteheadi</i>	22(11;11)	8 (8;0)	30	Pre, F, Po	III
	<i>Gilchristella aestuaria</i>	434 (433;1)	1345 (1337;8)	1 779	Ys, Pre, Po	Ia
Cynoglossidae	<i>Cynoglossus capensis</i>	0 (0;0)	1 (0;1)	1	Pre, F, Po	III?
Elopidae	<i>Elops machnata</i>	7 (1;6)	0 (0;0)	7	Po	IIa
Engraulidae	<i>Engraulis japonicus</i>	4 (1;3)	2 (0;2)	6	Po	III
	<i>Stolephorus holodon</i>	1 (0;1)	10 (10;0)	11	Po	IIc
Gobiidae	<i>Caffrogobius gilchristi</i>	22 (21;1)	1830 (1830;0)	1 852	Ys, Pre, F, Po	Ib
	<i>Glossogobius callidus</i>	816 (816;0)	932 (932;0)	1 748	Po	Ib
	<i>Psammogobius knysnaensis</i>	178 (150;28)	254 (65;189)	432	Ys, Pre, F, Po	Ia?
	Gobiid 1	141 (97;44)	105 (99;6)	246	Pre, Po	I?
Gobiesocidae	Gobiesocid 1	4 (4;0)	5 (5;0)	9	Pre	III?
	Gobiesocid 2	1 (0;1)	0 (0;0)	1	Pre	III?
Haemulidae	<i>Pomadasys olivaceum</i>	21 (0;21)	0 (0;0)	21	Po	III
Monodactylidae	<i>Monodactylus falciformis</i>	9 (4;5)	2 (1;1)	11	Pre, Po	IIa
Mugilidae		191 (4;187)	314 (5;309)	505	Po	IIa,b,c,V?
Sciaenidae	<i>Argyrosomus japonicus</i>	1 (0;1)	3 (1;2)	4	Pre	IIb
Soleidae	<i>Heteromycteris capensis</i>	43 (1;42)	265 (2;263)	308	Pr,Po	IIb
	<i>Solea bleekeri</i>	5 (2;3)	5 (1;4)	10	Po	IIb
Sparidae	<i>Diplodus sargus capensis</i>	285 (4;281)	56 (3;53)	341	Po	IIc
	<i>Rhabdosargus globiceps</i>	416 (2;414)	108 (1;107)	524	Po	IIc
	<i>Rhabdosargus holubi</i>	814 (46;768)	74 (9;65)	888	Po	IIa
	<i>Spondyllosoma emarginatum</i>	1 (0;1)	11 (0;11)	12	Po	III
Syngnathidae	<i>Syngnathus acus</i>	12 (12;0)	3 (2;1)	15	Po	Ib
Tetraodontidae	<i>Arothron immaculatus</i>	40 (19;21)	27 (25;2)	67	Pre, F, Po	IIIa

Figure 3 shows the pre- and post-release family composition of larval fish at all sampling sites using all gear types during the study period. Only dominant families are represented with the Atherinidae ranked first during the pre-release period and the Gobiidae during the post-release period.

Diversity indices were calculated over the entire study period incorporating all species caught and total numbers caught per species (Table 2). The family Mugilidae was treated as a separate species for the purposes of this analysis. Margalef's species richness was represented by a value of 2.99. High species diversity ($H' = 1.96$) reflects the occurrence of marine species in the catch. However, the Pielou evenness value ($J' = 0.58$) indicated that numerical distribution amongst species was confined to a few dominant taxa and other species made a small or insignificant numerical contribution.

Diversity indices were also calculated for the pre- and post-release larval fish community (Table 2). Diversity indices for pre- and post-release catches were compared using a two-sample t-test. Analyses treated beach-seine net and plankton catches separately and combined. No significant difference ($P > 0.05$) in pre- and post-release species richness, evenness or diversity was recorded.

In total, larvae of 29 fish species were identified and categorised according to their association with the estuary. A full description of these categories can be found in Whitfield (1998). The number of species recorded per estuary association category is shown in Fig. 4. Estuary association categories for individual species are shown in Table 1.

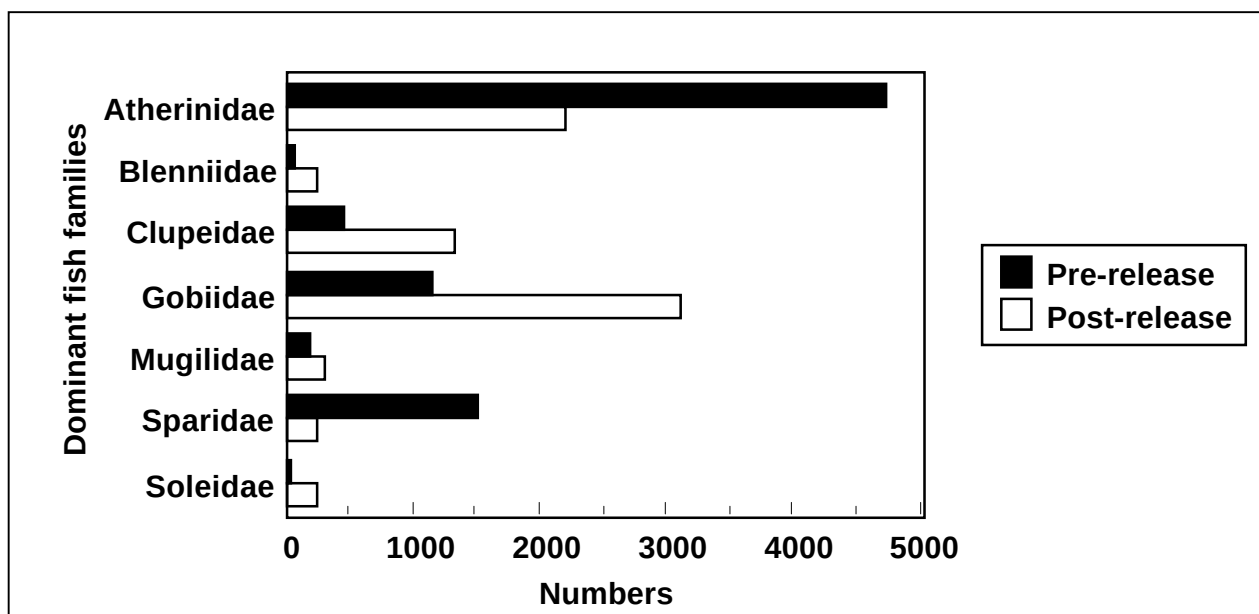


Figure 3. Pre- and post-release family composition of larval fish (plankton and seine net catches combined) in the Kromme Estuary.

Table 2. Diversity indices for the larval fish assemblage in the Kromme Estuary.

	SPECIES	TOTAL NUMBER OF INDIVIDUALS	MARGALEF'S SPECIES RICHNESS (d)	SHANNON- WIENER DIVERSITY (H')	PIELOU'S EVENNESS (J')
Total	30	16 109	2.99	1.96	0.58
Pre-release	27	8 275	2.88	1.62	0.49
Post-release	25	7 834	2.68	1.98	0.62

Individual species of the family Mugilidae were not identified but probably included *Mugil cephalus* (IIa), *Liza dumerilii* (IIb), *Liza richardsonii* (IIc) and *Myxus capensis* (V). Categories IIa (marine species dependent on estuaries), IIb (marine species mainly in estuaries but also at sea), IIc (marine species in estuaries but more abundant at sea) and V (catadromous species) each include one of the four likely species representative of the family Mugilidae. Therefore, a species presence for the family Mugilidae was assigned to each of these categories to cater for the joint classification of the mugilids.

The dominant estuary association category shown in Fig. 4 is marine straggler species (IIIa) with no dependence on the estuarine environment. These species comprised 34 % of the total number of species caught in the estuary with all other estuary association categories having smaller contributions. Estuary-resident species (Ia) (complete their life-cycle in estuaries) comprised 9 % while estuary-resident species that also spawn in the marine environment (Ib) comprised 18 % of the species catch. Marine species that are very dependent on estuaries (IIa) comprised 9 % of the catch while marine species mainly found in estuaries but also found in the marine environment (IIb) comprised 18 %. Marine straggler species mainly found in the marine environment but occur in estuaries (IIc), comprised 9 % while catadromous (V) species comprised < 3 % of the total catch. Freshwater species belonging to category IV (Whitfield 1994b) were not recorded in the Kromme Estuary.

Pre- and post-release catches of fish larvae were separately placed into estuary association categories and compared. For the purposes of this analysis, species were broadly categorised into estuary-resident species (larvae belonging to fish which breed in estuaries), estuary-dependent species (larvae belonging fish spawning in the marine environment but dependent on estuaries during their early life-history stages) and marine stragglers (larvae belong to marine fish that have no dependence on estuaries as nursery areas). These pre- and post-release results are shown in Fig. 5. No major changes in the estuary association of the larval fish community were evident in the data after the release of freshwater into the estuary.

Temporal and spatial trends in seine and plankton catches

The number of larvae caught by modified beach-seine net were statistically analysed using a two-sample t-test for differences in mean CPUE of larval fish caught before and after the

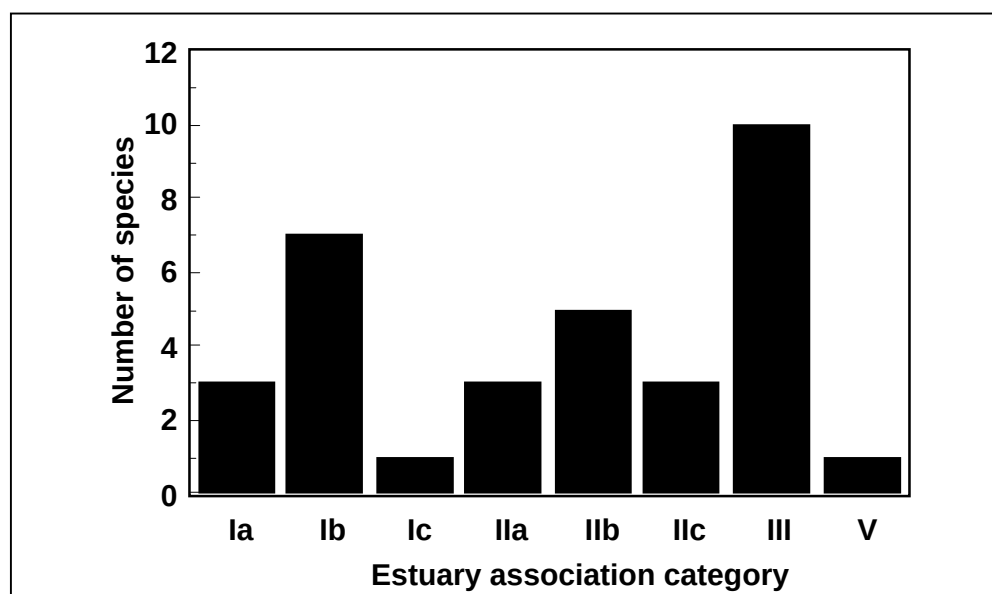


Figure 4. Estuary association categories (Whitfield 1998) for larval fish recorded in the Kromme Estuary (October – November 1998).

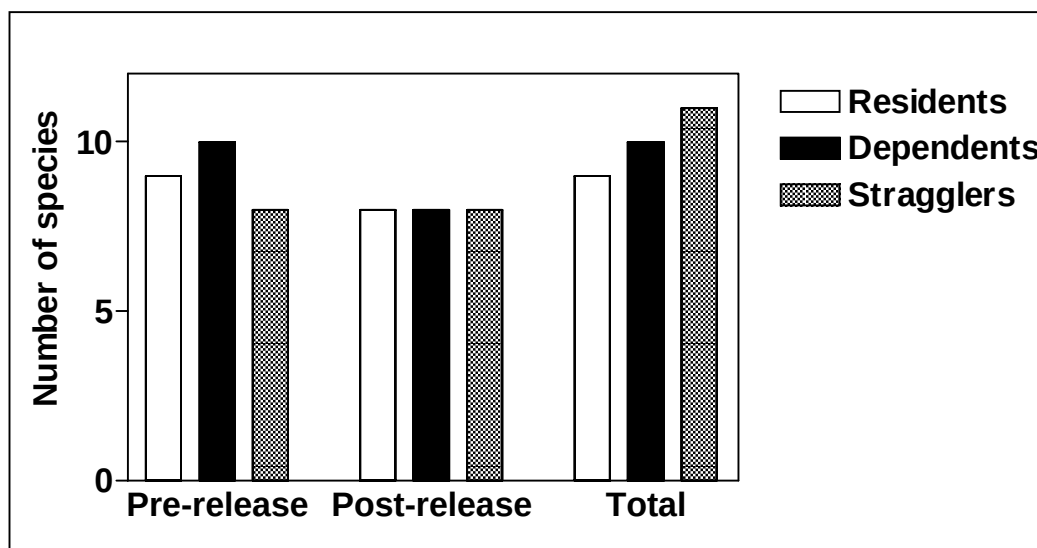


Figure 5. Comparison of estuary association categories for larval fishes caught in the Kromme Estuary before and after the freshwater release.

freshwater release. There was no difference ($P > 0.05$) in mean weekly CPUE of larval fish before and after the release. Mean CPUE was also analysed on the basis of the site in the estuary. There was no difference ($P > 0.05$) between the numbers of larval fish caught before and after the release. Mean CPUE of larval fishes in terms of sampling week and site for the study period are shown in Figs 6 and 7 respectively.

Plankton catches were analysed, using a two-sample t-test, for variations in density (number / 100 m^3) of larval fish caught before and after the artificial freshwater release. Analyses incorporated all sites in the Kromme Estuary. No difference ($P > 0.05$) in mean weekly density of larval fish before and after the release was recorded (Fig. 8). Mean larval fish density was also analysed on the basis of estuary site, before and after the release. Inter-site differences were recorded ($P < 0.05$) between the density of larval fish caught before and after the release. When sites P6 and P7 (situated in the Geelhoutboom Tributary) were removed from the analysis, inter-site results showed no significant differences ($P > 0.05$) between the pre- and post-release periods. The mean weekly larval fish density is shown in Fig. 8. Mean pre- and post-release site density of larval fishes is shown in Fig. 9.

The Geelhoutboom Tributary

The inclusion of the Geelhoutboom Tributary sites shows a distinct difference in pre- and post- release densities of larval fish (see above). The tributary was included in the sampling program to serve as a control for comparison with the main estuary. During the week of the release, local rainfall resulted in the tributary also receiving a pulse of freshwater. The freshwater input into the tributary served to initiate a breeding response by certain estuary-resident fish species and as a result, the Geelhoutboom Tributary acted as a major source of yolk-sac and preflexion larvae during post-release observations in the estuary. Figure 10 shows a comparison of larval densities of estuary resident species in the Kromme Estuary and the Geelhoutboom Tributary.

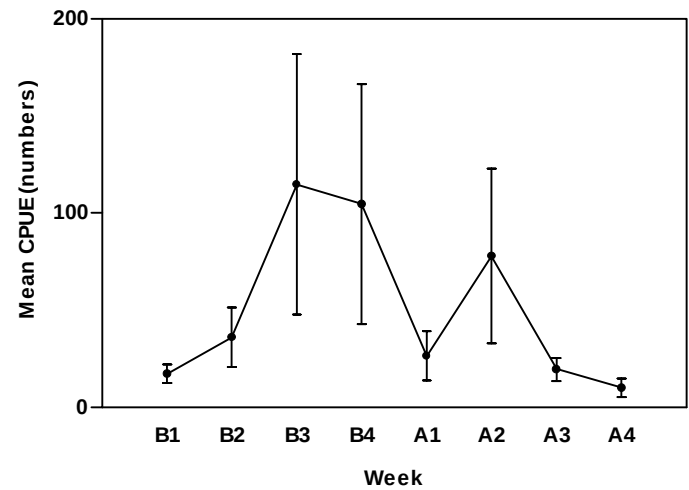


Figure 6. Pre- and post-release mean ($\pm$ SE) CPUE for fish larvae caught by seine net at weekly intervals from the Kromme Estuary (B = pre-release, A = post release)

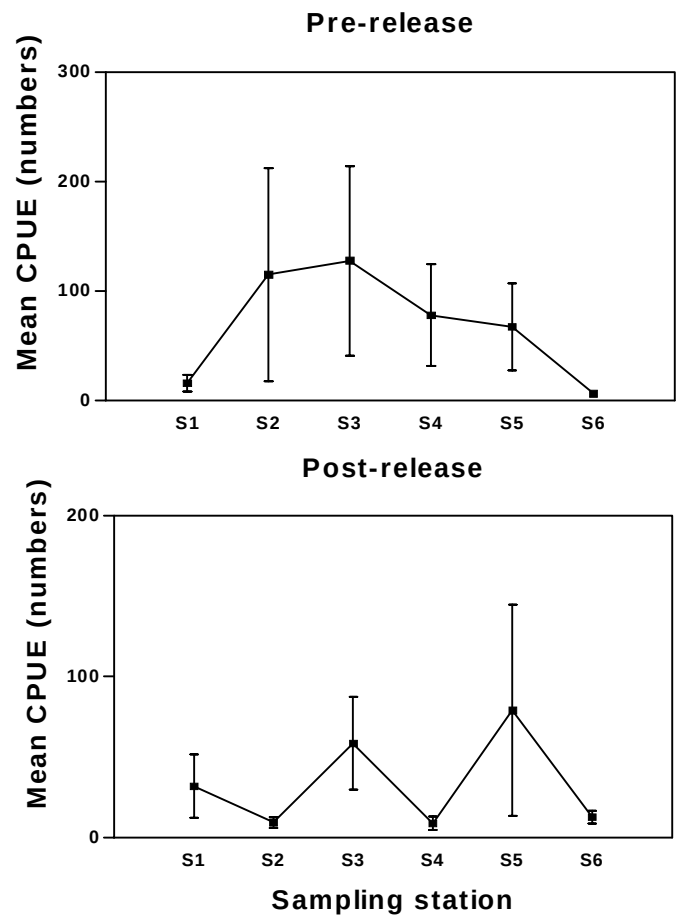


Figure 7. Pre- and post-release mean ($\pm$ SE) CPUE for fish larvae caught by seine net at sampling stations in the Kromme Estuary.

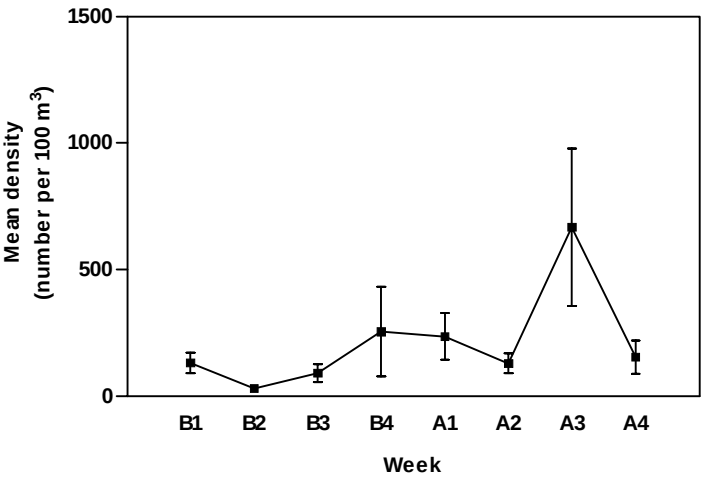


Figure 8. Pre- and post-release mean ($\pm$ SE) CPUE for fish larvae caught in plankton trawls at weekly intervals from the Kromme Estuary (B = pre-release, A = post release).

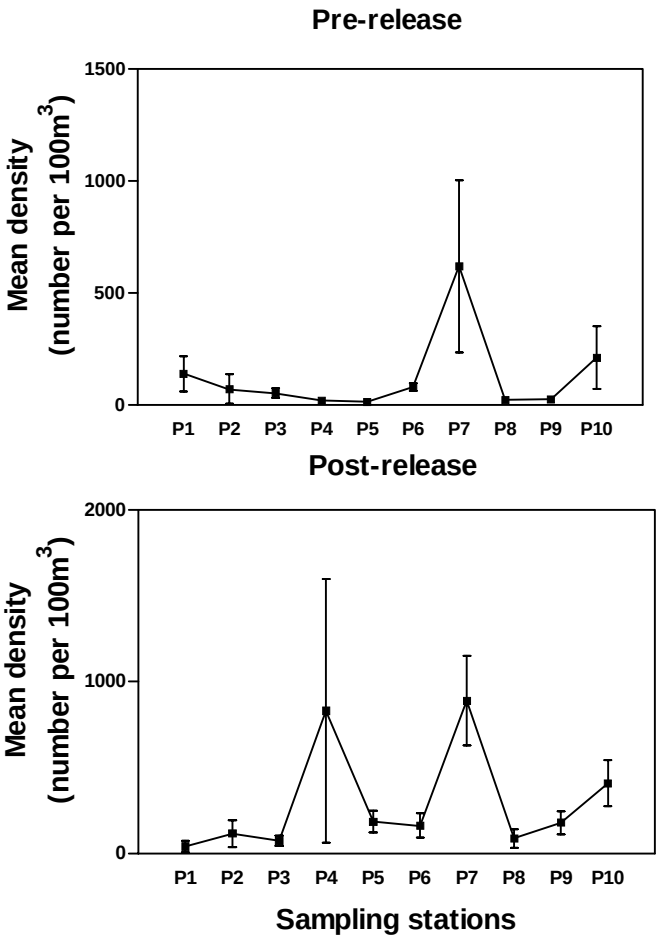


Figure 9. Pre- and post-release mean ($\pm$ SE) CPUE for fish larvae caught by seine net at sampling stations in the Kromme Estuary.

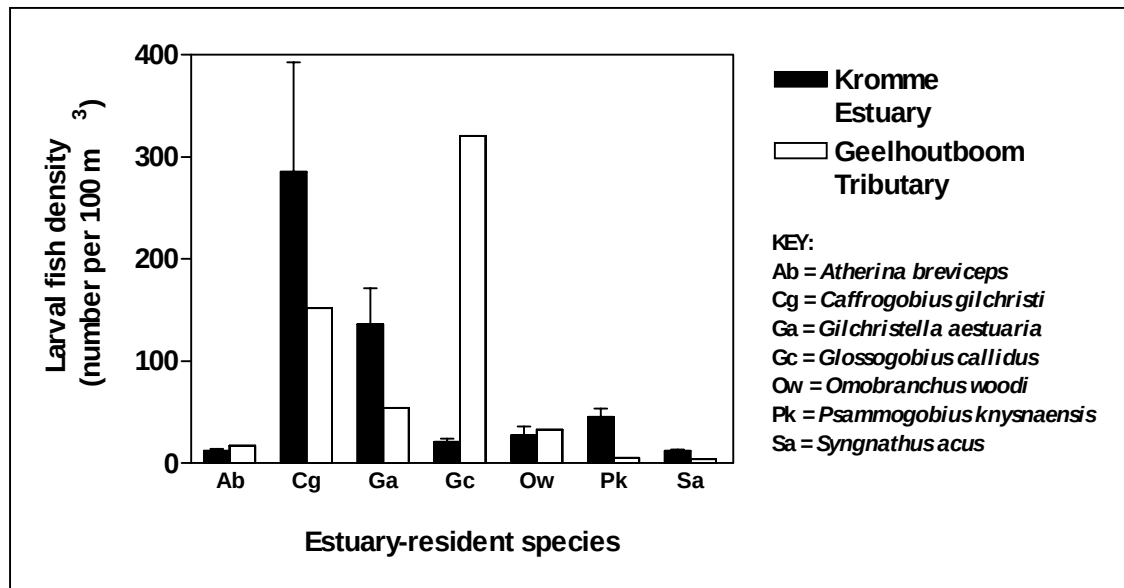


Figure 10. Mean larval fish densities ($\pm$ SE) of estuary-resident species caught in plankton trawls in the Kromme Estuary and Geelhoutboom Tributary.

Figure 11 shows a more detailed account of the estuary-resident species and the relative contributions of larval fish made by the Kromme Estuary (eight sites) and the Geelhoutboom Tributary (two sites). Larvae of the river goby *Glossogobius callidus* appeared to be mainly supplied by the Geelhoutboom Tributary, since numbers in the Kromme Estuary were extremely low, possibly due to the estuary having lost its link with the river. The larvae of other estuary-resident species also occurred in large numbers in the Geelhoutboom Tributary.

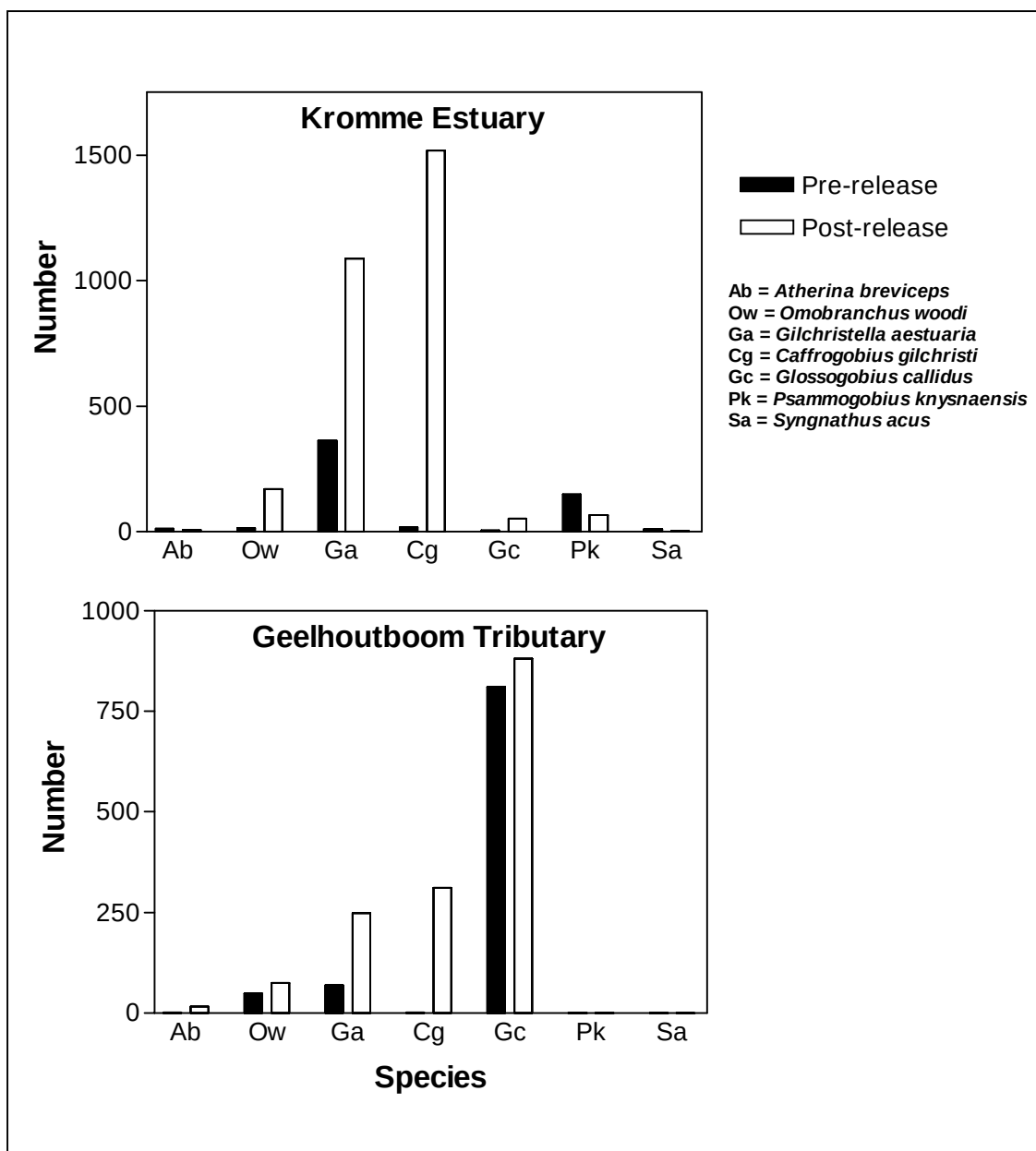


Figure 11. Pre- and post-release occurrence of estuary-resident fish species caught in plankton trawls at eight sites in the Kromme Estuary and at two sites in the Geelhoutboom Tributary.

DISCUSSION

The present study provided an ideal opportunity to gain more insight into the freshwater requirements of Southern African estuaries. This project may be considered pioneering work with respect to freshwater releases as a management option for regulated rivers and their associated estuaries in South Africa. Dams, built to serve metropolitan areas and freshwater abstraction for agricultural purposes, have resulted in freshwater deprivation in the Kromme Estuary and have altered the biological characteristics of the estuary. This is particularly evident in the frequent absence of a typical salinity gradient and the resultant dominance of marine fish species in this system.

The $2 \times 10^6 \text{ m}^3$ freshwater release from the Mpofu Dam into the Kromme Estuary resulted in minor changes to the salinity regime of the estuary. The most notable effects were observed in the surface waters of the estuary with mixing of the freshwater pulse and the existing estuarine waters being limited to the upper 2 m of the water column. Typical estuarine salinity conditions (i.e. the presence of a salinity gradient) were short-lived, with marine-dominated conditions being restored within two weeks of the freshwater release. Even when present, the longitudinal salinity gradient was too weak to facilitate adequate recruitment of estuary associated fish species. Whitfield (1994a) has shown that a longitudinal salinity difference of at least 19 ‰ is required before an efficient cueing process can be established for immigrating postflexion fishes.

The dominance of marine species in the Kromme Estuary is particularly evident in the changes that the larval assemblage has undergone since the first survey of larval fish in the estuary by Melville-Smith (1981), prior to the building of the Mpofu Dam. The sampling sites used in the present study are the same plankton sampling sites used by Melville-Smith (1981) in the main estuary and Geelhoutboom Tributary. The catch included 12 identified species, one unidentified species and two taxa identified to family level. Exclusively marine species comprised 14 % (2 species) of the catch composition. In the present study, exclusively marine species comprised 25 % (6 species) of the species captured in plankton trawls. Beach-seine net catches in this study included 8 marine species that comprised 32 % of the catch. Species diversity in the Kromme Estuary is also considerably higher ($H' = 1.96$) than the species diversity observed in the nearby Gamtoos Estuary ($H' = 1.09$) by Strydom (1998).

In both studies, diversity indices are provided for mid-channel and littoral water sampling. The higher species diversity in the Kromme Estuary is a result of the increased number of marine fish species utilizing the system.

Comparisons of the pre- and post-release larval fish assemblages in the main estuary and Geelhoutboom Tributary showed that the release had no major effects on the fish family composition, species diversity or estuary association of larval fish. Beach-seine net catches revealed no significant changes in abundance of larval fish thus indicating that no recruitment by estuary-dependent marine species occurred. Plankton catches showed that the Geelhoutboom Tributary, that also received a pulse of freshwater as a result of local rainfall during the main release period, serves as an important source of larvae of estuary-resident fish species. These larvae are then distributed into the main estuary channel through tidal action. The Geelhoutboom Tributary is therefore serving as the only remaining natural breeding environment for these estuarine fish species, thus partially compensating for the loss of estuarine habitat and natural pulses of freshwater in the marine-dominated main estuary. Increases in numbers of yolk-sac and preflexion larvae in post-release plankton catches also showed a small breeding response by estuary resident fish in the main estuary. Evidence from this study suggests that estuary resident species are sensitive to riverine flow, which signals increased nutrient input and therefore increased estuarine primary production, and respond by spawning soon after the event.

Despite the breeding response being stimulated by the input of freshwater into the estuary, some resident fish species produce larvae that have an obligatory marine phase in their development. The larvae of estuarine gobiids, (e.g. *Caffrogobius gilchristi*) have a marine phase in their development (Whitfield 1989, Neira & Potter 1992). Larvae are flushed into the marine environment as preflexion larvae and undergo flexion in the sea, after which they recruit back into nearby estuaries as postflexion larvae. The success of this recruitment probably depends on the cueing effect of estuarine waters. The Kromme Estuary may therefore lose many of these larvae as a result of the marine dominance within the system and the lack of this probable cueing effect. It is also possible that larvae produced in the Kromme Estuary may recruit into neighbouring estuaries with stronger riverine inputs, e.g. the Gamtoos Estuary.

Freshwater-starved systems, like the Kromme Estuary, that are tidally linked to an adjoining tributary that does receive freshwater, should not be considered as separate entities. Tidal action renders these two parts of the system inseparable in terms of the supply of larvae of estuary-resident fish and management of the system should take this into account.

In conclusion, the changes to the salinity gradient in the Kromme Estuary, induced by the $2 \times 10^6 \text{ m}^3$ freshwater release were short-lived and weak, both horizontally throughout the estuary and vertically within the water column. As a result, the anticipated responses by larval fish to the release did not occur but valuable information was gained in the process. The existing freshwater allocation to the estuary is inadequate and a considerably larger volume of water is required to produce a positive recruitment response by the larvae of estuarine-dependent marine fish species.

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CHAPTER 6

INFLUENCE OF ALTERED FRESHWATER FLOW REGIMES ON ABUNDANCE OF LARVAL AND EARLY JUVENILE *GILCHRISTELLA AESTUARIA* (PISCES : CLUPEIDAE) IN THE UPPER REACHES OF TWO SOUTH AFRICAN ESTUARIES

(This work is published in the journal

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SYNOPSIS

Past investigations into South African estuaries that are subject to altered freshwater flow regimes have concentrated on the effects of reduced river flow on recruiting estuary-dependent marine fish species. This study compares larval and early juvenile abundance of an estuary-resident, *Gilchristella aestuaria*, in the upper reaches of the ‘freshwater deprived’ Kariega Estuary and the ‘freshwater rich’ Great Fish Estuary. Results showed that catches in the Kariega Estuary were significantly greater than those in the Great Fish Estuary. Larval and juvenile densities were correlated and regressed with salinity, temperature, turbidity, river flow in each system. River flow was found to be the most probable defining factor in terms of the contrasting catches in these systems. *Gilchristella aestuaria* larvae and early juveniles appear to be flushed out of the Great Fish system due to the excessive amount of river flow received from an inter-basin water transfer scheme. Although freshwater input into estuarine systems is vital for the lower reaches nursery function of South African estuaries, excessive supply can alter the larval and early juvenile composition of estuary-resident fish species in the upper reaches.

INTRODUCTION

The modification of natural flow regimes and the resulting degradation of habitat is one of the most extensive anthropogenic influences on rivers worldwide (Scheidegger & Bain 1995). In South Africa, fresh water is in high demand and more measures are being taken to meet these requirements by building dams and initiating water-transfer schemes (O’Keeffe & De Moor 1988). These practices influence the downstream supply of river flow and nutrients to estuaries. River flow into South African estuaries is critical for the natural functioning of these systems (Whitfield & Wooldridge 1994). Freshwater not only provides essential nutrients for sustainable primary and secondary production within estuaries (Wooldridge &

Bailey 1982, Baird & Heymans 1996) but also is a cue for recruitment of estuary-dependent larval and early juvenile marine fish into estuarine nursery areas (Whitfield 1994). A perennial base-flow interspersed by freshets has been identified as facilitating optimum estuarine biological functioning (Bate & Adams 2000). Together with this, Whitfield (1994) has shown that a longitudinal salinity gradient of at least 19 ‰ is required for an efficient cueing process for marine larval fish to be established.

Studies of estuaries that are subjected to altered flow regimes due to anthropogenic changes have shown the detrimental effects of excessive riverine abstraction (Baird & Heymans 1996, Grange *et al.* 2000, Strydom & Whitfield 2000), whereas few studies have focused on estuaries that receive an excessive supply of fresh water. The Great Fish Estuary is an example of an estuary that receives an elevated freshwater supply due to an inter-basin river transfer scheme (Pech *et al.* 1995).

In an effort to provide additional insight into the role of fresh water and its associated organic/inorganic and physical components in estuarine larval and early juvenile fish abundance, two permanently open anthropogenically altered Eastern Cape Province estuaries with differing freshwater inputs were selected as study areas. Instead of focusing on the lower and middle reaches of estuarine systems and the larvae of estuary-dependent fish recruiting from the marine environment (Whitfield 1994, Strydom & Whitfield 2000), this study attempts to evaluate the influence of altered river flow regimes on larval and early juvenile fish in the upper reaches of these systems and focuses on an estuary-resident fish species.

The resident estuarine roundherring, *Gilchristella aestuaria*, is abundant in clear and turbid estuaries and coastal lakes along the South African coast and occurs in a wide range of salinities (Whitfield 1998). Spawning peaks occur in the spring and summer months, although breeding has been noted throughout the year (Blaber 1979, Harrison & Whitfield 1990). The abundance and catchability of this species make it most suitable for the comparative work undertaken in this study. Past research has indicated that *G. aestuaria* is found in high densities in freshwater rich systems (e.g. Whitfield *et al.* 1994). The larval and early juvenile abundance of *G. aestuaria* were compared in the upper reaches of the Kariega

and Great Fish estuaries under different river flow conditions during the peak-breeding season in order to ascertain the effects of artificially low and artificially elevated freshwater inflow on the larvae of this estuary resident fish species.

METHODS

Study area

The Great Fish and Kariega estuaries (Fig. 1) are bar-built estuaries on the warm-temperate south-east coast of South Africa. The Kariega Estuary (33°41'S, 26°44'E) is ~18 km in length with a well developed flood tidal delta consisting primarily of marine sands (Grange & Allanson 1995). The main channel is narrow (40–90 m wide) and its morphometry is linked primarily to flood events, which have been reduced both in frequency and magnitude in recent years (Whitfield & Wooldridge 1994) as a result of large-scale impoundments in the catchment together with a series of abnormally severe droughts. Thus, although the system was formerly homogeneous with a horizontal salinity gradient increasing from the head to the mouth during periods of river flow, a reversed salinity gradient now prevails for much of the time (Hodgson 1987, Whitfield 1994). Shallowing of the estuary, particularly in the lower reaches, has increased owing to expansion of the flood-tidal delta up the system and accumulation of muddy sediments in the middle and upper reaches (Allanson & Read 1987).

The spring tidal range is between 1 m and 1.5 m in the lower reaches, decreasing up the system. The spring tidal prism averages about $1.9 \times 10^6 \text{ m}^3$. The ratio between the tidal prism volume and river flow shows that the tidal prism exceeds the river volume by more than 115 times (Allanson & Read 1987). Despite the lack of river flooding, this estuary is permanently open and water depths in the mouth channel are usually between 2 and 3.5 m at spring high tide. The mean annual river discharge is approximately $5 \times 10^6 \text{ m}^3$ but the estuary is often characterized by long periods (sometimes in excess of 12 months) of zero river flow, especially during low-rainfall periods. High-tide water temperatures (0.5 m below the surface) recorded in the lower estuary channel ranged from 16° to 22°C and those in the upper reaches from 11° to 25°C (Allanson & Read 1987, Whitfield 1994).

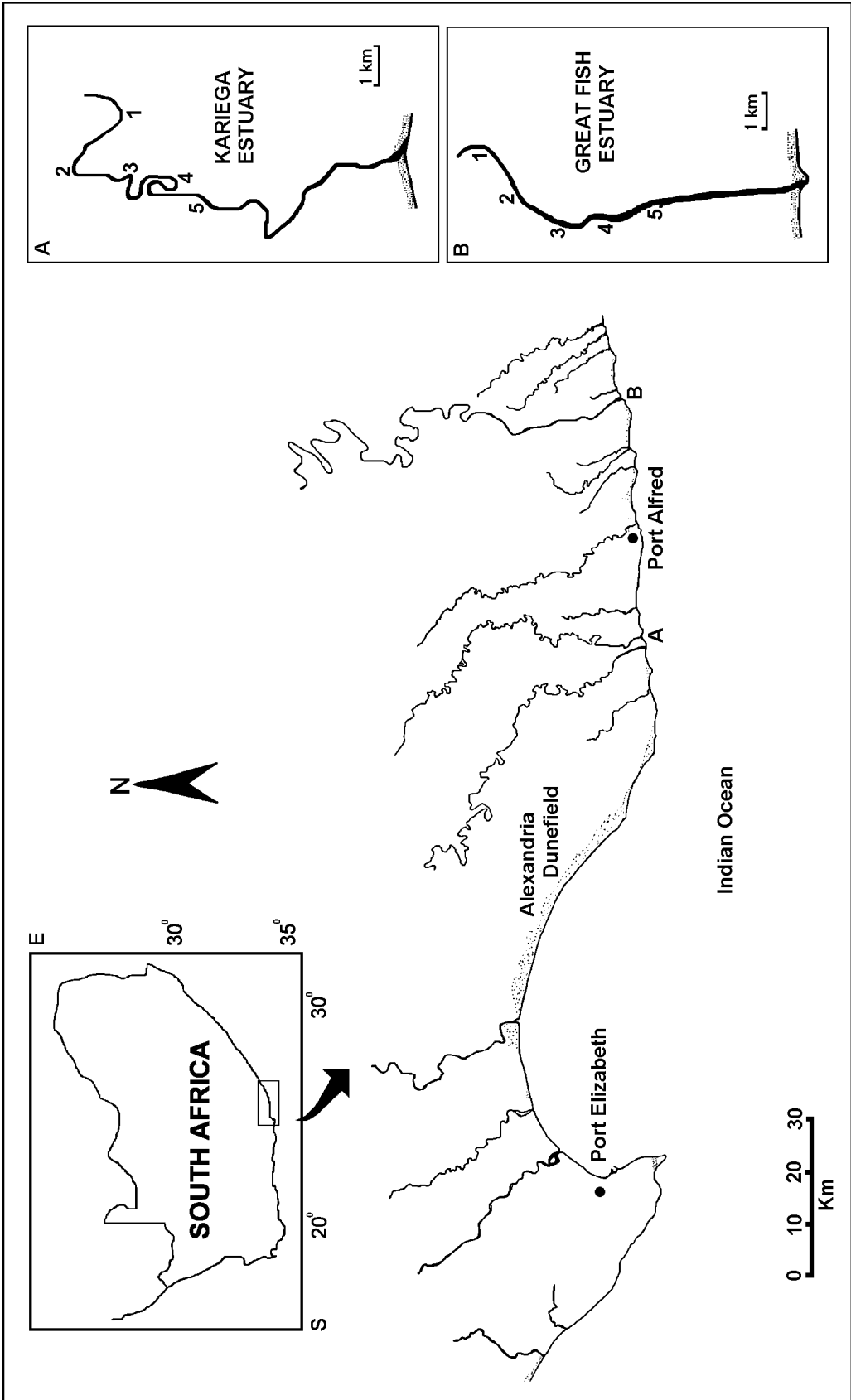


Figure 1. Geographical location of the Kariega and Great Fish estuaries, South Africa. Insets show position of sampling sites within each estuary.

The Great Fish Estuary (33°30'S, 27°08'E) is ~12 km in length with an absence of extensive sand or mudflats, except in the lower reaches where parts of the flood tide delta are exposed at low water. The main channel is narrow (30–100 m wide) and its depth (0.5–3.5 m) is dependent on river flood events. The catchment yields a large fluvial sediment load to the estuary, which results in shallowing of the system, particularly in the upper and middle reaches (Grange *et al.* 2000). During episodic floods these sediments are flushed out to sea but are then gradually replaced during periods of low river discharge by predominantly sand deposits in the upper reaches and mud in the lower reaches (Reddering & Esterhuysen 1982).

Spring tidal range is between 1 m and 1.5 m in the lower reaches, decreasing up the system. The spring tidal prism averages about $1.6 \times 10^6 \text{ m}^3$, with the tidal prism volume exceeding river water volume by only six times during an average tidal cycle (Allanson & Read 1987). Water depth in the channel at the estuary mouth is usually between 2 m and 3.5 m at spring high tide.

The mean annual river discharge is approximately $224 \times 10^6 \text{ m}^3$ and is usually sufficient to maintain a permanently open mouth. Oligohaline conditions (0.5–5.0 ‰) prevail in the upper reaches, mesohaline conditions (5.1–18 ‰) in the middle reaches and polyhaline conditions (18.1 – 35 ‰) in the lower reaches (Allanson & Read 1987, Whitfield 1994). Salinity stratification is often strongly developed in the lower and middle reaches of the estuary. During periods of high river discharge, oligohaline conditions extend into the lower reaches of the estuary, with turbid silt-laden waters penetrating many kilometres out to sea. High tide water temperatures (0.5 m below the surface) recorded in the lower estuary channel were 13–21°C and those in the upper reaches were 11–26°C (Allanson & Read 1987, Whitfield 1994).

The Great Fish Estuary is characterised by large volumes of fresh water derived via an inter-basin transfer from the Gariep River (O'Keeffe & De Moor 1988). The project was initiated to provide water for irrigation in the Great Fish and Sundays river valleys. Water is transferred to the Eastern Cape by means of the Orange–Fish Tunnel from the Gariep Dam in the central region of South Africa. The natural flow regime in the Great Fish River, prior to the initiation of the transfer scheme, was seasonal (Laurenson *et al.* 1989), with the river being reduced to pools during dry periods. The transfer scheme has resulted in a 500800 %

increase in runoff in the upper river, but abstraction in the lower Great Fish River results in a considerable reduction in flow. Nevertheless, the river has been modified from a seasonal to a perennial system (Reddering & Esterhuizen 1982) and now receives the highest river inflow of any estuary of the Eastern Cape Province. The flushing time of the Great Fish Estuary is one day, whereas that of the Kariega Estuary is 45 days (Whitfield 1994).

Field sampling and laboratory analyses

Summer sampling of the larval and early juvenile fishes in the upper half of the Great Fish and Kariega estuaries (Fig. 1) was conducted during 1991, 1992, 1994, 1995, 1999 and 2000. In each year, sampling took place at the end of January or beginning of February, with not more than one week spanning all dates. This period coincided with the known peak breeding period of the estuary-resident fish *Gilchristella aestuaria*. The estuaries were sampled on consecutive nights in order to minimise differences in tidal cycle between the two systems. Collections in all years were made at the same state of the tide. Sampling was conducted in complete darkness to limit any net avoidance by the fish.

WP2 plankton nets (57 cm mouth diameter with 0.2 mm mesh), each fitted with a calibrated digital flow meter, were used to sample larvae and early juveniles in the surface waters of each estuary. The nets were attached to a boom fitted on the bow of a flat-bottomed boat equipped with a 35 hp outboard engine. Sampling commenced ~30 min after nightfall on the new moon. The nets were towed alongside the boat for 3 min at a speed of ~1–2 knots and sampled the upper 0.6 m of the water column. Two replicate samples were collected at each site from the upper and middle reaches of each estuarine system (Fig. 1). Each site was sampled by means of manoeuvring the boat down the estuary but at the same time traversing the width of the estuary. After each tow, flow-meter readings were recorded and the sample immediately preserved in 5% buffered formaldehyde. The volume of water filtered by the plankton nets ranged between 15 and 25 m³ per sample.

Water temperatures (°C) were determined *in situ* at the time of sampling with a calibrated electronic thermometer, but salinity (‰) and turbidity (NTU) samples were collected in glass containers for subsequent laboratory analyses. Since all the fish were collected in the upper 0.6 m of the water column, all physico-chemical measurements were recorded at 0.3 m below

the water surface.

Water analyses were conducted within 12 h of returning from the field. Salinity was measured with a temperature-compensated optical salinometer and turbidities with a calibrated turbidimeter. All *G. aestuaria* were removed from samples and identified (Haigh & Whitfield 1993). Larvae and early juveniles were measured to the nearest 0.1 mm body length (BL) which represents notochord length in preflexion- and flexion-stage larvae and standard length in postflexion larvae / juveniles.

Data analyses

Fish density was expressed as the number of larvae or early juveniles per 100 m³. All data were log-transformed ($\log_{10}(x + 1)$) to conform to normality and homogeneity of variances. For all statistical analyses a significance level of $P < 0.05$ was used. Parametric statistical tests were used on all density data and included the F-test for differences in sample variance and Student's *t*-test for differences in sample mean. The Mann-Whitney U test was used to detect differences between environmental variables. Multiple linear stepwise regressions were used to assess relationships between suites of variables and fish density. Simple linear correlation was used to examine relationships between environmental variables and densities of larval and early juvenile fish.

RESULTS

Environmental variability

Salinity varied significantly between the two estuaries ($P < 0.001$). Salinity in the upper reaches of the Kariega Estuary ranged from 6 to 44 ‰ during the study period (Fig. 2). Hypersaline conditions were recorded in 1992 and 2000, with river flooding in 1995. Salinity in the Great Fish Estuary ranged from 0 to 22 ‰ during the study and despite the elevated flow in general still displayed the influence of wet and dry periods. Drier conditions caused elevated salinities in 1992, and river flooding in 1995 led to oligohaline conditions in the upper and middle reaches. Summer water temperatures ranged from 23 to 29 °C in the upper reaches of the Kariega Estuary and from 23 to 28 °C in the upper reaches of the

Great Fish Estuary and there was no significant difference between these ranges. Turbidity differed significantly ($P < 0.001$) between the Kariega Estuary (4–28 NTU) and the Great Fish Estuary (12 NTU during very dry periods to 1672 NTU after heavy rains) (Fig. 2). Flow also differed significantly ($P < 0.001$) between estuaries. Annual river flow (mean $\pm$ S.E.) in the Kariega River was $0.07 \pm 0.04 \times 10^6 \text{ m}^3 \text{ month}^{-1}$, with a range of 0 to $0.25 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ and a maximum of $9.9 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ during a flood month in January 1995; annual flow in the Great Fish River was $17.03 \pm 2.67 \times 10^6 \text{ m}^3 \text{ month}^{-1}$, with a range of $10.6\text{--}28.7 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ and a maximum of $106 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ during the January 1995 floods (Department of Water Affairs, Cradock, South Africa). In addition, monthly flow in the Great Fish Estuary ($18.1 \times 10^6 \text{ m}^3$) was almost double the highest recorded monthly flow in the past 10 years for the Kariega River.

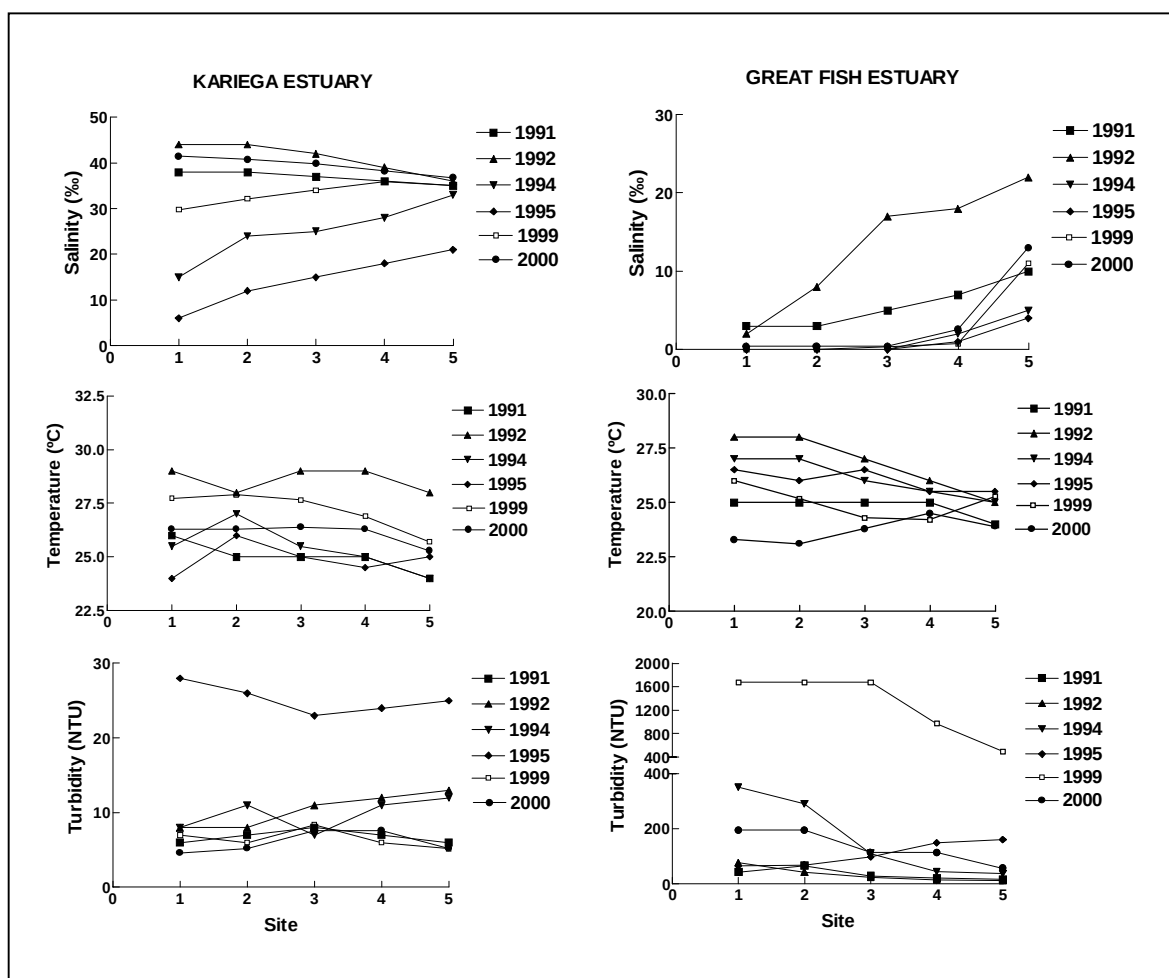


Figure 2. Salinity (%), temperature (°C) and turbidity (NTU) recordings in the Kariega and Great Fish estuaries during the study period.

Spatial and temporal trends in fish abundance

Mean catches of larval *G. aestuaria* were much higher ($F = 2.06$, $P < 0.05$) in the Kariega Estuary (457.2 per 100 m³, ± 66.59 S.E.) than in the Great Fish system (86.7 per 100 m³, ± 52.00 S.E.). Catches of juveniles were also significantly higher ($F = 1.56$, $P < 0.05$) in the Kariega Estuary (63.1 per 100 m³, ± 19.58 S.E.) than in the Great Fish Estuary (54.8 per 100 m³, ± 31.94 S.E.) (Fig. 3).

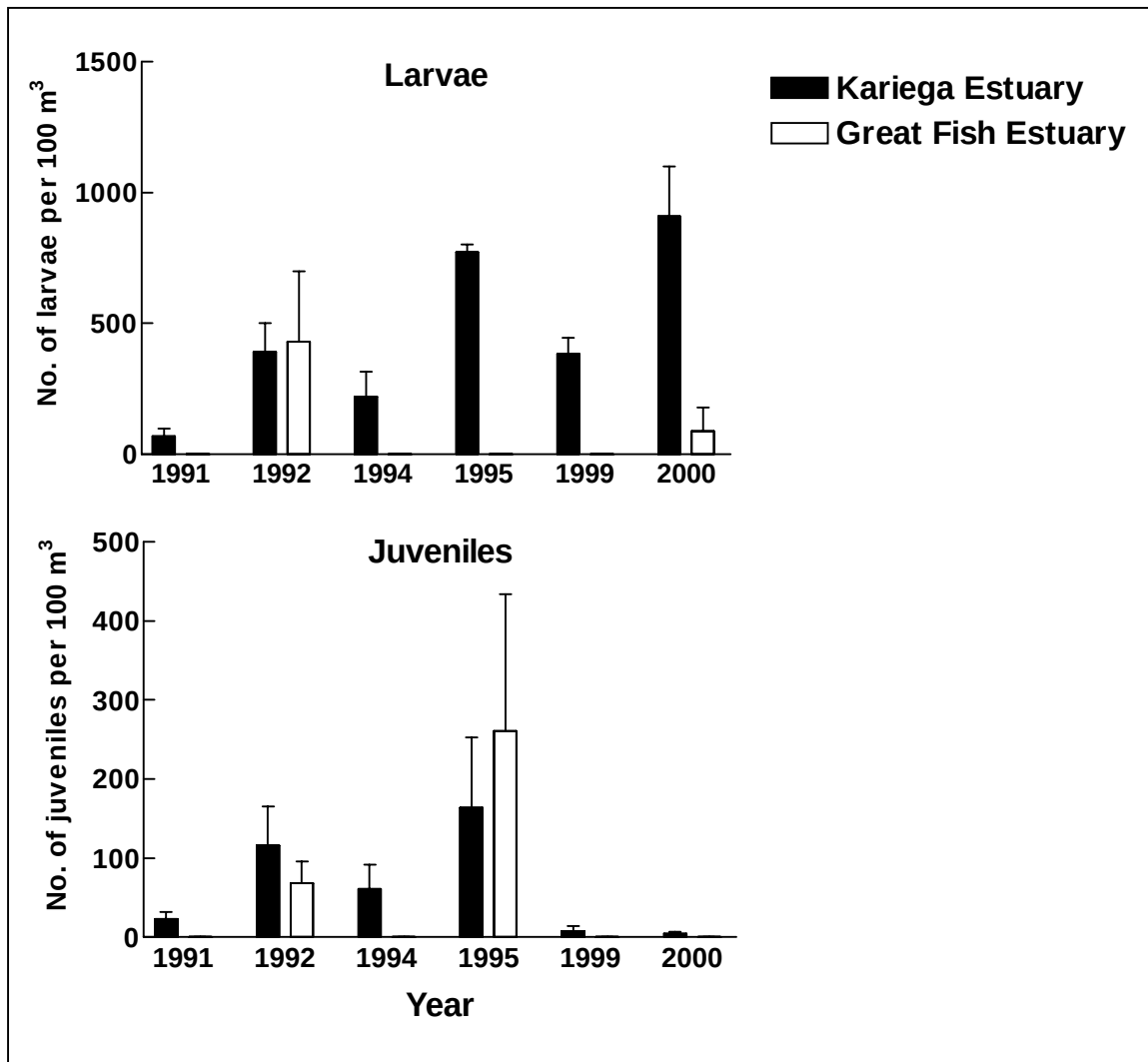


Figure 3. Mean ($\pm$ S.E.) densities of larval and early juvenile *Gilchristella aestuaria* caught in the Kariega and Great Fish estuaries between the 1991-2000 study period.

Larval and early juvenile density of *G. aestuaria* was assessed relative to interactive environmental variability by multiple linear regressions (Table 1) and individually correlated with salinity, temperature, turbidity and river flow (Table 2) for the two estuaries. Larval fish density was positively correlated with salinity in the Great Fish Estuary. Temperature significantly influenced the relationship between suites of environmental variables and larval catch in the Kariega and early juvenile catch in the Great Fish estuaries. Early juvenile fish density was negatively correlated with salinity in the Kariega Estuary and was positively correlated with temperature in the Great Fish Estuary.

Multiple linear regression showed no significant interaction between catch and turbidity. However, correlation results indicated that catches of larval *G. aestuaria* in the Kariega Estuary were positively correlated with turbidity, whereas catches of larvae in the Great Fish Estuary were negatively correlated with turbidity (Table 2).

Significant relationships between density of fishes and river flow were observed in the combined data set and more specifically in the Great Fish system (Table 1). Flow had a highly significant effect on catches in this system, especially on early juvenile fishes. In the Kariega Estuary, only catches of early juvenile fish were positively correlated with river flow (Table 2). In the Great Fish Estuary, catches of larvae and early juveniles were negatively correlated with river flow. Densities of larval and early juvenile fishes caught in the two estuaries are shown relative to river flow in the month of sampling in Table 3.

Table 1. Stepwise multiple linear regression statistics of fish density versus environmental variables for *G. aestuaria* in the Kariega and Great Fish estuaries. adjR2 = adjusted coefficient of determination; R = Correlation coefficient; F = F-statistic; sa = salinity; te = temperature; tu = turbidity; fl = flow. Significance levels: ns = not significant; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$.

	adjR2	R	F	Significant variable
All effects	0.38	0.63	19.31	fl**
Kariega Estuary	0.08	0.38	2.31	ns
Larvae	0.32	0.64	4.39	te**
Early juveniles	0.09	0.47	1.74	ns
Great Fish Estuary	0.42	0.67	11.50	fl****te*
Larvae	0.46	0.73	7.16	sa**
Early juveniles	0.70	0.86	17.63	fl****te****

Table 2. Correlation coefficient (r) for the relationship between larval and early juvenile density of *G. aestuaria* with individual environmental variables. Significance level: $P < 0.05$. ns = not significant.

	Salinity	Temperature	Turbidity	River Flow
Kariega Estuary				
Larvae	ns	ns	0.42	ns
Early juveniles	-0.42	ns	ns	0.38
Great Fish Estuary				
Larvae	0.67	ns	-0.43	-0.38
Early juveniles	ns	0.56	ns	-0.74

Table 3. Mean density of larval and early juvenile *Gilchristella aestuaria* ($\pm$ SE) recorded at specific flow rates during the study in the Kariega and Great Fish estuaries. Flow data obtained from the Department of Water Affairs, Cradock, South Africa).

	Flow (m ³ x 10 ⁶)	Larvae mean density per 100 m ³ ($\pm$ SE)	Juveniles mean density per 100 m ³ ($\pm$ SE)
Kariega Estuary	0	68.1 (30.2)	23.5 (8.8)
	0	391.6 (109.8)	116.2 (49.1)
	0.002	908.9 (190.1)	4.8 (2.7)
	0.027	384.2 (61.6)	8.3 (6.4)
	0.128	219.6 (94.4)	61.6 (30.8)
	0.245	772.7 (29.0)	164.1 (89.1)
Great Fish Estuary	10.6	0	260.6 (173.1)
	11.4	430.8 (269.2)	68.2 (27.7)
	15.5	0	0
	17.9	89.6 (89.6)	0
	18.1	0	0
	28.7	0	0

Length frequencies

Larvae caught in the Kariega Estuary were significantly ($F = 1.59$, $P < 0.05$) larger ($7.6 \text{ mm} \pm 0.11 \text{ S.E.}$; Fig. 4a) than larvae caught in the Great Fish Estuary ($5.9 \text{ mm} \pm 0.23 \text{ S.E.}$; Fig. 4b). Similarly, early juveniles caught in the Kariega system were significantly ($F = 0.58$, $P < 0.05$) larger ($23.5 \text{ mm} \pm 0.3 \text{ S.E.}$; Fig. 4a) than early juveniles caught in the Great Fish Estuary ($21.9 \text{ mm} \pm 0.18 \text{ S.E.}$; Fig. 4b).

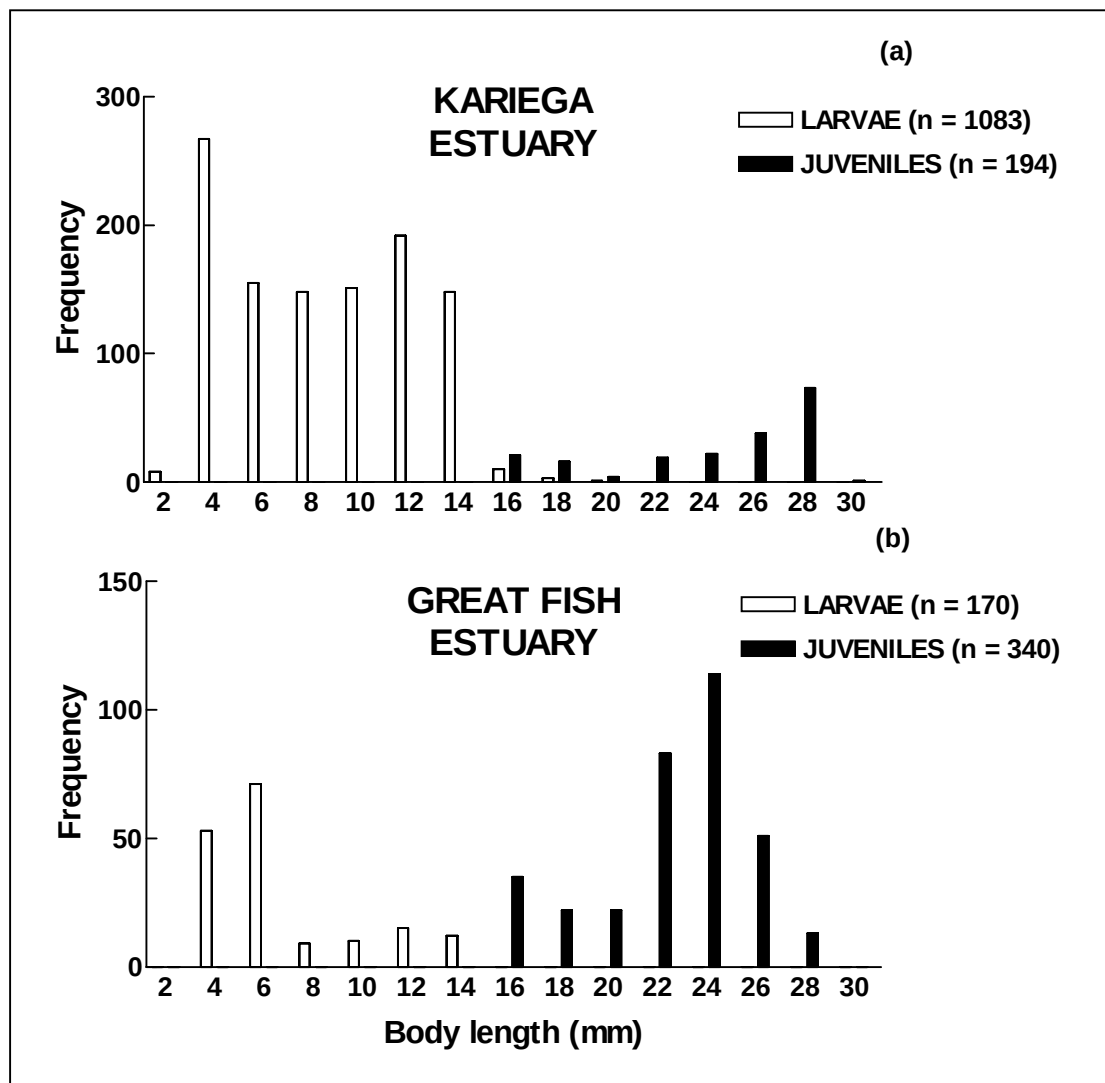


Figure 4. Length frequency distribution of larval and early juvenile *Gilchristella aestuaria* in the Kariega Estuary (a) and Great Fish (b) estuaries during the study period.

DISCUSSION

Freshwater input into estuaries significantly boosts nutrient input in estuarine systems and thereby promotes primary and secondary production (Hilmer & Bate 1991). Food availability for planktivorous larval and juvenile *G. aestuaria* (Whitfield & Harrison 1996) in the Great Fish Estuary is considerably higher than the production and availability of such organisms in the Kariega system and exceeds all other records for the estuaries in South Africa (Grange *et al.* 2000). It would therefore be expected that the Great Fish Estuary should support larger stocks of planktivorous fish larvae and early juveniles.

Indeed, Grange *et al.* (2000) have shown that higher numbers of larvae and early juveniles of estuary-dependent marine fish species occur in the lower and middle reaches of the Great Fish Estuary than of the Kariega Estuary. This increased ichthyoplankton density in the Great Fish Estuary has been attributed to the cueing properties of estuarine and riverine waters entering the marine environment as well as the availability of prey items for young fish in the lower estuary (Whitfield 1994). Similarly, low salinity conditions have been shown to have favourable influences on larval concentrations in other estuaries, such as those found by Allen & Barker (1990) in the North Inlet Estuary, South Carolina, USA. Results from the present study, however, show that the reverse appears to be true for larvae and juveniles of *G. aestuaria* frequenting the upper reaches of Kariega and Great Fish estuaries. Despite the availability of freshwater and therefore prey items in the Great Fish Estuary, larvae and juveniles of this species occur in very low numbers and, at times, are even absent.

This study and past investigations in both estuaries showed that food availability, salinity, turbidity and river flow are the major characteristics that separate the Kariega and Great Fish systems. Invariably, river inflow has a major impact on the physico-chemical characteristics and hence the biology of these estuaries. The high numbers of larvae recorded in the present study in the Kariega Estuary after the small-scale flooding in 1995, like the higher numbers of larvae of *G. aestuaria* after river inflow in other South African estuaries (Martin *et al.* 1992, Strydom & Whitfield 2000), suggest pulse spawning by adults in response to freshwater events (Newton 1996). This species appears to continue low-scale breeding during euhaline conditions but responds positively to freshwater pulses, which may trigger spawning events. Temperature was not considered a critical factor in the variations between

catches in this study because there was no statistical difference between recordings made throughout the study period despite the fact that temperature did show an interactive role in the effects of suites of variables on larval catches in the Kariega and early juvenile catches in the Great Fish Estuary. The lack of effect of turbidity in interactive relationships between variables and catches may be due to the over-riding effect of other variables in the analysis. Correlation analyses were, however, more sensitive and turbidity was positively correlated with larval fish catches in the Kariega Estuary. Turbid water is usually associated with riverine input and this result is similar to the correlation between early juvenile catches and salinity. In the Great Fish system, larval fish abundance was negatively correlated with turbidity. The Great Fish Estuary generally carries high sediment loads, especially during high flow periods. Fish larvae have been found to be sensitive to abnormally high levels of suspended sediments in the water column (Auld & Schubel 1978, Miner & Stein 1993) and/or the flushing effect of high river flows passing through an estuary (Harvey 1987, Salveit *et al.* 1995). River flow is the over-riding factor in this system and the most significant variable affecting fish density, with densities of larvae and early juveniles in the Great Fish Estuary showing a negative correlation with river flow. This absence of young fishes in the water column during high flow periods, combined with the knowledge that fish still spawn after river pulsing and flooding (Martin *et al.* 1992, Strydom & Whitfield 2000), suggests that larval fish are being flushed out of the estuary. Earlier larval cohorts may be flushed down the estuary during high flow periods and therefore reduce the number of early juvenile recruits. Juvenile stocks can only be replenished by the spawning adults if conditions are optimal for larval development and river flows are low enough for a proportion of the larvae to be retained within the estuary.

This study indicates that larvae spawned and residing in the upper reaches of a high-flow estuary, like the Great Fish, are at a much greater risk of being flushed out to sea. Early developmental stages of fish larvae are more susceptible to flushing (Harvey 1987, Dower *et al.* 1998), particularly when larvae hatch in the underdeveloped state characteristic of this clupeid. These factors further contribute to the loss of larvae from the estuary into the marine environment.

Pulsed spawning by adults during high rainfall periods may also increase the chances of at least one spawning event coinciding with lower river flows. Opportunities for refuge may occur in the lower estuary where river flow is considerably reduced, but even so, this is limited because of the small size and underdeveloped nature of *G. aestuaria* larvae. *G. aestuaria* larvae are known to use tidal currents in stratified water columns, as also observed in other larval fish (Heggenes & Traaen 1988), to maintain their position within an estuary (Melville-Smith *et al.* 1981), but the effectiveness of this is reduced in the mouth regions of estuaries where current stratification is reduced by turbulence (Beckley 1985).

High turbulence, a characteristic of fast flowing water, can interfere with the successful feeding of young fish (Browman & Skiftesvik 1996, Dower *et al.* 1998). All components of the predation cycle (search, location, pursuit, attack and capture, ingestion and retention) may be affected by turbulence via excessive river flow. Turbulence may be influencing prey ingestion rates of larvae and juveniles of *G. aestuaria* in the Great Fish Estuary and may thereby influence their growth and mortality.

Despite the negative correlation of larval and early juvenile *G. aestuaria* with river flow in the upper reaches of the Great Fish Estuary, numbers of early juveniles did exceed all catches in the Kariega Estuary when average monthly flow in the Great Fish Estuary declined to around $10\text{--}11 \times 10^6 \text{ m}^3 \text{ month}^{-1}$. Similarly, densities of *G. aestuaria* peaked in the Kariega Estuary after freshwater flow reached $9.9 \times 10^6 \text{ m}^3 \text{ month}^{-1}$. It appears that a tentative range of between 9 and $12 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ provides for optimum breeding and survival of this species. Beyond this range, larvae and early juveniles were not recorded in the Great Fish Estuary despite the presence of adults in the WP2 nets. Flow rates between 1 and $10 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ were not sampled for the Kariega and Great Fish estuaries in the present study as these two systems represent extreme flow regimes for estuaries in the region. It is assumed that *G. aestuaria* still actively spawns during flows of between 1 and $10 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ because larvae and juveniles occur in other Eastern Cape estuaries with river flows extending into this range (Melville-Smith & Baird 1980, Harrison & Whitfield 1990). However, more information is still needed on the effects of flow regimes on the population dynamics of *G. aestuaria* in these regulated systems.

Freshwater is scarce in South Africa and more inter-basin water transfer schemes will be required to provide for the ever-increasing demands for fresh water (O’Keeffe & De Moor 1988). It is imperative that the full ecological consequences of such transfers are realized and monitored. In-depth investigations have been made on the hydrology, chemistry, benthic invertebrate and ichthyofaunal (lower reaches) changes to the Great Fish system following the initiation of the inter-basin transfer scheme (O’Keeffe & De Moor 1988, Grange *et al.* 2000). The present study is the first to address the effects of elevated river flows on the larvae and early juveniles of an estuary-resident fish species.

The optimum riverine flow into an estuary should take into account both the upper and lower limits of freshwater input. Past research has tended to focus on the lower limits of river flow required to sustain estuarine functioning. It appears that in artificially altered systems, such as the Great Fish Estuary, the upper limit of freshwater inflow also needs to be considered. This is especially important in the case of estuary-resident fish species that breed in the system and have larvae hatching with limited swimming capabilities. More information is needed on the far-reaching effects of inter-basin water transfer schemes on other estuary-resident fish species, as well as the effects on freshwater fish species breeding in the riverine sections of these systems.

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CHAPTER 7

SYNTHESIS AND CONCLUSIONS

South African estuaries can be divided into five main types, namely permanently open, intermittently open, estuarine lakes, estuarine bays and river mouths (Whitfield 1998). Permanently open and intermittently open estuaries are the dominant types in South Africa. The warm temperate Eastern Cape coastline has the highest number of estuaries, with permanently open systems and intermittently open estuaries comprising 49 % of the estuary total in South Africa (Whitfield 1998). Estuaries are important nursery areas for both fish larvae (Beckley 1985, Miskiewicz 1986, Whitfield 1989a, Gaughan, *et al.* 1990, Strydom, 1998) and juveniles (Day *et al.*, 1981, Dando, 1984, Wallace *et al.*, 1984) of many estuarine and marine fishes. Estuary-dependent marine fish species recruit into sheltered, food-rich estuarine nurseries from inshore and offshore spawning grounds (e.g. Claridge *et al.* 1986, Whitfield 1989a, Tzeng & Wang 1992, Neira & Potter 1994, Harris & Cyrus 1995, Harris *et al.* 1995). Recruitment of fish larvae into permanently open estuaries in South Africa has been particularly well studied. These studies have highlighted either active migration or passive drift, via tidal currents, as recruitment mechanisms used by these fishes to gain entry into estuarine nurseries (Beckley 1985, Whitfield 1989a, 1994a, Harris & Cyrus 1995, Harris *et al.* 1995, Strydom 1998).

Intermittently open estuaries have recently also been identified as important nursery areas for fishes. Early developmental stages gain entry during estuary openings and overwash events (Harrison & Cooper 1991, Cowley *et al.* 2001). Early stage fish assemblages, particularly larval stages, in intermittently open estuaries are poorly studied with an isolated unpublished investigation from the Eastern Cape Province (Dundas 1994). Surf zone investigations of assemblages of early stage fishes off intermittently open estuaries have been made in isolated studies in the subtropical KwaZulu Natal region (Harris & Cyrus 1996), in the warm temperate Eastern Cape (Cowley *et al.* 2001) and cool temperate Western Cape (Whitfield 1989b). These studies highlighted that assemblages off intermittently open estuaries are composed of predominantly estuary-dependent marine species. This predominance of estuary-dependent fishes in the surf off these estuaries was attributed by Whitfield (1989b) to seepage through the bar acting as a cue.

In the present study (Chapter 2) the lack of higher catches of early stage fishes in the surf adjacent to the mouth of the intermittently open Kabeljous and Van Stadens estuaries during the closed phase indicated that no seepage, as measured by salinity or turbidity changes, was taking place into the surf zone. This was reiterated in the lack of variation in catches between sites sampled in the surf adjacent and away from the closed mouths of these estuaries. The surf zone assemblages were found to be almost exclusively dominated by postflexion larvae of species having varying degrees of dependence on estuaries as nurseries. Seasonal fluctuations in surf zone catches were evident and similar to findings by Roper (1986), Whitfield (1989b) and Harris & Cyrus (1996). Distinctions between surf zone catches were made during natural estuary opening events. Catches were considerably higher in the Kabeljous surf zone, attributed to the effects of a large estuary opening event. Early stage fishes showed a significant relationship with salinity in the surf during the open phase. Catches of postflexion estuary-dependent fishes were significantly higher at sampling stations falling within the estuary outflow plume in the surf zone. Similar findings of larval fishes associating with plumes have been observed by Grimes & Kingsford (1996). A smaller cueing response was also observed in the Van Stadens surf during two opening events even though no measurable physical variable in this study showed any significant relationship with the increase in CPUE. Additional aspects of estuarine water quality, other than salinity per se, may be driving this affinity by the larvae of estuary-dependent fishes for out-flowing estuarine waters. Catchment odours (Creutzberg 1961, Miles 1968) may be playing a greater role than was previously thought and could explain the cueing response observed in the Van Stadens surf. This could link the lack of cueing from a regulated water release into the Kromme Estuary from the Mpofu Dam (Strydom & Whitfield 2000) to the possible loss of catchment odours in water that has been dammed for an extensive period.

Early developmental stages of estuary-dependent species enter estuaries and initially concentrate in the lower reaches of these systems (Neira & Potter 1992a, Whitfield 1994a). Tippers Creek light trap catches (Chapter 3) showed that larval fishes in the lower reaches of the Swartkops Estuary showed preferences for non-vegetated marginal areas rather than vegetated areas characteristic of older juvenile fishes in these systems (Beckley 1983, Hanekom & Baird 1984, Connolly 1994, Ter Morshuizen & Whitfield 1994a). Estuary-dependent marine species were distributed mainly along the margins of the sampling area and

straggler marine species occurred mainly in the channel region. Estuary-resident species showed no distinctive pattern and were indiscriminately distributed between littoral and channel areas. Larger sizes of both estuary-resident and estuary-dependent marine fishes were, however, found along the marginal areas of the creek. Active migration to the margins serves as an ebb tide avoidance mechanism (Beckley 1985) and fishes are thereby able to maintain their position within the estuary and avoid strong currents prevalent in the main channel (Whitfield 1989a). Concentration of young fishes in shallow water also serves as a predator avoidance mechanism as larger piscivorous fishes are excluded at these depths (Copp 1990, Bryan & Scarnecchia 1992, Paterson & Whitfield 2000).

Estuary-dependent fishes may be using shallow littoral regions of the estuary en route to more suitable settlement habitat within the system, with recruitment to vegetated areas only occurring later in their development (Hannan & Williams 1998). This mechanism may be an adaptive response by the larvae of estuary-dependent marine fishes to dynamic tidal environments where position maintenance and predator avoidance in the initial stages of recruitment is imperative to the survival of these fishes. Larval fish have been shown to associate with vegetation beds and floating mats of algae at early stages in their development in habitats devoid of strong currents, e.g. lakes (Conrow *et al.* 1990, Bryan & Scarnecchia 1992). The lower affinity for vegetated areas displayed by postflexion larvae in the present study may have further advantages in lowering predation from larger piscivorous juvenile fish already associated with vegetated areas of the estuary and secondly, lowering the risk of entrapment in eelgrass during the receding tide.

Once recruitment into estuaries has taken place, early stage fishes disperse into these systems and new patterns of composition and distribution emerge within the different estuarine types. Physico-chemical and hydrodynamic variability within permanently open and intermittently open estuarine systems influences the early stage fish communities residing in and utilizing these habitats as nursery areas (Chapter 4). Although each estuarine system is distinct from the next, driven by the physical variables governing each system, general trends emerge in spatial and temporal variability in assemblage and community structure of larvae and early juveniles. Community structure within permanently open estuaries is distinct from smaller intermittently open systems in terms of species composition. Similar differentiation of

species composition in permanently open and intermittently open estuaries has been observed for juvenile and adult fishes in warm temperate estuaries of the Eastern Cape (Vorwerk 2000) and in similar systems of temperate Australia (Potter *et al.* 1990).

In both permanently open and intermittently open Eastern Cape estuaries, the larvae and early juveniles of estuary-resident fishes numerically dominated catches (Chapter 4). Similar findings were made in permanently open systems in subtropical KwaZulu-Natal by Harris & Cyrus (2000) and as similar trend observed for temperate systems of Australia (e.g. Neira *et al.* 1992). Dominant species in permanently open estuaries in the present study, namely *Gilchristella aestuaria*, *Caffrogobius gilchristi*, *Psammogobius knysnaensis* and *Omobranchus woodi*, were also recorded in earlier single estuary investigations (Melville-Smith & Baird 1980, Melville-Smith 1981, Beckley 1985, Whitfield 1989a, Harrison & Whitfield 1990). First-time records of larval *Redigobius dewaali* and *Glossogobius callidus* were also made in these estuaries, particularly in those systems receiving an adequate supply of freshwater. Estuary-dependent marine species, namely *Rhabdosargus holubi*, *Heteromycteris capensis*, *Solea bleekeri*, *Liza richardsonii* and *Monodactylus falciformis* were regularly recorded in the present survey and were also abundant in these systems as shown by past investigations. Additional recordings of species such as *Elops machnata*, *Pomadasys commersonnii* and *Myxus capensis* made sizable contributions to the larval fish catches in the present study. The documentation of small shoals of postflexion *P. commersonnii* also marks the first record of larval recruitment of this species into temperate South African estuarine systems. Larval stages of freshwater genera such as *Labeo* and *Eleotris* were also recorded for the first time in an estuarine system in the subcontinent. Further elucidation of early developmental stages of fishes residing in intermittently open systems in the Eastern Cape Province was made. This information contributes to the limited amount of information available for fish communities in these systems. These systems were however low in species richness and diversity, mainly as a result of the limited access that estuary-dependent marine larval fishes have to these systems. As a result, catches of early stage fishes in intermittently open systems were dominated by estuary-resident species. This finding is similar to recordings made by (Neira & Potter 1992b) in a similar temperate Australian estuary. Diversity of fishes in intermittently open temperate Australian estuaries (e.g. Neira & Potter 1992a) is considerably higher than catches of early stage fishes in

intermittently open estuaries in the present study. This may be attributable to the larger size of similar estuary types occurring in Western Australia.

Family and species recordings made during this multi-estuary comparison (Chapter 4) show that species diversity in these Eastern Cape estuaries is much higher than any previous single estuary larval fish study has shown (Melville-Smith & Baird 1980, Melville-Smith 1981, Beckley 1985, Strydom 1998). This diversity is however indicative of a warm temperate climate and is much lower than the subtropical estuaries of South Africa (Harris & Cyrus 1995, Harris *et al.* 1995). Whitfield (1994b) characterised South African estuaries as having typically low species diversity and a dominance by relatively few species. This was also evident in early stage fishes where species like *G. aestuaria* dominated catches throughout these estuarine systems. The permanently open Swartkops Estuary was differentiated from all other systems in terms of species richness and diversity. The Swartkops Estuary also has the largest lower reaches surface area dominated by extensive salt marshes and eelgrass beds (Baird *et al.* 1986) with a wide variety of nursery habitats. This characteristic separates this system from the more channel-like lower reaches found in other permanently open estuaries sampled. Freshwater rich and freshwater deprived systems had similar richness and diversity index values. This was attributed to the increased recruitment of estuary-dependent species in the freshwater rich systems (Whitfield 1994a) and conversely, the increased numbers of marine stragglers prevalent in the freshwater deprived estuaries (Strydom & Whitfield 2000).

Seasonal variations in early stage fish abundance and diversity were evident within most estuarine systems studied (Chapter 4). Catches peaked in summer in both permanently open and intermittently open estuaries. These increases in abundance coincide with recruitment peaks for most fish species (Whitfield 1998) and with peaks in primary and secondary production in these estuaries (Whitfield & Marais 1999). Within these estuaries, salinity zones appeared to have a major influence on early stage fish communities in terms of species density and composition in all estuary types. Mesohaline zones supported the highest densities of early stage fishes, and are known to support chlorophyll-a and nitrate maxima (Hilmer & Bate 1990, Snow *et al.* 2000) as well as elevated levels of zooplankton productivity (Wooldridge & Bailey 1982, Jerling & Wooldridge 1991). These regions may be driving the establishment of food chains by virtue of the increased primary productivity

and zooplankton abundance characteristic of these zones and may have feeding implications for early stage fishes.

River-estuary interface (REI) regions have recently been well studied in selected permanently open Eastern Cape systems (Whitfield & Wood *in press*). Larval fishes were not included in this REI study and the present study may shed some light on the implications of this zone for early stage fishes utilizing estuary nursery areas. Intermittently open estuaries have not been investigated and the higher abundance of early stage fishes in mesohaline regions of these systems may indicate that REI zones also exist in closed estuaries, and could have ecosystem implications for biological productivity within these small systems.

A hypothesis for the distribution of early developmental stages of estuary-dependent fishes in these warm temperate estuaries emerges here. Estuary-dependent marine fishes enter estuaries predominantly at the larval stage. These fishes mainly occupy the marginal areas of the estuary, avoiding strong water currents and larger fish predators. Postflexion larvae gradually make their way further into the estuarine system, via active migration and flood tidal movement. Larvae mainly occupy the non-vegetated areas, in so doing, they avoid high concentrations of larger juvenile fishes already occupying eelgrass-covered areas and avoid possible entrapment in eelgrass on the receding ebb tide. Once above the lower reaches of the estuary, planktonic postflexion larvae and pelagic early juveniles make their way into the mesohaline zone of the system, either by actively targeting this region or following an increasing food gradient. This zone will probably support rapid growth and development of these larvae, followed by settlement, after which the juvenile fishes, larger in size and more mobile, will disperse throughout the estuary, being particularly attracted to submerged macrophyte beds.

The role that estuaries fulfill as nursery areas for early developmental stages of estuary-dependent fishes is crucial to the survival of many coastal fish populations. Management and conservation of estuaries becomes imperative for the continuation and success of the intricate recruitment processes and the availability of habitat niches required by these fishes in estuaries. Anthropogenic changes in freshwater supply to estuaries in South Africa are widespread and present an ever-increasing problem (Whitfield & Wooldridge 1994). River

supply manipulation, in the form of dams, weirs and various types of abstraction for agricultural, industrial and urban use may result in large-scale fish recruitment loss to estuarine systems. Freshwater deprivation impacts on small intermittently open estuarine systems by affecting the quantity and quality of opening events that generate large-scale cueing responses and recruitment potential by early stage fishes. Permanently open estuaries are also greatly affected by such manipulations since the large rivers supplying these systems with freshwater are invariably selected for the building of large-scale impoundments and water abstraction schemes.

In an attempt at managing freshwater-deprived permanently open estuaries, a pulse of dam water was released into the euhaline Kromme Estuary (Chapter 5). The study provided an ideal opportunity to gain more insight into the freshwater requirements of South African estuaries, particularly for larval fish recruitment into these systems. Freshwater releases as a management tool for regulated rivers and their associated estuaries are a relatively new option for severely altered estuaries in South Africa. Changes in the larval fish assemblage after the building of the Mpofu Dam are evident in the current dominance of marine straggler species when compared to the assemblage in the estuary prior to dam construction (Melville-Smith 1981). Larval fish recruitment was monitored after $2 \times 10^6 \text{ m}^3$ of freshwater was released from the Mpofu Dam into the estuary. The changes to the salinity gradient were limited, both on a spatial and temporal scale. As a result, the anticipated responses by larval fish to the release did not occur. The existing freshwater allocation to the estuary is inadequate and a considerably larger volume of water is required to produce a positive recruitment response by the larvae of estuary-dependent marine fishes. The Geelhoutboom Tributary adjoining the main estuary was found to serve as an important source of larvae of estuary-resident fish species and therefore serves as the only remaining natural breeding environment for these taxa, thus partially compensating for the loss of estuarine habitat in the marine-dominated main estuary. Increases in the numbers of yolk sac and preflexion larvae of estuary-resident fishes in post-release catches, mainly in the Geelhoutboom Tributary that received a simultaneous natural pulse of freshwater after rains, indicated that a small breeding response had occurred. This phenomenon was also observed by Martin *et al.* (1992) in the St Lucia Estuary after a cyclone-induced flood. This response is likely to be triggered by increased nutrient loads entering the estuary via freshwater inflow that in turn, signals greater

food availability (Grindley 1982) for these fishes. Within the main Kromme Estuary, there is a loss of potential marine recruits of estuary-dependent species because of the marine dominance in the system and the lack of riverine/estuarine cues reaching surf zone and nearshore ichthyoplankton. These fishes may therefore recruit into neighbouring estuaries receiving a more natural supply of freshwater.

Freshwater deprived estuaries have received much attention (Day *et al.* 1954, Grange *et al.* 2000, Strydom & Whitfield 2000) but lesser known problems arise from freshwater rich systems which are subject to anthropogenically altered freshwater flow regimes. The Great Fish Estuary served as a case study and a comparison was made between two extremes of severely altered estuaries in terms of river supply and its impact on a resident fish residing in the upper reaches of these systems (Chapter 6). The larvae and early juveniles of the estuary-resident *Gilchristella aestuaria* were compared in the upper reaches of the freshwater deprived Kariega Estuary and the freshwater rich Great Fish Estuary.

Freshwater input generally boosts nutrients (Hilmer & Bate 1991) and therefore food availability for planktivorous fishes (Whitfield & Harrison 1996). The abundance of estuary-dependent larvae and juveniles is also considerably higher in the lower and middle reaches of freshwater rich estuaries when compared to the systems characterized by large impoundments and major abstraction (Allen & Barker 1990, Whitfield 1994a, Grange *et al.* 2000). A reverse trend was observed for *G. aestuaria* larvae and early juveniles in the upper reaches of these systems. Catches of this resident species were higher in the Kariega Estuary that receives very little to no freshwater when compared to the freshwater rich Great Fish. River flow, an over-riding factor in the upper reaches of the Great Fish system, was negatively correlated with larval and early juvenile fish density. Young fishes were absent from the water column during high flow periods suggesting that early stage fishes are being flushed out of the estuary (Harvey 1987, Salveit *et al.* 1995). Larvae spawned and residing in the upper reaches of a high-flow system such as the Great Fish are at a much greater risk of being flushed out to sea. Early developmental stages of fish larvae are more susceptible to flushing (Harvey 1987, Dower *et al.* 1998), particularly when larvae hatch in the underdeveloped state characteristic of this clupeid.

Opportunities for refuge may occur in the lower estuary where river flow velocity is considerably reduced, but even so, this is limited because of the small size and under-developed nature of *G. aestuaria* larvae. These larvae are known to use tidal currents in stratified water columns, as also observed in other larval fish (Heggenes & Traaen 1988), to maintain their position within an estuary (Melville-Smith *et al.* 1981). The effectiveness of this mechanism however, is lowered in the mouth regions of estuaries where current stratification is minimised by turbulence (Beckley 1985). High turbulence, a characteristic of fast flowing water, can also interfere with the successful feeding of young fish (Browman & Skiftesvik 1996, Dower *et al.* 1998) and thereby influence growth and mortality. In addition, fish larvae have been found to be sensitive to abnormally high levels of suspended sediments in the water column (Auld & Schubel 1978, Miner & Stein 1993), a characteristic of river water passing through the Great Fish Estuary.

Numbers of larvae and early juveniles in the Great Fish Estuary did exceed those in the Kariega Estuary when average monthly flow into the former estuary declined to approximately $10 - 11 \times 10^6 \text{ m}^3 \text{ month}^{-1}$. Similarly, densities of *G. aestuaria* peaked in the Kariega Estuary after freshwater flow reached $9.9 \times 10^6 \text{ m}^3 \text{ month}^{-1}$. A tentative range of $9 - 12 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ therefore appears to provide for optimum breeding and survival of *G. aestuaria*. *G. aestuaria* still actively spawns during flows ranging between 1 and $9 \times 10^6 \text{ m}^3 \text{ month}^{-1}$ because larvae and early juveniles are abundant in other Eastern Cape estuaries with river flows within this range (Melville-Smith & Baird 1980, Harrison & Whitfield 1990).

Fresh water is scarce in South Africa and more inter-basin water transfer schemes will be required to provide for the ever-increasing demands of the human population (O'Keeffe & De Moor 1988). It is imperative that the ecological consequences of such transfers are realized and monitored. Optimum river flow into an estuary should take into account both the upper and lower limits needed to sustain biological functioning as well as the natural variability inherent in estuarine systems. In-depth investigations have been conducted on the hydrology, chemistry, zooplankton and ichthyofauna of the Great Fish system following the initiation of the inter-basin transfer scheme (O'Keeffe & De Moor 1988, Grange *et al.* 2000). The present study was the first to address the effects of elevated river flows on the larvae and juveniles of an estuary-resident fish species residing in the upper reaches of this system.

More information is needed on the far-reaching effects of inter-basin water transfer schemes on other estuary-resident fish species, as well as the effects on freshwater fish species breeding in the riverine sections, particularly species that have preflexion larvae with limited swimming capabilities.

Holistic approaches such as multi-estuary comparisons and multi-habitat studies are imperative to an understanding of the dynamic nature of early stage fish use of estuarine nurseries in South Africa. Understanding the occurrence of early stage fishes in these estuaries has repercussions for understanding the biological functioning of these systems and sheds light on the intricacies of the effects of estuary type and associated environmental variability on structuring early stage fish communities in South African estuaries. This has implications for estuarine research and management both nationally and internationally. Despite advancements in larval fish research in South Africa, much still needs to be done. Baseline information pertaining to taxonomy, physiological tolerances and further elucidation of factors driving recruitment into estuaries are still required. The cueing of early stage estuary-dependent fishes is an important aspect in the dynamics of the life cycle of these species (Boehlert & Mundy 1988). More information is needed on those aspects of water quality that are responsible for odours that early developmental stages of estuary-dependent fishes may be responding to. The freshwater requirements of estuaries also need further investigation. This is particularly important in light of findings during this study that suggest that dam releases may not be able to provide the essential cues necessary to induce a recruitment response, as is found with natural pulses of river water. The importance of nearshore regions and surf zones for assemblages of larval fishes need further investigation. Transport mechanisms used by larval fishes to gain entry into estuarine nurseries from surf and nearshore habitats have not been investigated in South Africa and may provide further reasons for the concentration of estuary-dependent fishes in these zones.

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