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Fishes and freshwater in southern African estuaries – A review

Alan K. Whitfield[a]

South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa

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Abstract – The functioning of estuaries relies on a natural dynamism imposed on these systems by riverine and marine influences. The increasing abstraction of fresh water from both large and small river catchments in southern Africa has had the effect of forcing some estuaries into artificial cycles, i.e. natural successions now have human imposed trajectories that are changing estuarine variability and forcing some systems into extreme states. The ichthyofauna has responded to these changes in a variety of ways. Where river flow has declined considerably, or ceased altogether for extended periods, fish recruitment has shown a considerable decrease. This can be related to the collapse in planktonic productivity which negatively affects zooplanktivorous fishes, as well as decreased amounts of olfactory cues entering the sea for the attraction of larval and juvenile marine fishes into these estuaries. Hypersaline conditions can result in both a reduced species diversity and abundance. However, where estuaries lose their normal estuarine salinity gradient and become "arms" of the sea, there is often an increase in fish species diversity due to stenohaline marine taxa entering the estuary. Unfortunately the gain in small numbers of marine stragglers is insufficient to compensate for the decline in estuarine dependent fishes that usually dominate these systems. Conversely, major river flooding often causes temporary decreases in both species diversity and abundance due to a rapid decline in salinity, increased suspended sediments, reduced dissolved oxygen levels, and a collapse in the availability of pelagic and benthic food resources. However, the "resetting" of estuaries by episodic events is part of the essential cycle that maintains and enhances estuarine productivity and habitat diversity. Recovery by estuary associated fishes from such events is usually rapid and linked to a variety of factors, especially estuary morphometry which has a direct influence on the flushing or retention of estuarine biota. Freshwater flows interact directly and indirectly with the fishes that inhabit estuaries, e.g. river floods directly influence estuarine morphometry, water temperature, salinity, pH, turbidity, nutrient status, organic inputs, dissolved oxygen concentrations and olfactory cues; and indirectly affect mouth status, tidal prism, habitat diversity, primary and secondary productivity, fish recruitment, food availability and competition. Depletion or removal of components of river flow to an estuary have major short and long-term negative impacts on the ichthyofauna, some of which can be ameliorated by the provision of an environmental freshwater allocation that is appropriate to that particular system.

Key words: River flow / Salinity / Fish / Estuary / South Africa

Résumé – Poissons et eau douce des estuaires d'Afrique du Sud – une synthèse. Le fonctionnement des estuaires dépend de la dynamique naturelle imposée à ces systèmes par les influences fluviales et marines. L'accroissement des détournements d'eau douce, prises d'eau de rivières ou de fleuves en Afrique du Sud a eu pour effet d'imposer des cycles artificiels à certains estuaires, c'est-à-dire des successions de trajectoires naturelles imposées par l'homme qui modifient la variabilité de l'estuaire et forçant certains à des états extrêmes. L'ichtyofaune a répondu à ces modifications de façon fort variée. Là où le courant a diminué considérablement ou cessé lors de longues périodes, le recruitement en poissons a montré une diminution considérable. Ceci peut être lié à la chute de la productivité planctonique qui affecte négativement les poissons zooplanctonophages, ainsi que la baisse des indicateurs olfactifs venant de la mer qui servent d'attraction aux larves et juvéniles des poissons marins dans les estuaires. Des conditions hypersalines peuvent conduire à la fois à une diminution de la diversité des espèces et à leur abondance. Cependant, où les estuaires perdent leur gradient normal de salinité et deviennent des « bras » de mer, il y a souvent une augmentation de la diversité des espèces due à l'entrée de taxons marins sténohalins. Malheureusement, le gain en retardataires marins est insuffisant pour compenser le déclin des poissons estuariens qui dominent habituellement dans ces systèmes. Réciproquement, d'importantes décharges d'eau douce causent une diminution temporaire à la fois en diversité d'espèces et abondance due à la chute rapide de la salinité, à l'accroissement des sédiments en suspension, réduisant les niveaux d'oxygène dissous, et à l'effondrement des ressources en nourriture benthique et pélagique. Cependant, le réenclenchement des estuaires par périodes épisodiques est une part du cycle essentiel qui maintient et relance la productivité estuarienne et la diversité de l'habitat. La reconstitution des poissons associés aux estuaires, après de telles épreuves, est habituellement

[a] Corresponding author: A.Whitfield@ru.ac.za

rapide et liée à de nombreux facteurs, spécialement la morphométrie de l'estuaire qui a une influence directe sur la rétention ou le lâchage du vivant. Les courant d'eau douce interagissent directement et indirectement avec les poissons d'estuaires, ex. le courant agit directement sur la morphométrie de l'estuaire, la température de l'eau, la salinité, le pH, la turbidité, le statut des substances nutritives, des entrées organiques, de l'oxygène dissous, des concentrations et des indicateurs olfactifs, et indirectement affecte le statut de l'embouchure, du prisme des marées, de la diversité de l'habitat, de la productivité primaire et secondaire, du recruitement en poissons, de la disponibilité en nourriture et la compétition. La diminution ou la suppression des composantes du courant fluvial d'un estuaire a des conséquences négatives importantes à courts et à longs termes sur l'ichtyofaune, certaines peuvent être améliorées par la provision et l'allocation d'eau douce appropriée à un système en particulier.

1 Introduction

Although a considerable amount of research has been conducted on the biology and ecology of fishes in southern African estuaries (Blaber 1979; Cyrus 1991; Wallace 1975; Whitfield 1998), no synthesis of information on the response of estuary associated species to changing river flows has been undertaken. This review attempts to draw together information from a wide range of disparate studies, many of which were not designed to address the role of freshwater in estuaries but nevertheless yielded valuable information.

Much of southern Africa has a semi-arid climate with a highly seasonal and variable rainfall pattern. The average precipitation in South Africa is only 497 mm compared with a world average of 860 mm (Department of Water Affairs and Forestry 1986). In addition, years of above-average rainfall frequently alternate with dry cycles, the latter often punctuated by heavy rains of varying magnitude and extent. These natural extremes provide the perturbations that contribute to the range and temporal variability of estuarine systems, especially with respect to physico-chemical states which in turn affect biotic processes (Forbes and Cyrus 1993).

Growing demand for fresh water in southern Africa has led to widespread impoundment and extraction of surface and underground water resources, often without adequate consideration of the impacts on aquatic ecosystems (Jezewski and Roberts 1986). In addition, invasive alien trees are having a considerable negative influence on the water yields from catchment areas (Dye and Poulter 1995). When river flow patterns are altered, and the intensity and frequency of flood events are modified, these disturbances change natural fluctuations within the riverine and estuarine ecosystems. Base flows and small flood events are commonly removed from the river discharge spectrum altogether and large floods may be attenuated according to the available dam storage capacity at the time of the flood (Davies and Day 1986). Imposition of these anthropogenic disturbances often results in estuarine processes deviating from natural successionary patterns, the implications of which need to be understood before effective management strategies can be devised to maintain or restore the diversity of estuarine ecosystems along the coast.

Studies in a wide range of estuarine and coastal marine systems around the world indicate that reductions in river flow have had a predominantly negative impact on the fish species utilizing these environments (for a global review see Drinkwater and Frank 1994). In addition, more recent international studies have shown that natural river flow variation, through its effect on environmental conditions in estuaries, influences annual and inter-annual changes in fish community structure (Garcia et al. 2003; Garcia et al. 2004; Hurst et al. 2004). Similarly, the review of Grimes and Kingsford (1996) has pointed to a strong positive influence by riverine/estuarine plumes on coastal fish larvae and their subsequent recruitment into nearby habitats. The outcome of the above research indicates that the ecology of rivers, estuaries and the coastal zone needs to be well understood in order to inform the planning process for large-scale freshwater modification projects, thus minimizing the negative impacts of such developments on the aquatic biota of these ecosystems.

In the following review, the influence of freshwater deprivation on different types of southern African estuaries is discussed, with particular reference to the response of the ichthyofauna to changing river flows, salinities and food web structure.

2 Freshwater requirements of estuaries

The continued functioning of most estuarine processes relies on the maintenance of a natural dynamism and the range of oscillations imposed on these systems by riverine and marine influences. Under certain conditions (e.g. droughts) river flow in many South African catchments often ceases and the estuary mouth may close, thus preventing marine-estuarine interactions (Cooper 1994). However, if there is a permanent cessation of river flow then the system effectively ceases to be an estuary, even if the mouth remains open and sea water penetrates upstream to replace the estuary water.

A major global review on the impact of changes in freshwater flow on estuarine habitats and associated biota has been conducted by Gillanders and Kingsford (2002). These authors concluded that, in some areas of the world, freshwater entitlements exceed the available water supply yet few proposals for regulating quantities extracted are scrutinised in terms of possible environmental consequences. In South Africa, Whitfield and Bruton (1989) synthesized some of the principal effects of freshwater deprivation on the physical and biotic components of large and small estuaries in the Eastern Cape Province. Both the above reviews highlighted the false perception that freshwater is 'lost' when it enters an estuary or flows into the marine environment. The studies also emphasized that our knowledge of estuarine freshwater requirements is very limited and that a considerable amount of research is still required to gain a proper understanding of how altered river flows influence estuaries and adjacent marine systems.

Rivers and estuaries are increasingly being regarded as renewable natural resources that can only be exploited within sustainable limits. This change in attitude has resulted in further attempts to develop methods of assessing instream flow needs (Davies et al. 1993; Slinger and Breen 1995). In 1998 the South African Government promulgated a new Water Act and the Department of Water Affairs and Forestry now requires that, for any river system affected by a water resource development scheme, an assessment should be made of the quantity and quality of fresh water that should flow downstream to maintain the river and estuary in some predetermined condition. This required amount of water for the environment is determined by scientists and engineers in co-operation with interested and affected parties, and is called the Ecological Reserve. Reserve determinations have already been conducted on a number of South African systems, e.g. Mtata Estuary (Adams et al. 2002).

3 Effects of impoundments on estuaries

One of the main effects of impoundments in southern Africa is to reduce the incidence and amplitude of minor floods in rivers and estuaries (Whitfield and Bruton 1989). Floods are a critical determinant of the physical structure (van Heerden 1986), functioning (Cooper 1989) and evolution (Reddering and Rust 1990) of estuaries, and a change in the pattern and magnitude of floods can lead to an alteration in morphometry, sedimentary processes, depth profiles, mouth configuration, duration of the open phase, and size of the tidal prism within an estuary. Both river floods and the associated physical variables described above have a direct and indirect effect on the estuarine biota (Marais 1982; McLachlan and Grindley 1974; Talbot et al. 1990).

The effects of freshwater deprivation will vary according to estuary type and locality. Estuaries in regions of low rainfall and high evaporation rates are more likely to be adversely affected by freshwater abstraction and resulting elevated salinities than similar systems in higher rainfall areas (Harrison 2004). This is reflected in the virtual absence of hypersaline conditions in KwaZulu-Natal estuaries when compared with the frequent occurrence of such conditions in some of the drier Eastern and Western Cape estuaries (Allanson and Read 1987). This does not imply that estuaries in higher rainfall areas are not susceptible to reductions in river flow; indeed, the aquatic biota of these regions are likely to be well adapted to elevated riverine inputs and may therefore be very sensitive to intensive freshwater abstraction from the catchments.

Estuaries on the subcontinent seem to have innumerable small-scale spatial and temporal abiotic successions that are superimposed on the weak overall ecological succession, and thus constantly move back and forth along a continuum of successionary states (Whitfield and Bruton 1989). These gradual changes can also be drastically altered by episodic events, e.g. the September 1987 floods in KwaZulu-Natal (Perry 1989). In addition, the frequency and intensity of episodic events within a single estuary vary, thus producing a range of possible successionary trajectories. The effects of certain human perturbations (e.g. impoundments) are to hasten the succession along trajectories which often result in the temporary or permanent disruption of certain estuarine functions. For example, most of the estuarine fishes and invertebrates were temporarily lost from the Seekoei Estuary in the Eastern Cape as a result of extreme hypersaline conditions occurring 1988/89 (Whitfield 1989).

In instances where freshwater pulses are prevented from reaching estuaries, the natural sequence of estuarine biota responses is altered, and small scale successions (e.g. zooplankton community changes) become less frequent (Wooldridge and Melville-Smith 1979). Loss of estuarine variability through reduced river flow fluctuations is becoming increasingly evident in certain estuaries with heavily impounded catchments, with both plant and animal communities responding accordingly (Adams et al. 1992; Adams and Talbot 1992; Whitfield and Paterson 2003). A likely consequence of this reduction in variability is that certain species that are well adapted to fluctuating estuarine conditions will decline in abundance relative to those species that benefit from a more ‘constant’ environment.

Table 1. Summary of biotic and abiotic characteristics in two Eastern Cape estuaries with high and low river flow (modified from Grange et al. 2000): Kariega estuary (33°40′55”S; 26°41′15”E) and Great Fish Estuary (33°39′37”S; 27°08′10”E).

Characteristics	Kariega Estuary	Great Fish Estuary
Abiotic		
Mean annual river flow	Low	High
Allochthonous input	Low	High
Turbidity	Low	High
Sediment load	Low	High
Nutrient load	Low	High
Biotic		
Seston load	Low	High
Phytoplankton stocks	Low	High
Zooplankton abundance	Low	High
Ichthyofaunal abundance	Low	High
Ichthyofaunal diversity	High	Low

Long-term freshwater deprivation can lead to a complete restructuring of energy flow within the affected estuary. In general, a high proportion of primary production in those southern African estuaries which receive adequate riverine input is contributed by phytoplankton (Campbell et al. 1991). Conversely, when riverine discharge into an estuary has been drastically curtailed, food webs usually become centred around benthic primary production (Allanson and Read 1995). This shift in estuarine system properties has been highlighted in a comparison between the Swartkops and Kromme estuaries (Baird and Ulanowicz 1993) who recorded a 1:5 ratio between pelagic and benthic primary production in the Swartkops Estuary but a 1:81 ratio in the freshwater deprived Kromme Estuary. Both systems have similar physical dimensions, lie in the same climatic region, but differ in the amount of riverine input by an order of magnitude. The resulting shifts in ecosystem properties suggest that river flow is vital to both pelagic productivity and the maintenance of a range of food chains within these estuaries (Schlacher and Wooldridge 1996a).

A similar comparison between the nearby Kariega and Great Fish estuaries (Grange et al. 2000) highlights how differences in riverine inflow can influence the structure and functioning of selected biotic components in permanently open systems (Table 1). Maximum chlorophyll a values in the freshwater deprived Kariega Estuary were 1 $\mu g\,l^{-1}$ whereas maximum values in the freshwater enriched Great Fish Estuary

Table 2. Relative abundance of fishes in two Eastern Cape estuaries with high and low riverine flow (data from Whitfield et al. 1994).

Characteristics	Kowie Estuary (33°36′11"S; 26°54′10"E)	Great Fish Estuary (33°39′37"S; 27°08′10"E)
Physical		
Annual river flow	20×10^6 m^3	224×10^6 m^3
Estuary length	21 km	12 km
Estuary width	30–150 m	30–100 m
Estuary depth	2–8 m	1–4 m
Ichthyofauna		
Fish larval densities	26 larvae per 100 m^3	77 larvae per 100 m^3
Seine net fish CPUE	569 fish per 10 seine hauls	1534 fish per 10 seine hauls
Gill net CPUE	130 fish per 100 gill net hours	352 fish per 100 gill net hours

were 22 μg l^{-1}. Sestonic particulate organic material in the Kariega Estuary was also considerably lower than in the Great Fish Estuary, with values in the former system ranging between 11 and 23 mg l^{-1} and in the latter between 29 and 76 mg l^{-1}. Mean zooplankton biomass in the lower, middle and upper reaches of the Kariega Estuary reflected the depleted food resources and was always below 50 mg m^{-3}, whereas in the same reaches of the Great Fish Estuary these values ranged from 256 to 4253 mg m^{-3}. Similarly, mean larval and early juvenile fish densities in the mouth region of the Kariega Estuary were 49 individuals per 100 m^2 compared to 279 individuals per 100 m^2 in the Great Fish Estuary.

Temporal changes in river flow reinforce the importance of allochthonous inputs to the functioning of Eastern Cape estuaries. A comparison between a dry and wet period in the freshwater deprived Kariega Estuary revealed mean nitrate and phosphate concentrations increasing from 6 to 102 μmol l^{-1} and 1 to 6 μmol l^{-1} respectively (Allanson and Read 1995). Phytoplankton stocks responded positively to freshwater pulses in both the Kariega and Great Fish estuaries. Similarly, peaks in zooplankton biomass in Great Fish Estuary increased rapidly in response to high food resource availability resulting from elevated river discharge (Grange 1992). The higher ichthyoplankton and ichthyonekton densities in the Great Fish Estuary, when compared to the Kariega Estuary, were attributed to a combination of stronger olfactory cues for larval immigrants from the sea and elevated food stocks in the former system (Whitfield 1994).

A similar comparison between fish stocks of the Kowie and Great Fish estuaries (Table 2) indicated an approximate three fold increase in relative abundance of larval, juvenile and adult fishes in the latter system. The Kowie Estuary may be larger, deeper and possess a wider variety of habitats (e.g. extensive *Zostera* beds) than the Great Fish, but a key element in supporting the higher fish densities per unit area appears to be the elevated perennial river flow entering the Great Fish system (Whitfield et al. 1994).

An aspect that has, until recently, been ignored in a southern African context is the contribution of rivers and estuaries to nutrient supplementation and productivity of the marine environment. Increasing evidence is accumulating that estuaries on the southeast African coast make an important contribution to the cohort strength of many marine fish species (A.D. Connell pers comm.), some of which do not utilize estuaries as nursery areas. The possible significance of catchment run-off into oligotrophic, nutrient poor coastal systems is finally being recognised and given the research attention that it should have received decades ago.

4 River flow reduction and estuary responses

Estuarine responses to changing river flows will be strongly influenced by estuary type. In a southern African context five major types of estuaries (Table 3) have been recognised (Whitfield 1992). What are the likely impacts of freshwater deprivation on each of the estuarine types and what are the potential impacts on these systems and their biota?

4.1 Permanently open estuaries

Less than 50 South African estuaries maintain permanent tidal inlets with the sea (Reddering and Rust 1990) and it is these large systems that are most threatened by reduced freshwater inputs. The extent to which river water is impounded varies, but in some catchments the combined capacity of existing impoundments already exceeds the mean annual runoff of the river system. In the Kromme system, for example, the mean annual catchment run-off is 105×10^6 m^3, with the combined capacity of the Churchill and Mpofu dams being 133×10^6 m^3 (Bickerton and Pierce 1988). Large episodic floods (>80×10^6 m^3) will probably flow over the walls of these impoundments, depending on water volumes held at the time of the flood. However, smaller floods do not appear to reach the Kromme Estuary, with a resultant loss of nutrient inputs and scouring action within the system (Emmerson and Erasmus 1987). In addition, segmentation of catchment rivers by dam walls has major deleterious consequences for the migrations and population sizes of anguillid eels and other diadromous fish species (Bruton et al. 1987).

According to Bennett (1994) there has been an upstream penetration of seawater into the Berg Estuary as a result of the 30% loss in annual river flow. This has led to the polyhaline zone being reduced in size and has caused changes in species composition among benthic invertebrates and declines in the commercial gill net catches of fishes within the estuary. Reduced river flow also leads to a reduction in the size of the river-estuary interface (REI) zone, thus limiting the available nursery area for certain marine fish species such as the sciaenid *Argyrosomus japonicus* (Whitfield and Wood 2003).

The prevailing water column mixing process in permanently open estuaries is tidally and riverine driven, and mean salinities usually fluctuate between 15‰ and 35‰ (Table 3) with oligohaline conditions often present at the head of these estuaries and euhaline conditions in the mouth region. However, where major impoundments prevent base flows from entering these systems, tidal mixing processes become dominant and temporarily change the estuary into an "arm" of the sea

Table 3. Some general characteristics of southern African estuarine systems (modified from Whitfield 1992).

System type	Riverine/marine balance	Spring tidal prism	Mixing process	Mean salinity (‰)
Estuarine bay	Marine dominance	Large (>10 × 10^6 m^3)	Mainly tidal	25–35
Permanently open estuary	Marine dominance	Moderate (1–10 × 10^6 m^3)	Tidal/Riverine	15–40
River mouth	Riverine dominance	Small (<1 × 10^6 m^3)	Riverine	1–15
Estuarine lake	Variable	Negligible (<0.1 × 10^6 m^3)	Wind	1 – >35
Intermittently open estuary	Variable	Absent when closed	Wind	1 – >35

(Allanson and Read 1995). Hypersaline conditions (>40‰), particularly during summer, have been recorded in the upper reaches of certain permanently open estuaries deprived of freshwater inflow e.g. Kromme, Bushmans and Kariega systems (Allanson and Read 1987). Certain freshwater fish species that may have penetrated the REI zone under normal circumstances are therefore excluded from these estuaries (Whitfield and Paterson 2003).

Oligohaline conditions (<5‰) in the upper reaches of permanently open estuaries can extend into the middle and lower reaches for brief periods during major river floods, and may even cause extensive mortalities of the biota in these regions (McLachlan and Grindley 1974; Whitfield and Paterson 1995). However, these extreme low salinity events will probably become less common and of shorter duration as more dams are built in the catchments, with an increasing proportion of river floods being captured by these impoundments.

Further results of reduced flood events in permanently open estuaries, particularly those along the Eastern Cape coast, could take the form of an increase in the size of sand shoals situated in the lower reaches and a greater degree of mud compaction in the middle and upper reaches (Reddering 1988). These modifications have two main effects. Firstly, disproportionately large flood-tidal deltas tend to constrict the channel of the lower estuary. This reduces tidal exchange between the sea and the estuary, and consequently the tidal prism, coupled with a reduced freshwater scouring action, cannot maintain an open tidal inlet as before. Secondly, when a river flood does occur, the amount of accumulated sediment in the delta would be larger than normal and would require a flood of greater magnitude to remove the increased amount of sediment. In the case of muddy estuaries, or sections of an estuary where mud is the dominant sediment, these substrata would attain a higher degree of erosion resistance. As an overall result, smaller estuary channel dimensions are established under prolonged conditions of reduced freshwater inflow (Reddering 1988). Shallowing of an estuary channel may limit the entry of large fish into an estuary, and closure of a previously permanently open system will result in the fish assemblage undergoing major structural and functional changes (Vorwerk et al. 2003).

The biota of permanently open estuaries in the Eastern Cape Province undergo several important changes following significant long-term reductions in riverine input (Baird and Heymans 1996). Primary food resources in the water column (e.g. phytoplankton) decline (Grange and Allanson 1995) while macrophyte production increases due to the spread of marine plants such as *Zostera capensis* (Adams and Talbot 1992). Loss of planktonic production will reduce zooplanktivorous fish stocks such as *Gilchristella aestuaria* (Whitfield and Harrison 1996) and expansion of seagrass beds will favour macrophyte associated marine fish species such as *Rhabdosargus holubi* (Hanekom and Baird 1984). Zooplankton abundance declines in association with reduced sestonic food availability and the estuary is left with a predominantly zoobenthic driven food web. Baird and Heymans (1996) concluded that reduced freshwater supplies have changed the Kromme Estuary from a plankton-dominated system to one driven by submerged benthic vegetation. This conclusion is reinforced by stable carbon isotope information from the freshwater deprived Kariega Estuary, which showed that phytoplankton is relatively unimportant to the fish assemblage of this system (Paterson and Whitfield 1997).

The positive effect of freshwater inflow on phytoplankton biomass usually involves two processes; firstly, the development of vertical stratification creates hydrodynamically more stable conditions that retain phytoplankton inside the estuary and favour the formation of blooms (Hilmer and Bate 1991). Secondly, the bulk of inorganic nutrients in the estuarine water column are allochthonous, and increases in river flow result in an increase in nutrient availability to estuarine primary producers (Allanson and Winter 1999). Increased phytoplankton productivity is usually reflected in a higher zooplankton biomass (Wooldridge 1999) which, in turn, is able to support increased fish stocks when compared to those estuaries where pelagic productivity is low (Strydom et al. 2002).

4.2 Intermittently open estuaries

Most of these systems have small river catchments (< 500 km^2) and extended periods when the river flow is minimal or even ceases altogether (Whitfield 1992). The magnitude of river flow into some of these estuaries has declined considerably in recent years as a result of the growing number of farm dams that retain increasing proportions of freshwater flow from the catchments. The effect of farm dams is most noticeable during and after prolonged periods of drought and at the beginning of the rainy season.

Large amounts of sediment, which accumulate during the lagoonal phase (Cooper 1989), are removed from temporarily open estuaries during river flooding (Reddering and Esterhuysen 1987). Since mouth opening and closing of the above systems is directly linked to the amount of runoff feeding the inflowing rivers, impoundments within the catchment can have a major influence on the duration of the estuarine open and closed phases. Reduced river inflow will lead to prolonged mouth closure and a shorter open phase, thus inhibiting invertebrate and fish migrations between the estuary and the sea (Forbes and Benfield 1986; Kok and Whitfield 1986; Wooldridge 1991). If the link with the sea is permanently broken then the marine species eventually disappear and only a few estuarine and freshwater taxa remain within the previous estuary (Sinclair et al. 1986).

In addition to influencing mouth phase, freshwater deprivation during droughts can also lead to hypersaline conditions (>60‰) developing within closed systems, resulting in the loss of major components of the food web. Whitfield (1989) documented an extensive fish kill in the Seekoei estuarine lagoon (salinity 98‰), whereas no fish kill was recorded in the adjacent Kabeljous system (salinity 55‰). The Seekoei catchment, which is similar in size to the Kabeljous catchment, has more farm dams than the latter system. The inference here is that abstraction of fresh water from the Seekoei catchment during the 1988/89 drought was sufficient to elevate hypersaline conditions in this estuary, thereby resulting in the loss of a high proportion of the aquatic biota.

4.3 Estuarine lakes

Most estuarine lakes in southern Africa evolved from drowned river valleys (Hill 1975) that were filled in by sediments to varying degrees and are now separated from the sea by vegetated sand dune systems. In some instances (e.g. Lake Sibaya) the dune barrier has completely isolated the lake, which then loses its estuarine character and is referred to simply as a coastal lake (Whitfield 1992). The transformation of estuarine lakes into coastal lakes may be accelerated if reductions in freshwater supplies to these systems are of sufficient magnitude and duration.

Salinities in estuarine lakes are highly variable and depend on a variety of factors, the most important of which is the balance between freshwater input, evaporation, and water exchange across the mouth. Salinity variations in the St Lucia system can range from less than 5‰ to more than 100‰ (Millard and Broekhuysen 1970). Although salinity extremes have always been a natural feature of Lake St Lucia, the magnitude of the salinity peaks in recent decades has increased following increased freshwater abstraction from the catchment basin (Hutchison 1977). Unless Mfolosi River connections can be re-established with the St Lucia Estuary, the amplitude and temporal scale of the salinity fluctuations within this lakes system are likely to increase in the future, i.e. hypersaline conditions will be higher and last longer than under natural conditions. The adverse impact of salinities above 50‰ on the fauna and flora of Lake St Lucia has been well documented (Boltt 1975; Wallace 1975; Whitfield 1977), and management strategies aimed at reducing the magnitude of future hypersaline conditions are being investigated.

Reduced freshwater supplies to Western Cape Province estuarine lakes such as Swartvlei and Botriviervlei are unlikely to cause hypersaline conditions but could result in prolonged mouth closure. These conditions favour estuarine animal species which can complete their life cycle in brackish waters, but would result in a decline in marine dependent invertebrate and fish populations due to natural mortality and a breakdown in recruitment processes (Bennett et al. 1985; Wooldridge 1991). An extreme version of this scenario is illustrated by the loss of marine fish species from Groenvlei, an isolated coastal lake in the warm temperate region where estuarine species still occur (Ratte 1989). Similarly, subtropical Lake Sibaya was once an estuary that contained the full spectrum of marine, estuarine and freshwater species. With the loss of its major river system, Sibaya became a coastal lake that retained only a relict estuarine fauna and became dominated by freshwater taxa (Allanson et al. 1966). Long-term reductions in river flow would also lead to reduced nutrient inputs, with concomitant declines in pelagic primary production within already oligotrophic lake systems such as Swartvlei (Robarts 1976; Howard-Williams 1977).

4.4 Estuarine bays

Increased freshwater abstraction from inflowing rivers would result in an increase in salinities in the upper reaches of these systems, but little change would be recorded in the lower reaches and middle due to strong tidal exchange patterns (Largier et al. 2000). Water temperatures in the lower and middle reaches are primarily influenced by the sea due to the relatively large tidal prism (Table 3) and this influence would extend further up the estuary if river flow declined or ceased altogether.

The loss of riverine nutrient and organic inputs may have a profound effect on the productivity of estuarine bays, especially the planktonic food web in the upper reaches of these systems. However, little impact is likely in the lower reaches where, apart from major river pulses, allochthonous nutrient and organic exchanges are mostly dominated by the sea (Allanson et al. 2000; Russell 1996). Similarly, the ichthyoplankton in the lower reaches of estuarine bays is also dominated by marine taxa (Harris and Cyrus 1999), with many of these species having little or no association with estuaries or riverine inputs into these systems.

The fauna and flora of estuarine bays tend to be dominated by marine species (Day and Morgans 1956), some of which are not recorded in other types of estuaries. The more stenohaline marine taxa are unlikely to be adversely affected by a reduction in freshwater input and may even be able to extend their distribution further up the bay under such conditions. However, loss of river flow into an estuarine bay would have a negative impact on oligohaline and migratory species (e.g. freshwater prawns *Macrobrachium* spp. and the freshwater mullet *Myxus capensis*) which use the riverine portions of estuaries when available (Bok 1979; Reavell and Cyrus 1989).

4.5 River mouths

Freshwater deprivation in these systems would lead to marine conditions extending higher up the estuary, provided the mouth remained open. If the estuary mouth closed, oligohaline conditions are likely to prevail behind the sand bar during the lagoonal phase, depending on overtopping events during mouth closure (Begg 1978).

A task group was set up in 1989 to assess the water requirements of the Orange (Gariep) River Estuary. This task group found that more than 20×10^6 m^3 of fresh water per month would be required to maintain a permanently open estuary mouth and that less than 4×10^6 m^3 per month would result in closure of the mouth (Prins 1990). A similar conclusion was reached for the Thukela Estuary where flows above 25×10^6 m^3 per month would ensure a permanently open mouth condition, with regular closure occurring at flows below 13×10^6 m^3 per month (Huizinga and van Niekerk 1997).

Freshwater and estuarine species tend to dominate the biota of river mouths. Marine and estuarine organisms are usually confined to the lower reaches (Brown 1958), extending upstream during periods of reduced freshwater input. In general, river mouths have a relatively depauperate aquatic biota both in terms of biodiversity and biomass (Day 1981a). Under high river flow conditions the estuarine zone may even be pushed out to sea, thus limiting the usefulness of this type of system to estuary associated organisms.

A reduction in river flow is probably beneficial to both estuarine and marine fish species in these systems. This would apply particularly if the mouth remained open during low flow conditions and salinities within the estuary increased. In the Thukela Estuary there was an inverse relationship between the CPUE of fishes within the system and river flow, i.e. highest fish densities were recorded when river flow was lowest and vice versa (Whitfield and Harrison 2003). Similarly, there is recent evidence (S.J. Lamberth pers. comm.) of increasing marine and estuarine fish diversity and abundance in the Orange (Gariep) River Estuary as a result of reduced river flow, when compared to the earlier surveys conducted by Brown (1958) under more pristine river catchment conditions.

Closure of river mouth type estuaries would result in a temporary increase in water surface area and volume (Cooper 1993). These conditions would be beneficial to those fishes which had already migrated into the system prior to mouth closure. The increased residence time of waters within the estuary would probably also give rise to increased levels of phytoplankton production which would benefit the zooplanktonic component in particular. Prolonged mouth closure, in the absence of regular marine overtopping of the bar, would normally lead to oligohaline conditions which may result in osmoregulatory stress for certain marine fish species trapped within the lagoon. However, most river mouth estuaries are small water bodies relative to the size of their catchments (Whitfield 1992), so even under very low river flow conditions the closed phase is likely to be of short duration.

5 Salinities and fishes

The most essential adaptation by fish that enter estuarine systems is an ability to adjust to changes in salinity (Panikkar 1960). The change may be gradual, as normally occurs in a temporarily closed estuary, or sudden, as often takes place in tidal estuaries. The magnitude of the change in salinity depends mainly upon the balance between freshwater inflow and the tidal regime, with evaporation playing a major role in lacustrine systems with a high surface area to volume ratio (Hutchison and Midgley 1978). Although this review focuses on the southern African situation, global studies have also shown that salinity can be a primary factor in the structuring of estuarine fish assemblages (e.g. Barletta et al. 2005).

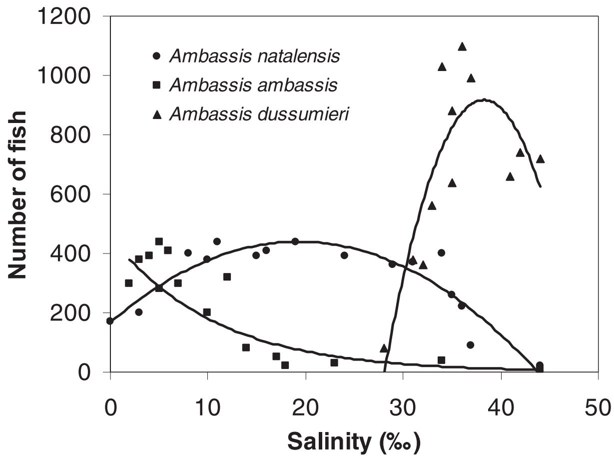

Fig. 1. Numerical abundance of seine netted *Ambassis* spp. in relation to the salinity at collecting sites (after Martin 1988).

Salinity preferences and tolerances of fishes differ both between species and at different life stages of the same species. A southern African example of how salinity preferences differ within the ambassids is shown in Fig. 1 (Martin 1988). Numerous examples also exist of 0+ marine juveniles of certain species (e.g. *Argyrosomus japonicus*, *Caranx sexfasciatus* and *Pomadasys commersonnii*) being attracted to the low salinity headwaters of permanently open estuaries, whereas the older juveniles and adults of the same species are common only in the lower and middle reaches of the same estuaries (Ter Morshuizen et al. 1997). These differential preferences may also extend to differential tolerances of extreme salinities and therefore account for the apparent absence of 0+ juveniles when recording fish mortality events attributed to low salinity.

A characteristic of many fish species entering southern African estuaries is an ability to adapt to both low and high salinity regimes, although it is noteworthy that less than 25 species have their upper recorded limits above 65‰, whereas more than 85 species can survive in water with a salinity of <5‰ (Whitfield 1998). Similarly, only 8 fish species in Lagune Madre (Gulf of Mexico, Texas) were recorded in salinities above 65‰, whereas 15 taxa (including the 8 hypersaline tolerant species) were recorded in salinities below 5‰ (Hedgpeth 1967). Fishes are therefore more tolerant of low rather than high salinity conditions (Whitfield et al. 1981) and this adaptability to low salinities is important in a southern African context since most estuaries are subject to periods of freshwater flooding whereas salinities seldom rise above sea water except in Lake St Lucia and a few temperate systems to the south (Day 1981b). Furthermore, the closure of estuaries is usually associated with declining salinities, and only fishes tolerating these conditions are able to utilize the rich food resources available within these systems (Harrison and Whitfield 1995).

A few southern African freshwater teleosts have developed hypotonic regulation but most species are incapable of this adaptation and are therefore excluded from estuaries. Only eight freshwater species are occasionally recorded in saline waters and, of these, only the cichlid *Oreochromis mossambicus* may be classified as truly euryhaline (Whitfield 1998).

O. mossambicus were abundant in Lake St Lucia during hypersaline conditions and were even recorded in areas where the salinity exceeded 100‰ (Wallace 1975). Freshwater species such as *Clarias gariepinus* often undergo mass mortalities in Lake St Lucia when exposed to increased salinity (>10‰) arising from wind-induced seiches entering inflowing rivers, or being washed into high salinity waters by sudden flooding of the rivers into the lake (Blaber 1981).

The shark *Carcharinus leucas*, stingray *Himantura uarnak* and sawfish *Pristis zijsron* have all been recorded in estuarine waters with a salinity <3‰ (Whitfield et al. 1981). *C. leucas* has also been regularly netted at Lake St Lucia in salinities up to 47‰ by Bass et al. (1973). Large numbers of the spotted ragged-tooth shark *Carcharias taurus* move into the euhaline Kariega Estuary, especially during coastal upwelling events. In addition, Paterson (1995) recorded juveniles and adults of the electric ray *Torpedo fuscomaculata* and stingray *Dasyatis chrysonota* in the lower half of this estuary. None of these species have been recorded in the Kariega system under mesohaline conditions (<18‰).

Most South African marine fish species associated with estuaries are strong osmoregulators, capable of surviving under both oligohaline and hypersaline conditions. Apart from a few species that have been tested (Blaber 1973), the prevalence of euryhalinity within marine fish taxa is largely unknown. However, of the approximately 1200 marine species found in northern KwaZulu-Natal coastal waters, only about 200 (17%) have been recorded entering estuaries in the region (Whitfield 1980). Fewer than 50 of these species are common in estuaries within the region, with the implication that less than 5% of all coastal marine fishes use estuaries to any great extent.

Do salinity ranges within coastal systems limit the use of estuaries by marine fish? Observations from the Kariega and other estuaries in the Eastern Cape Province suggest that some stenohaline marine species do penetrate estuaries which have limited freshwater input, but that these taxa are poorly represented and usually confined to the mouth region or lower reaches (Ter Morshuizen and Whitfield 1994). Conversely, several euryhaline marine fish species sometimes penetrate considerable distances up the rivers of southern Africa. Pooley (1975) recorded *Acanthopagrus berda* and *Mugil cephalus* on the Phongolo floodplain approximately 100 km from the sea, and Bok (1979) found both *Myxus capensis* and *Mugil cephalus* 120 km upstream from the head of the Gamtoos Estuary. In the Great Fish system, marine species tend to dominate the fish assemblage immediately above the ebb and flow region (Fig. 2). The relatively high conductivity of catchment flows, and presence of marine fishes in the lower portions of the above river system, suggests that dissolved salts of terrestrial origin may be important in reducing osmoregulatory stress for these temporary riverine residents. However, during flooding the conductivity of the river water declines and marine fish species decrease in both diversity and abundance above the head of the estuary (Ter Morshuizen et al. 1996).

Both species composition and abundance seem to respond to temporal salinity changes. Research in Lake St Lucia has shown that between 10‰ and 80‰ there is an inverse relationship between salinity and numbers of fish species (Fig. 3). Abundance is also affected, with gill net catch rates

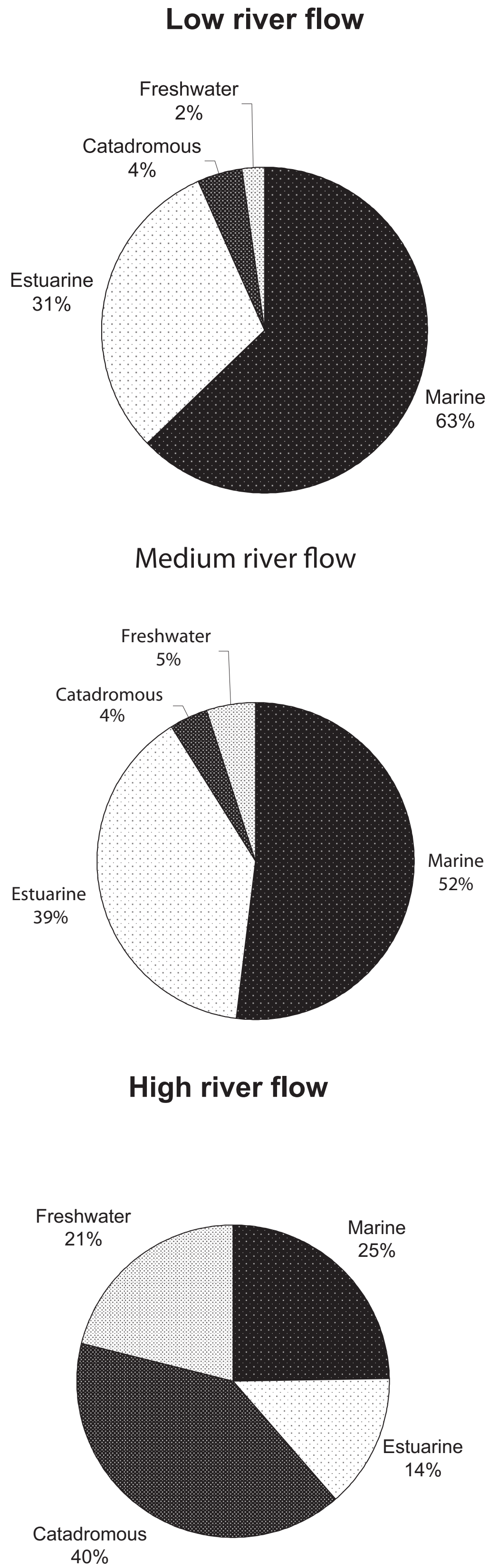

Fig. 2. Fish catch composition above the headwaters of the Great Fish Estuary under conditions of low (<10×10^6 m^3 $month^{-1}$), medium (10–20×10^6 m^3 $month^{-1}$) and high (>20×10^6 m^3 $month^{-1}$) riverine flow (after Ter Morshuizen et al. 1996).

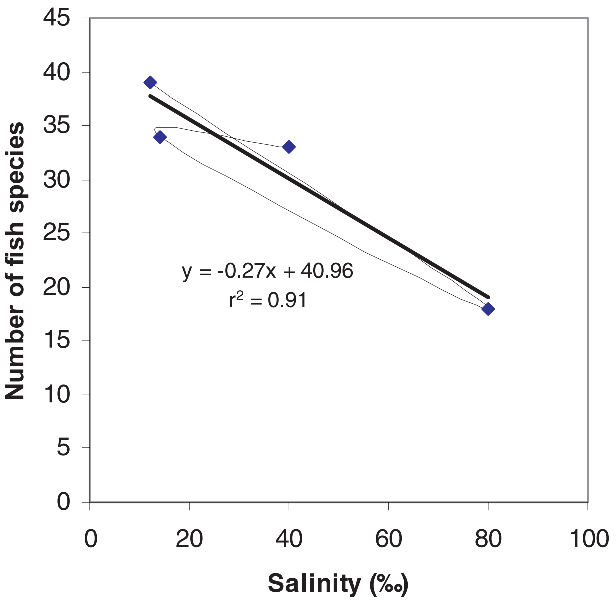

Fig. 3. Numbers of fish species recorded in northern Lake St Lucia under different salinity regimes (data from van der Elst et al. 1976).

at <20‰ being double those when salinities exceeded 50‰ (van der Elst et al. 1976). These results are supported by Mann et al. (2002) who found an inverse relationship between anglers CPUE and lake salinities (Fig. 4).

Although the lower gill net and angler catches during the hypersaline period could have been due to osmoregulatory stress forcing particular fish taxa out of the area, the disappearance of certain food resources (Boltt 1975) may also have played a role in reducing fish abundance. According to Forbes and Cyrus (1993) piscivores, zooplanktivores, zoobenthivores and detritivores were all represented under both low and high salinity conditions in Lake St Lucia. However, the normally abundant *Pomadasys commersonnii* and *Rhabdosargus sarba*, captured in areas where the salinity was in excess of 70‰, were no longer feeding on normal molluscan and crustacean prey but were consuming filamentous algae (Wallace 1975).

Prolonged closure of an estuary, in association with dilution of lagoonal waters from catchment rivers, can cause osmoregulatory stress in many marine fish species (Bennett 1985). However, estuarine spawners appear to be more tolerant of prolonged oligohaline conditions, with all species recorded in salinities below 10‰ and most also occurring in fresh water (Whitfield 1998). In contrast to marine taxa, the estuarine group does not appear well adapted to hypersaline conditions, with only *G. aestuaria* being recorded in salinities above 60‰ (Whitfield et al. 1981). Although the eggs and larvae of estuary associated species are found under both oligohaline and euhaline conditions, it would appear that the eggs of many marine taxa such as *Mugil cephalus* cannot survive low salinity waters (Sylvester et al. 1975) but the fry of these species are attracted to brackish regions of estuaries (Mires et al. 1974).

Detailed information on the salinity tolerance of fishes on the subcontinent is limited to a few species (Blaber 1973). Field records on the occurrence of fishes in different salinities are extensive and indicate that not all species utilizing estuaries are adapted to the same extent (Whitfield 1998). This would account for the fact that selected fish species are recorded during mass mortalities on certain occasions but absent at others. However, when fish kills are documented there are usually a large number of species recorded simultaneously, especially at extremely low or high salinities (Bennett 1985; Kyle 1989; Whitfield 1995a). Single species mortalities under extreme salinity regimes have not been recorded but there have been instances in the St Lucia system where different groups of species succumbed at different stages of hypersaline development (R.H. Taylor, pers. comm.).

Most mass mortalities of fish in southern African estuaries are associated with a combination of low salinities (<3‰) and low water temperatures (<14 °C). More than 100 000 fish belonging to at least 11 species were recorded dying in subtropical Lake St Lucia during June 1976, when the salinity declined below 3‰ and the temperature dropped to 12 °C (Blaber and Whitfield 1976). Although the lake (surface area ±325 km^2) is linked to the sea by a 20 km long winding channel, the relatively uniform salinity conditions prevailing over the entire system may have prevented the marine fish species from returning to sea before critical conditions developed. A similar mortality of marine fishes has been recorded in the nearby Kosi lakes system where low salinities combined with abnormally low winter temperatures (Kyle 1989).

Examination of dead and dying fish in Lake St Lucia during the winter of 1976 revealed skin lesions and haemorrhaging over large areas of the body, although most commonly encountered around the caudal peduncle, fin bases, opercula and mouth (Blaber and Whitfield 1976). The large mortality was probably due to either a lethal combination of low salinities and sudden low temperature leading to osmoregulatory failure, or to fungal infection of the skin lesions that usually follows severe osmoregulatory stress. The disorientation behaviour shown by dying fish in the lake is symptomatic of osmoregulatory failure recorded in *Rhabdosargus holubi* (Blaber 1974), and the development of skin lesions under freshwater conditions has also been documented in *Lithognathus lithognathus* (Mehl 1973).

Mass mortalities have also been recorded in the warm-temperate Botriviervlei. Salinity concentrations in the lake declined to 2–3‰ and the temperature was less than 18 °C when at least 7000 fish belonging to nine species died in the system (Bennett 1985). Indications that the marine ichthyofauna was attempting to avoid the lowest salinities is provided by the fact that most dead fish were found in the southern areas of the estuary where salinity readings were highest (3‰). It should be emphasized that the marine fish killed in October 1981 had survived salinities less than 8‰ for four months, and 3‰ for at least two weeks prior to the mortality. If the duration of exposure had been shorter, or the water temperature higher, these species might not have succumbed. Another factor which may have played a role was the age of the fish. All the fish that died in the Bot system were estimated to be older than three years, indicating that juveniles may be more tolerant of low salinities than subadult and adult fish (Bennett 1985).

Mass mortalities under hypersaline conditions appear to be less frequent than under oligohaline conditions, and such kills usually occur when fish are trapped in an estuary that lacks freshwater inflow for prolonged periods. During April

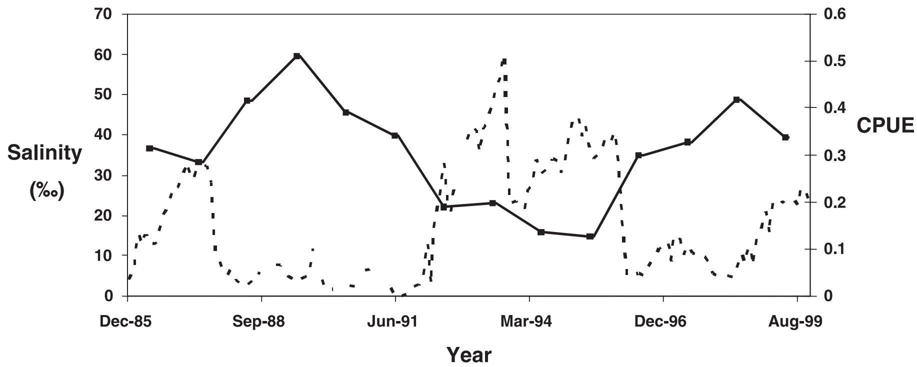

Fig. 4. Total catch per unit effort (fish per angler per hour) of all angling fish species in South and North Lake combined (solid line) versus the averaged salinity (dashed line) measured in these compartments (data from Mann et al. 2002).

1989, the temporarily closed Seekoei Estuary on the Eastern Cape coast experienced salinities above 90‰ as a result of a protracted drought and excessive freshwater abstraction by farmers in the catchment. More than 6000 juvenile and adult fish, belonging to at least 11 species (comprising both marine and estuarine taxa), were recorded dying in the estuary (Whitfield 1989). In contrast to the above mass mortalities, Wallace (1975) documented the fish fauna in the St Lucia system under salinities ranging from 60‰ to 110‰. He recorded very few dead fish at these salinities and suggested that the lower species diversity in the most hypersaline regions was indicative of a movement towards lower salinity areas in the south of the system before critical levels were reached. However, during October and November 2003 extensive mass mortalities of marine fish species were recorded in the St Lucia system when drought conditions resulted in some lake compartments experiencing salinities in excess of 70‰ (R.H. Taylor pers. comm.). The ichthyofauna was unable to avoid the extreme hypersaline conditions because evaporative declines in the lake water level had compartmentalised the system, effectively cutting off any potential escape routes.

6 River flow and fish responses

Variations in the position of the salt wedge and salinity stratification within estuaries is directly related to freshwater inputs (Read 1983; Schumann and Pearce 1997). Changing salinity attributes within the water column, which is usually directly or indirectly linked to river flow, can have major implications for the distribution and abundance of both fishes and their food resources in estuaries (Bennett 1994; Read 1985; Schlacher and Wooldridge 1996b).

River flow into estuaries influences not only the salinity but also the biochemical properties of the water body, including the introduction of catchment olfactory cues to both the estuary and adjacent ocean. Fishes have a highly developed sense of smell (Hara 1992) and it is possible that olfactory cues guide the larvae of species such as the longfin eel *Anguilla mossambica* up estuaries and into the river catchments. Olfactory cues, which can be of freshwater or estuarine origin (Stabell 1992), may also act as a guide to marine larvae and 0+ juveniles that are attempting to locate estuarine nursery areas (N.C. James et al. in prep.). Indirect evidence to possibly support this view

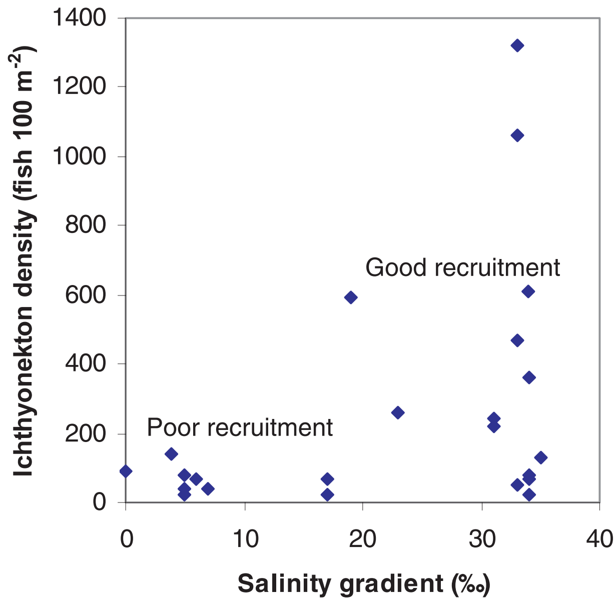

Fig. 5. Relationship between longitudinal salinity gradient, which is the difference in mean salinity between the tidal head and mouth of an estuary, and postflexion marine fish recruits in three permanently open estuaries along the Eastern Cape coast (modified from Whitfield 1994).

is provided by the high densities of estuary associated marine fish larvae in the surf zone that were attracted to plumes of river water leaving the Kabeljous Estuary in the Eastern Cape Province (Strydom 2003).

Permanently open Eastern Cape estuaries with longitudinal salinity gradients greater than 19‰ have considerably higher densities of 0+ juvenile marine fishes (Fig. 5) than those systems where salinity gradients are small or absent (Whitfield 1994). A similar finding was arrived at by Martin et al. (1992) who found that the densities of postlarval marine migrants in the St Lucia Estuary increased markedly following an episodic flushing of the system. Although the inference from the above studies is that the salinity gradients are the attractant for these 0+ juvenile fishes, it is more likely that the increased amounts of olfactory cues that are exported to the marine environment on each ebb tide are vital to the recruitment process.

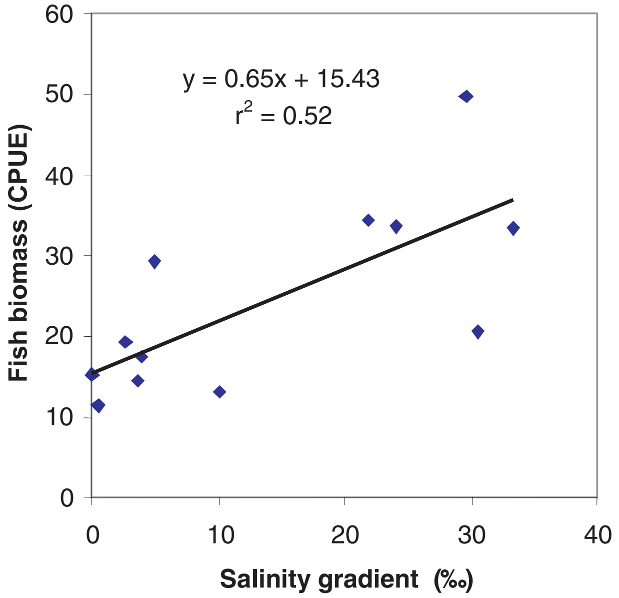

Fig. 6. Relationship between longitudinal salinity gradient, which is the difference in mean salinity between the tidal head and mouth of an estuary, and gill net fish biomass (CPUE) in a range of permanently open estuaries along the warm temperate Eastern Cape coast (data from Marais 1988).

If river flow is related to the magnitude of marine fish recruitment, then an estuary receiving a higher river flow will need to be able to support greater fish populations than an equivalent system with a low freshwater input. The work of Bate et al. (2002) has shown that the river-estuary interface (REI) in permanently open Eastern Cape Province estuaries is a highly productive zone and an important nursery area for several marine fish species (Ter Morshuizen et al. 1997). Since the size of the REI zone is dependent on the relative volume of freshwater entering the estuary, a high river flow will result in a large REI zone (Whitfield and Wood 2003). Conversely, loss of river flow can lead to an elimination of this zone with major deleterious consequences for the ability of the estuary to support large numbers of juvenile fishes, including the loss of certain marine species (Whitfield and Paterson 2003).

Indications are that estuaries with strong riverine inputs are also attractive to subadult and adult marine immigrants because data presented by Marais (1988) shows that gill net catches in Eastern Cape estuaries are positively correlated with increasing longitudinal salinity gradients (Fig. 6). Marais (1988) determined that in the Eastern Cape Province there was a highly significant positive correlation ($r = 0.46$, $p < 0.001$) between estuarine fish abundance and catchment size, as well as between overall fish biomass and catchment area ($r = 0.59$, $p < 0.001$). He suggested that it was not the actual catchment size that influenced fish stocks, but rather the hydrological consequences of increased river inflow with increasing catchment area. The higher run-off from larger catchments almost invariably leads to positive estuarine salinity gradients and increased water turbidity, both of which are often associated with increased nutrient inputs (Scharler 2000) and high fish abundance (Whitfield et al. 1994).

A factor not included in the Marais (1988) analysis is the tendency towards higher nutrient and organic matter loading of estuaries with larger catchments, and hence the potential for elevated primary and secondary productivity within these systems. Another possible factor accounting for the positive correlation between fish abundance and catchment size in Eastern Cape estuaries is the magnitude of olfactory cues entering the marine environment. Large perennial rivers are going to transmit greater volumes of land based cues to potential marine fish recruits, when compared to small seasonally flowing systems. However, river mouth type estuaries in other parts of the country also deliver large volumes of water to the marine environment yet these systems often have a depauperate fish fauna. This situation is probably linked to the oligohaline estuarine conditions in river mouths as well as a lack of pelagic and benthic food resources caused by limited water resident times within the estuary and highly mobile sediments.

River pulses also seem important in influencing the abundance of estuarine spawners. Whitfield and Wooldridge (1994) have described the cascading effect freshwater pulses have on southern African ecosystems, primarily through the stimulation of the planktonic food web. Martin et al. (1992) recorded considerably higher abundances of virtually all estuarine resident species following the flushing of the St Lucia Estuary. They found that an order of magnitude increase in the abundance of the clupeid *Gilchristella aestuaria* could be indirectly linked to the phytoplankton bloom and increased zooplankton stocks that followed the flooding. Conversely, the decimation of the rare estuarine pipefish *Syngnathus watermeyeri* has been attributed to the indirect effect freshwater deprivation has had on the three Eastern Cape estuaries where this endemic species had previously been recorded (Whitfield 1995b).

Despite the positive effects of frequent minor freshwater pulses, river flooding into estuarine systems can result in a temporary depletion of both marine and estuarine fish species (Marais 1983). In both the Great Fish and Thukela estuaries there was an apparent decline in ichthyofaunal abundance under high river flow conditions (Ter Morshuizen et al. 1996; Whitfield and Harrison 2003). This decline (Fig. 7) can be attributed to both direct physiological stress to the biota (Hill 1981) and a temporary reduction in estuarine food resources, mostly linked to impacts on the zoobenthos and zooplankton stocks (Grindley 1964; Hanekom 1989). The ichthyoplankton of estuarine spawners is similarly influenced by river flooding (Fig. 8), with large numbers of pelagic larvae being swept out sea under such conditions (Strydom et al. 2002).

River floods carrying high suspensoid loads can be lethal to both marine migrant and estuarine resident fish species. Whitfield and Paterson (1995) recorded extensive mortalities of both groups of fishes in the Sundays Estuary following a major flash flood. Although the suspended silt resulted in a clogging of the gills of fishes which died in the mass mortality, it is also plausible that reduced oxygen levels associated with the floodwaters contributed to the asphyxiation of fishes in this estuary.

The morphology of an estuary may also influence the response of certain fish taxa to major flooding events. Marais (1982) found that densities of Mugilidae increased in the broad Swartkops Estuary after river floods but decreased markedly

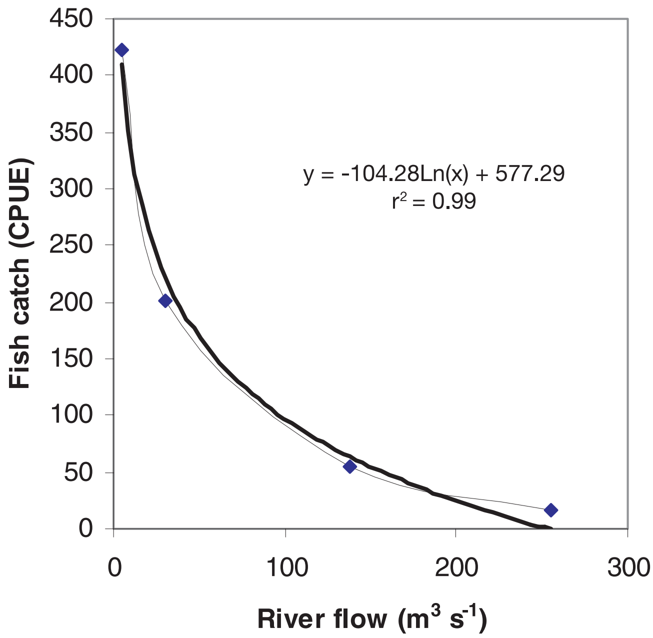

Fig. 7. Seine net fish catches in the Thukela Estuary under four different river flow regimes (after Whitfield and Harrison 2003).

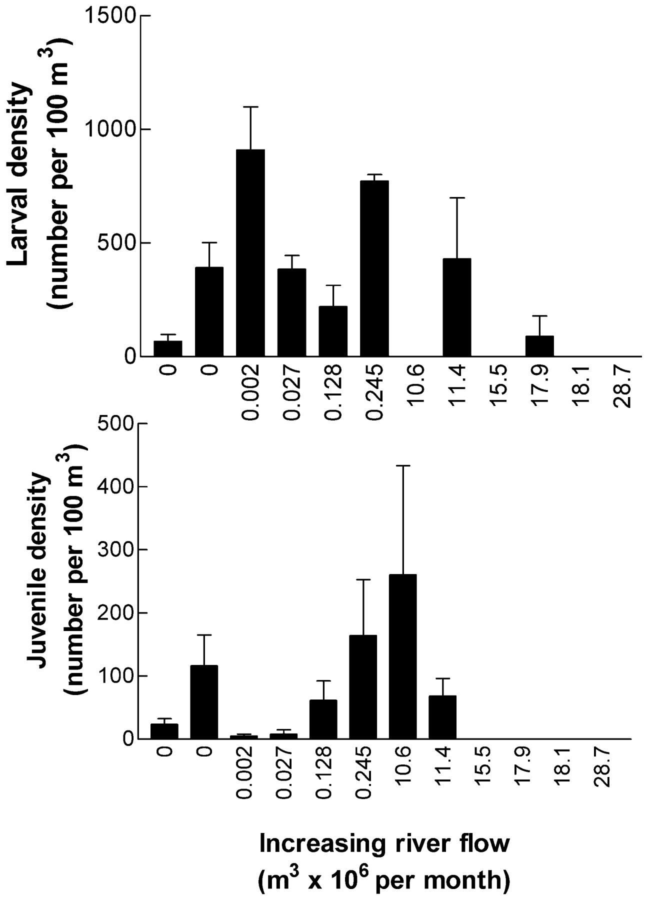

Fig. 8. Densities (mean ±SD) of estuary spawned *Gilchristella aestuaria* (Clupeidae) larvae and juveniles under different river flow regimes in the Kariega and Great Fish estuaries (data from Strydom et al. 2002).

in the channel-like Sundays Estuary. He postulated that the organic rich mud and silt that was deposited in the floodplain-like middle and lower reaches of the Swartkops Estuary acted as a food source for the mugilid species, whereas the rich epibenthic layer in the Sundays Estuary was washed away by heavy floods.

7 Conclusion

The biotic and abiotic factors that determine the distribution and abundance of fishes in southern African estuaries are strongly driven by riverine inputs. Freshwater flows interact directly and indirectly with the fishes that inhabit estuaries, e.g. river floods directly influence estuarine morphometry, water temperature, salinity, pH, turbidity, nutrient status, organic inputs, dissolved oxygen concentrations and olfactory cues; and indirectly affect mouth status, tidal prism, habitat diversity, primary and secondary productivity, fish recruitment, food availability and competition.

Previous estuary associated fish studies, particularly those which have been laboratory based, have tended to examine the effects of one or two environmental factors in isolation, e.g. salinity and temperature. However, with the realisation that multiple factors impinge on the lives of fishes in estuaries, research emphasis is now moving away from attempting to determine the influence of isolated physico-chemical variables and adopting a more holistic approach.

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