Fishes and salinities in the St Lucia estuarine system—a review

Alan K. Whitfield · Ricky H. Taylor · Caroline Fox · Digby P. Cyrus

Abstract   The recorded salinity ranges of freshwater, estuarine and marine fish species in Lake St Lucia, a Ramsar and World Heritage Site, are documented. The freshwater group is most diverse and abundant under oligohaline conditions, although the Mozambique tilapia (*Oreochromis mossambicus*) was common under all salinity regimes. Estuary resident species also favoured oligohaline conditions but, in contrast to the freshwater taxa, were well represented in salinities up to 40 ‰. The marine group was most diverse and abundant within the salinity range 10–40 ‰, but a large number of species could also be found in salinities up to 70 ‰. Very few fish species were able to tolerate salinities between 70 ‰ and 110 ‰, with only *O. mossambicus* surviving for extended periods in salinities above 110 ‰. All the aquatic macrophytes and most of the zoobenthos within the lake appear to die out within the salinity range of 50–60 ‰, thus creating additional stress to those fish present under such conditions. The food resources least affected by extreme hypersalinity are the microphytobenthos and detritus food chains, with detritivorous fishes being dominant when the lake is in this state. Mass mortalities of fishes in Lake St Lucia have been recorded under both low (< 5 ‰) and high salinity (>70 ‰) conditions. The fish kills are often triggered by exceptionally low or high water temperatures which affect the osmoregulatory abilities of these species. Hypersaline conditions and fish mortalities under the most recent closed estuary mouth conditions (2002–2005) are reviewed. If the surface area of St Lucia (35,000 ha) is compared to the total surface area of all South African estuaries (approximately 70,000 ha), then the possibility exists that the loss of the Lake St Lucia nursery area for estuary-associated marine fish species over the past few years may cause significant short-term declines in the future abundance of these taxa on both a local and regional scale.

Keywords   Estuary · Fish · Food chains · Mass mortalities · Salinity ranges

A. K. Whitfield (✉)
South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa
e-mail: a.whitfield@ru.ac.za

R. H. Taylor · C. Fox
Ezemvelo KwaZulu-Natal Wildlife, Private Bag X1, St Lucia 3936, South Africa

D. P. Cyrus
Coastal Research Unit of Zululand, Department of Zoology, University of Zululand, Private Bag X1001, KwaDlangezwa 3886, South Africa

Introduction

Lake St Lucia is the largest estuarine system in Africa and the oldest protected estuary in the world, with the lake and its immediate surroundings having

been officially proclaimed as the "St Lucia Game Reserve" in 1895. A primary goal in the establishment of this reserve, which included the entire water body and a narrow land margin surrounding the lake, was the protection of the largest remaining hippo and crocodile populations in South Africa. In addition, the lake is an important refuge for a diverse array of water birds, including many that breed within this protected area (Berruti 1983). Currently, the lake system forms part of the Greater St Lucia Wetland Park (Taylor 1991) which has both World Heritage and Ramsar Site status.

Although invertebrates and fishes were not considered in the original St Lucia proclamation giving protection to the area, this system is a major nursery ground for prawns, crabs and fishes (e.g. Joubert and Davies 1966; Wallace and van der Elst 1975; Hill 1979; Bickerton 1989). Currently, this estuarine lake system supports a diverse array of marine, estuarine and freshwater fish species and the extremely wide salinity fluctuations (0–120 ‰) offer unique opportunities to study the impact of short- and long-term salinity changes on the ichthyofauna (Blaber and Whitfield 1976; Martin et al. 1992) as well as other components of the aquatic biota (e.g. Millard and Broekhuysen 1970; Boltt 1975; Blaber et al. 1983; Martin et al. 1992; Forbes and Cyrus 1993; Owen and Forbes 1997).

More than 300 reports and formal scientific papers covering the St Lucia system were produced between 1963 and 1987 (Cyrus 1989). Published studies cover all the major biotic and abiotic components, e.g. hydrology (Hutchison and Midgley 1978), geomorphology (Hobday 1975), sediments (Wright and Mason 1990), turbidity (Cyrus 1988), suspensoids (Fielding et al. 1991), detritus (Steinke and Ward 1988), diatoms (Cholnoky 1968), zoobenthos (Blaber et al. 1983), hyperbenthos (Benfield et al. 1990), zooplankton (Forbes and Benfield 1986), ichthyoplankton (Harris and Cyrus 1995), fishes (Blaber 1979), parasites (Whitfield and Heeg 1977), birds (Berruti 1983), reptiles (Pooley 1973) and mammals (Whitfield and Blaber 1980).

The biology and ecology of fish species in Lake St Lucia, especially food and feeding studies, have been a major focus of research attention over the decades (e.g. Blaber 1976, 1979; Whitfield and Blaber 1978a; Cyrus 1991), but comparatively little effort has been directed towards assessing the impact

of salinity fluctuations on the plants and animals within the lake. This review is an attempt to draw together the available information on the response of fishes to salinity changes within the system, thereby contributing to a better understanding of the importance of freshwater supplies to estuaries on a local, regional and global scale (Whitfield and Wooldridge 1994; Drinkwater and Frank 1994; Gillanders and Kingsford 2002).

Study area

The St Lucia system comprises three main lake compartments linked to the sea by a winding channel approximately 20 km long and 100–200 m wide known as the Narrows (Fig. 1). The total lake area is 32,800 ha at mean lake level (Hutchison 1974) which, together with the Narrows and additional submerged marginal areas, amounts to a total surface area of approximately 35,000 ha. However, the actual surface area varies according to prevailing water levels within the system. The major lake compartments; False Bay, North Lake and South Lake are very shallow with an average depth of 0.98 m (Hutchison 1974) and a maximum depth of just over 2 m (Fielding et al. 1991). Parts of the Narrows are slightly deeper than the lake, with a maximum channel depth of 3–4 m (Forbes and Cyrus 1993).

The spring tidal range at the estuary mouth is 1.9 m, but decreases to < 0.1 m in the upper Narrows. There are no tidal fluctuations in the lakes but persistent winds may temporarily raise or lower the water level on the shores by as much as 0.3 m (Day 1981). This seiche action and wind-generated waves stir up sediments in the shallow lake waters, thus causing high levels of turbidity (Cyrus 1988). The Narrows are also turbid due to tidal and other water currents lifting fine sediments into suspension.

Freshwater currently enters Lake St Lucia by direct rainfall (273×10^6 m^3), by inflow from the Mkuze, Mzinene, Hluhluwe, Nyalazi and Mpate rivers, and by groundwater seepage, especially along the eastern shores of the lake compartments (Taylor et al. in press). Under natural conditions, the Mfolosi River also entered the St Lucia Estuary just inside the mouth, thus diluting the salinity of seawater flowing up the Narrows towards the lake. In 1952 the Mfolosi River was diverted southwards to form a separate
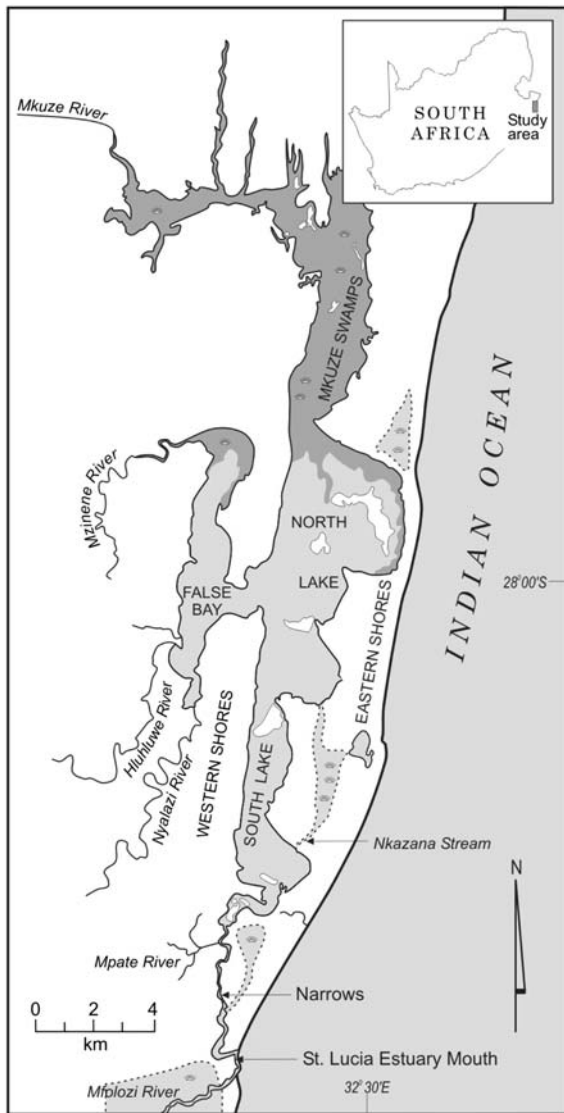
Fig. 1 Map of the St Lucia system showing the inflowing rivers, lake compartments, Narrows and estuary mouth

estuary because of the high sediment loads that were being carried into the St Lucia system (Day et al. 1954). The increased Mfolosi River sediments were a direct result of the canalization and destruction of the Mfolosi swamps in order to drain the floodplain for sugar cane cultivation and from degrading catchment areas. The loss of the Mfolosi River meant that the St Lucia system was deprived of the benefits of more than 700×10^6 m³ of freshwater per annum (Hutchison and Pitman 1977). The remaining rivers currently deliver an average of approximately 362×10^6 m³ to the system (natural conditions=417×10^6 m³ per

annum) with groundwater seepage contributing an additional 23×10^6 m³. Evaporation of approximately 420×10^6 m³ per annum means that during drought years there is a net deficit in freshwater supplies to the lake. Furthermore, increasing freshwater losses (abstractions for irrigation, increased evaporation from farm dams and transpiration from exotic tree plantations) from the Mkuze, Mzinene, Hluhluwe and Nyalazi rivers will accentuate the impact of droughts upon the lake ecosystem.

During dry years, evaporation exceeds freshwater inflow and the lake level drops below mean sea level. If the mouth remains open, seawater flows down the Narrows and into the lake, thus increasing the salt load within the system (Millard and Broekhuysen 1970). During periods of severe drought, evaporation results in hypersaline conditions, with the most saline waters developing in the northern areas of the lake (Fig. 2). This is a consequence of the lack of river flow entering False Bay and North Lake, as well as the continual transfer of additional salt loads from South Lake into the northern compartments. In contrast, seawater flowing up the Narrows and into South Lake during droughts has the effect of lowering salinities within this compartment.

If the St Lucia mouth closes and evaporation exceeds freshwater inflows, then the lake level declines and salinities within the compartments increase (Taylor 1993). Prolonged mouth closure under drought conditions (e.g. from 2002 to 2005) can result in the system shrinking to 25% of its original surface area and salinities increasing above 70 ‰ in the now isolated lake compartments. Under natural conditions, the estuary mouth closed from time to time (e.g. in 1823 and 1833) but the recently recorded shrinkage in water surface area and widespread hypersaline conditions within all the lake compartments would have been unlikely due to the positive influence of river flow from the Mfolosi system (P. Huizinga, pers. comm.).

Natural opening of the estuary mouth would probably have occurred by overtopping, followed by breaching of the beach berm at a water level of 3.0–3.5 m above mean sea level and resulted in more than 1000×10^6 m³ of water scouring the estuary mouth region (P. Huizinga, pers. comm.). An indication of the impact of such an event was provided by Cyclone Domoina which caused widespread flooding in Lake St Lucia and associated catchments, and was subse-
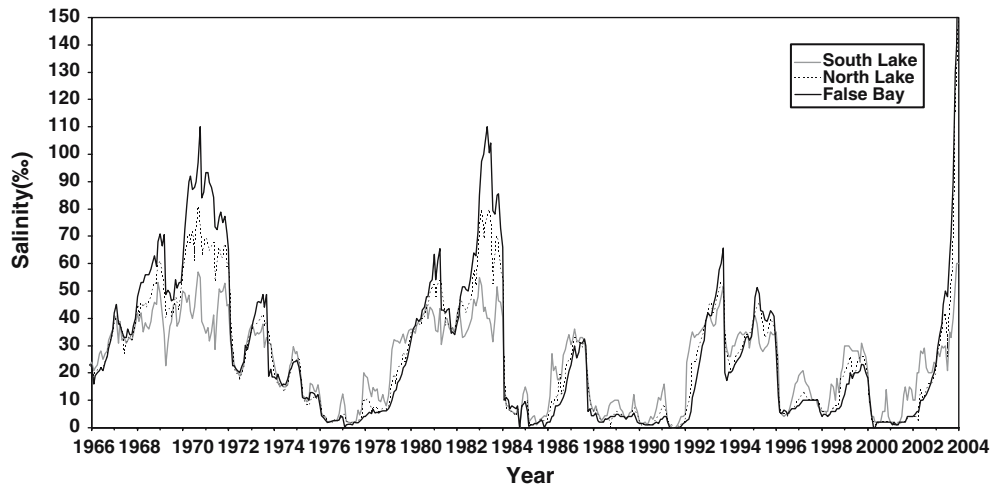
Fig. 2 Salinity fluctuations in the three major lake compartments of the St Lucia system

quently estimated to have removed $16{\times}10^6\,\mathrm{m}^3$ of sediment from the estuary mouth region (Forbes and Cyrus 1992). Salinities in St Lucia are likely to be low following mouth breaching but will increase once lake water levels have equilibrated and seawater starts flowing down the Narrows and into the system.

Fishes and St Lucia salinities

One of the most important homeostatic functions of all living organisms revolves around the regulation of the internal osmotic environment. Deviation from the normal range can jeopardize proper physiological function through water loss or gain, the changing of internal ionic concentrations, and shifts in osmotic gradients (Helfman et al. 1997).

Although most fishes are osmoregulators with respect to the external osmotic environment, individual species have differing abilities in this regard. Research on estuary-associated fishes found in Lake St Lucia has shown that internal osmotic concentrations can undergo considerable changes depending on the species. For example, juvenile Cape stumpnose (*Rhabdosargus holubi*) have an internal osmotic concentration of 370 mosmol l^{-1} when exposed to seawater (35 ‰), 381 mosmol l^{-1} when exposed to 65 ‰ and 216 mosmol l^{-1} when exposed to 1 ‰ (Blaber 1974). All three *Ambassis* species tested by Martin (1990) showed stable blood molalities (310– 390 mosmol l^{-1}) in salinities between 10 ‰ and 35 ‰.

However, the Malabar glassy perchlet (*Ambassis dussumieri*) showed the least tolerance of the three species to low salinities and experienced a 42% decrease in blood osmotic concentration when exposed to fresh water, whereas the decrease for Commerson's glassy (*Ambassis ambassis*) and slender glassy (*Ambassis natalensis*) was only 23% and 20%, respectively. Conversely, *A. dussumieri* was the most tolerant of the three species to higher salinities, as indicated by the lowest increase in blood osmotic concentration when exposed to a salinity of 50 ‰ (Martin 1990).

In general, those fishes tolerating only small changes in the solute concentration of their external environment are referred to as stenohaline whereas those with the ability to osmoregulate over a wide range of environmental salinities are euryhaline. As a result of the widely fluctuating salinities within estuaries, those fishes making extensive use of these systems tend to belong to the latter category (Whitfield 1999). Most fish species entering Lake St Lucia can be regarded as euryhaline, with the majority of freshwater taxa showing only limited osmoregulatory abilities with increasing salinities and the elasmobranchs having more restricted salinity tolerance ranges when compared to their teleost relatives (Whitfield et al. 1981). A number of fish species that have been recorded from the St Lucia system are limited to the mouth region where there is little or no dilution of the seawater (Millard and Broekhuysen 1970). These are usually inshore marine taxa that are

unable to cope with the osmoregulatory stress of lowered salinities and are thus ecologically distinct from estuarine forms (Wallace 1975).

During wet years there is a net outflow of water from the system to the sea. Gradually salt is flushed out the system via the Narrows and salinities in the lake decline (Forbes and Cyrus 1993). If the freshwater inflow is large enough over a protracted period then the salinity in parts of the lake nearest the rivers can become completely fresh. Marine fishes from the lake (e.g. large shoals of mugilids) have been observed 'hovering' in the water column of these inflowing streams and rivers which is similar to the behaviour of other marine fish species (e.g. Japanese meagre *Argyrosomus japonicus*) that have been recorded spending a few days in freshwater before returning to the estuary (Strydom 2000).

Recorded salinity ranges of fishes

Lake St Lucia is an ideal environment in which to assess the salinity tolerance ranges of individual fish species. This is because the hourly and daily salinity fluctuations that are prevalent in tidal estuaries are absent from the lake, with fish being exposed to particular salinity regimes for extended periods. In addition, the prevailing salinities within each lake compartment are often very similar, with False Bay and North Lake normally having higher salinity regimes than South Lake during droughts (Fig. 2). These differential salinities allow species to leave compartments where they are encountering osmoregulatory stress and move southwards into lower salinity waters. However, there are occasions where salinity gradients within the entire lake are minimal or where the compartments become isolated due to lowered water levels. Most fish kills that have been recorded in Lake St Lucia occur under such conditions and are an indication of the lower and upper tolerance limits of individual species. However, in contrast to open tidal estuaries where salinity fluctuations can be extremely rapid (minutes to hours), Lake St Lucia undergoes very small changes in salinity over long periods of time (weeks to months). The extent to which these slow incremental changes in salinity allow the fish species to tolerate more extreme salinities is unknown.

For the purposes of this review, the fish species recorded in Lake St Lucia are divided into freshwater, estuarine and marine categories (Whitfield 1994). Freshwater taxa are the least tolerant of increased salinities (Fig. 3), apart from the Mozambique tilapia (*Oreochromis mossambicus*) which is highly euryhaline. *Oreochromis mossambicus* regularly occupies parts of North Lake and False Bay when salinities are 70–120 ‰ and where most or all marine species are
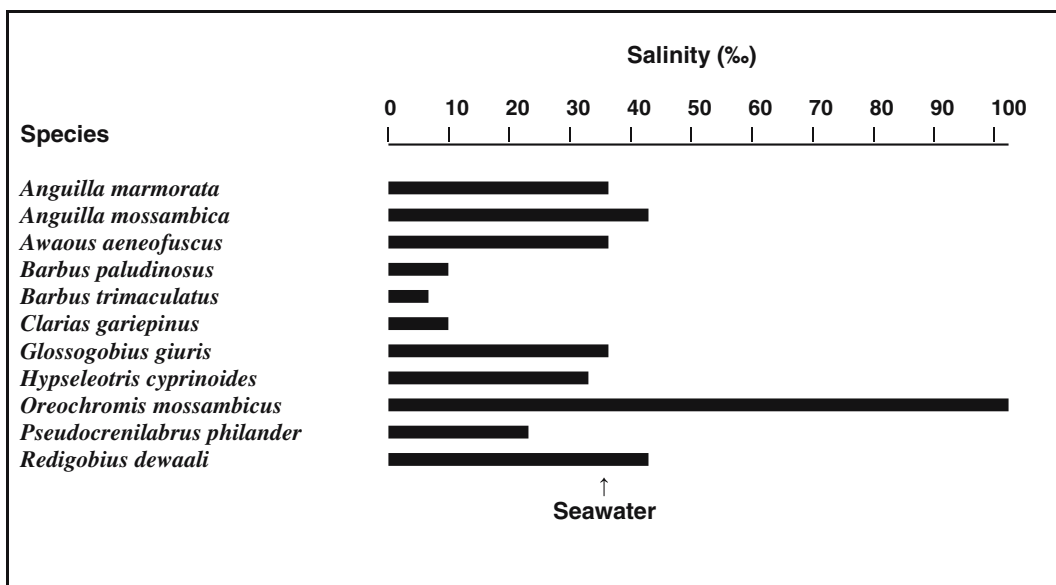
Fig. 3 Recorded salinity ranges of freshwater fish species from Lake St Lucia

absent (Cyrus et al. 2005). Indeed, large numbers of juvenile *O. mossambicus* were recorded in the northern parts of the lake during 1969 and 1970, thus indicating that successful breeding was occurring under hypersaline conditions (Wallace 1975). It would appear that salinity stability which tends to characterize South African estuarine lakes and lagoons is more important to the success of *O. mossambicus* than specific salinity levels (Whitfield and Blaber 1979a).

During very low lake levels associated with estuary mouth closure and drought conditions, groundwater flows along the eastern shores of the lake create shallow freshwater sheets and puddles that become vegetated, and within which freshwater species such as *O. mossambicus*, tropical carp gudgeon (*Hypseleotris cyprinoides*) and checked goby (*Redigobius dewaali*) find refuge from high lake salinities (Vrdoljak 2004). However, a recent survey by Cyrus et al. (2005) showed that even in those areas where groundwater seepage was absent and hypersaline conditions prevailed, both juvenile and adult *O. mossambicus* were present.

Freshwater species are known to enter St Lucia in large numbers following river flooding and the lowering of lake salinities below 5 ‰. The oligohaline conditions, together with the inundation of marginal

vegetation and creation of eulittoral pools associated with high lake levels, provide an ideal environment for these fishes (Whitfield 1977). Once lake salinities approach 10 ‰, some of these species (e.g. straightfin barb *Barbus paludinosus* and North African catfish *Clarias gariepinus*) are forced to retreat back up the rivers or perish.

The estuarine group of fishes in Lake St Lucia is also very tolerant of oligohaline conditions, with many species occurring in freshwater areas (Fig. 4). However, the tolerance of this group to hypersaline conditions is more limited, with only a few taxa having been recorded in salinities above 50 ‰. A number of these species (e.g. Gilchrist's round herring *Gilchristella aestuaria*, river goby *Glossogobius callidus* and barebreast goby *Silhouettea sibayi*) also occur in adjacent freshwater systems and would therefore be able to recolonize the St Lucia system once stream and river flow to the lake was restored.

Marine migrants are the dominant group of fishes in Lake St Lucia and most species are highly euryhaline (Fig. 5). Approximately 80% of these taxa can tolerate salinities < 5 ‰ whereas less than 40% were recorded in salinities above 65 ‰. This indicates a greater tolerance of low rather than higher salinities within the lake. Furthermore, the limited number of elasmobranch species found in Lake St Lucia,
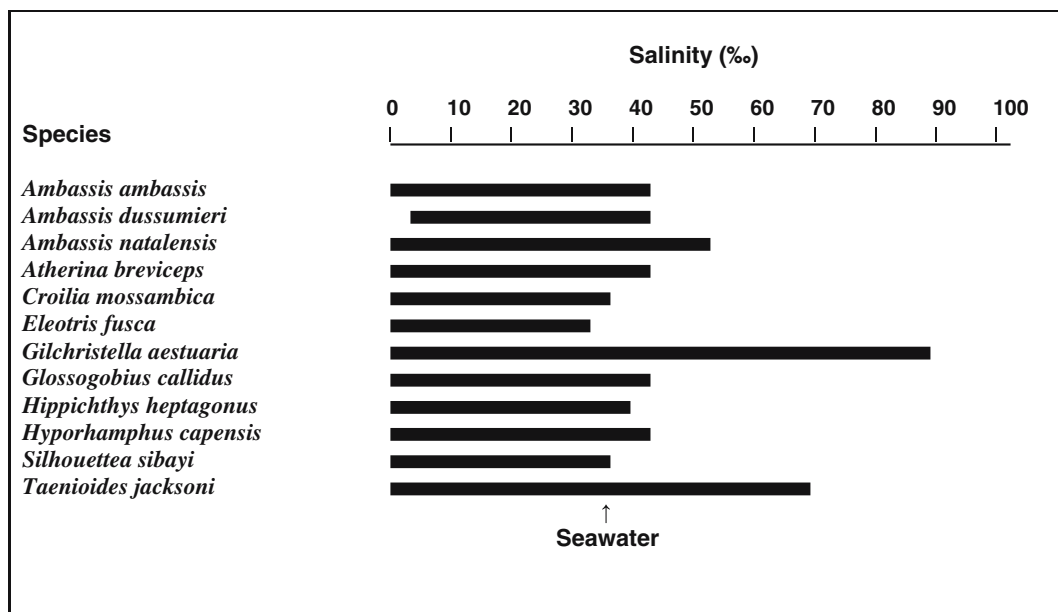
Fig. 4 Recorded salinity ranges of estuarine fish species from Lake St Lucia

together with their more reduced salinity ranges (Fig. 5), is perhaps an indication of the reduced osmoregulatory abilities of this component of the ichthyofauna (Whitfield et al. 1981).

A composite view of the change in fish group tolerance to increasing salinity categories is depicted in Fig. 6. All three groups undergo major declines in species diversity above the 30–40 ‰ category, with only a small proportion of species capable of surviving in salinities above 70 ‰. Although a relatively high proportion of the freshwater taxa survive in salinities up to 40 ‰, a number of these species (e.g. tank goby *Glossogobius giuris*, *H. cyprinoides* and *R. dewaali*) belong to marine families (Smith and Heemstra 1986) and are therefore more likely to

tolerate seawater salinities than primary freshwater taxa (Skelton 1993).

Support for the trend of declining species diversity with increasing hypersalinity is provided by fish catches from five different northern Lake St Lucia surveys (Fig. 7). In addition, the most recent St Lucia fish survey to monitor the impacts of drought under closed estuary mouth conditions (Cyrus et al. 2005) revealed only one surviving species (*O. mossambicus*) from an area of North Lake/False Bay where salinities exceeded 110 ‰.

Oreochromis mossambicus has been recorded breeding when salinities exceed 70 ‰ (van der Elst 1972), but very few fish in St Lucia appear to be able to carry out successful spawning under these
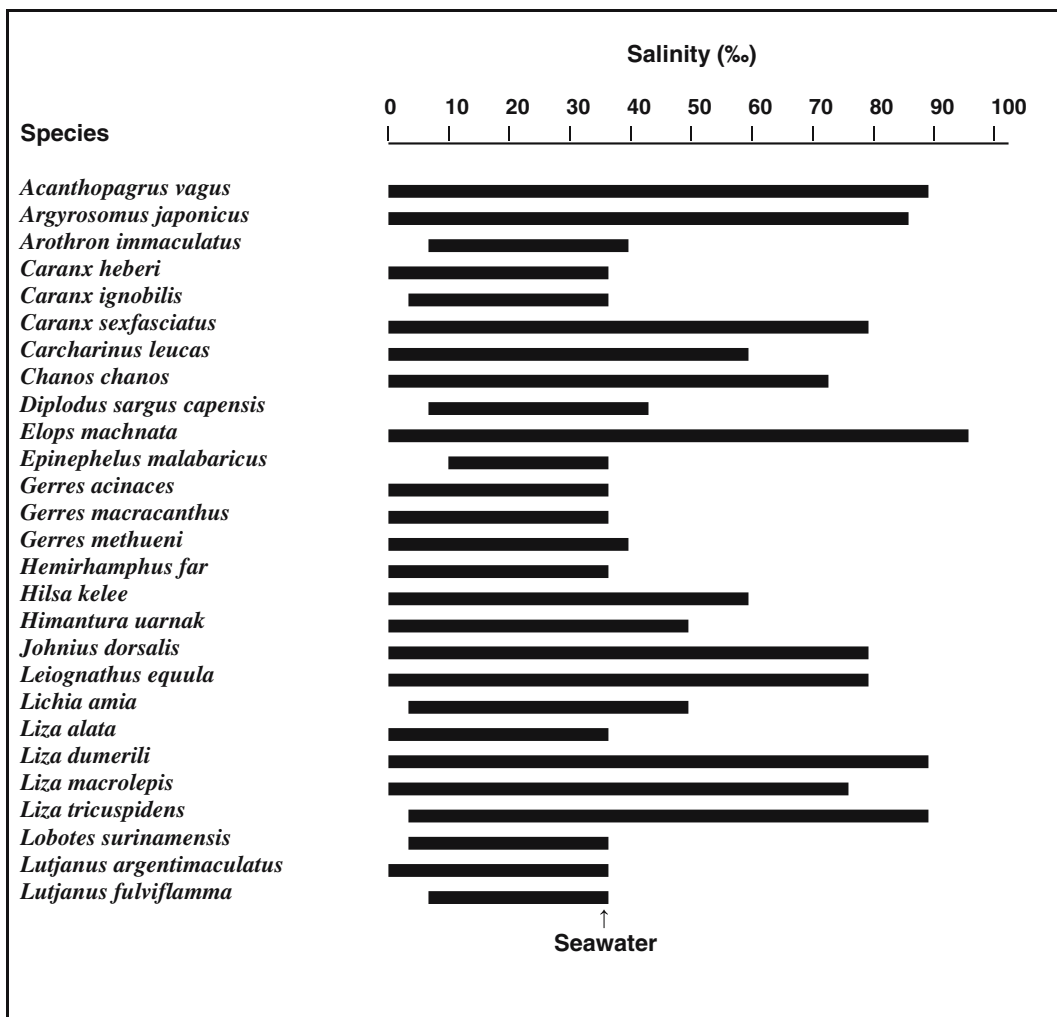

Fig. 5 Recorded salinity ranges of marine fish species from Lake St Lucia
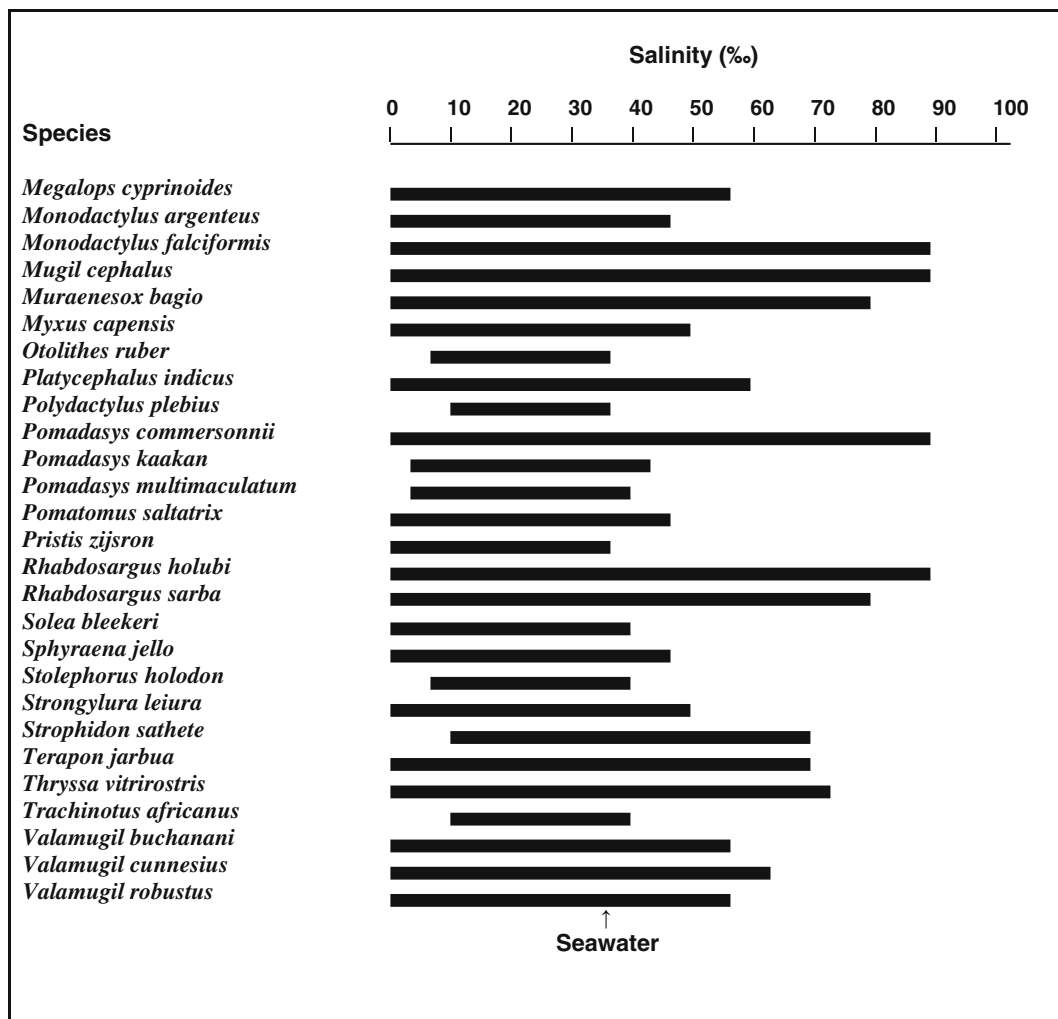
Fig. 5 continued

conditions. Estuarine resident species breed in the St Lucia system in a range of salinities below 40 ‰ (Blaber 1979; Harris and Cyrus 1995) and the fertilized eggs of marine migrant species have been documented in salinities approximating seawater (Connell 1996). Evidence presented by Cyrus et al. (2005) suggests that, apart from *O. mossambicus*, all fish spawning activity in Lake St Lucia ceases once hypersaline conditions prevail. Although the adults of many marine and estuarine species may be able to survive salinities above 50 ‰, successful breeding under these conditions is unlikely.

Spatial separation of fish species according to salinity has been clearly demonstrated by Martin (1988). He found that the co-existence and spatial separation of three *Ambassis* species, all of which are found in the St Lucia system, can be explained primarily by the survival capability of each species to different salinity ranges (Martin 1990). *Ambassis ambassis* is found mainly in areas of low salinity (< 10 ‰), *A. dussumieri* is restricted to higher salinity zones (>25 ‰) and *A. natalensis* occurs mainly in intermediate salinities (Martin 1988).

The spatial use of estuaries by fish larvae can also be strongly influenced by salinity (Chiappa-Carrara et al. 2003; Strydom et al. 2003). In addition, the osmoregulatory abilities of fertilized eggs and larval fishes may differ considerably from juveniles and adults of the same species. The flathead mullet (*Mugil cephalus*), an abundant species in Lake St Lucia, has
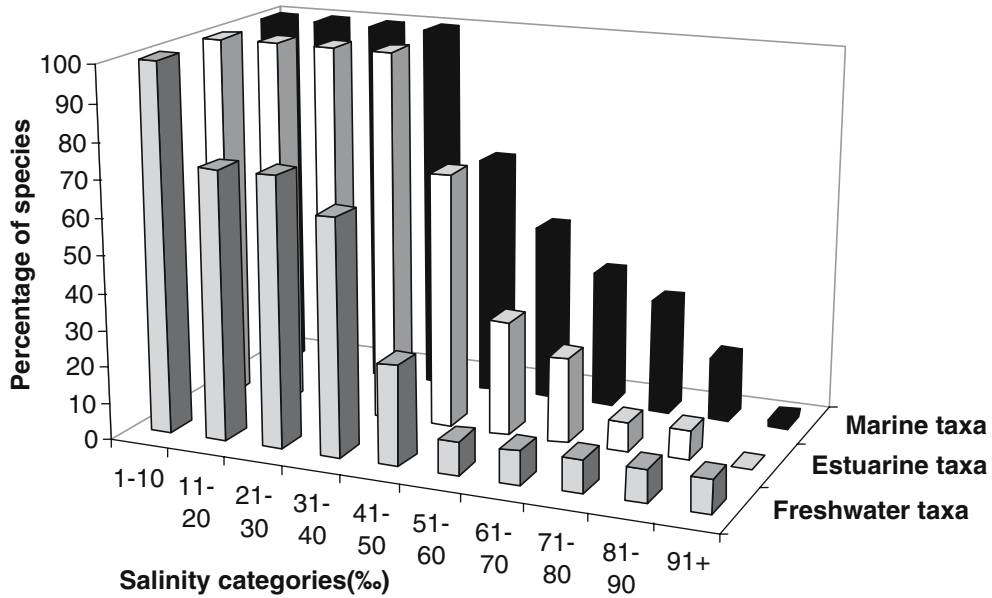
Fig. 6 A composite view of fish group tolerance to increasing salinities in Lake St Lucia
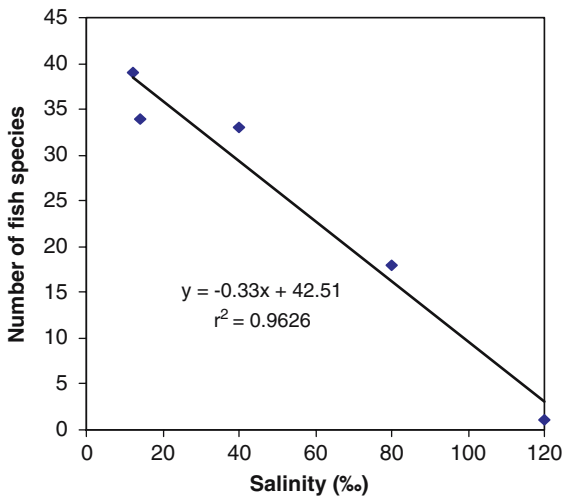

Fig. 7 Numbers of fish species recorded in northern Lake St Lucia under different salinity regimes (data from van der Elst et al. 1976; Cyrus et al. 2005)

eggs which cannot survive decreased salinities (Sylvester et al. 1975; Lee et al. 1992), but the early juveniles of these fish are attracted to low salinity estuaries and even rivers (Mires et al. 1974; Bok 1979). Increasing or decreasing salinities could result in the mortality of egg and larval stages but not influence the survival of juveniles and adults of the same species. Consequently, the presence of large numbers of estuarine and marine species in Lake St

Lucia at salinities below 5 ‰ and above 40 ‰ does not imply that the larvae of the same species can survive such conditions. Indeed, there is evidence in certain South African estuaries that the mesohaline zone is the most productive in terms of accumulator regions for larval fishes (Strydom et al. 2003).

McBride et al. (2001) have described how the metamorphosing larval ladyfish (*Elops saurus*) are attracted to the low salinity estuarine nursery areas with "positive" salinity gradients and later move to higher salinities within these systems. A similar leptocephalus larval migration pattern has been recorded for tenpounder (*Elops machnata*) entering South African estuaries, including St Lucia (Harris and Cyrus 1995; Whitfield 1998). What happens if the salinity gradient within these estuaries becomes "negative", as can occur at St Lucia? According to McBride et al. (2001) larval *Elops* can metamorphose and juveniles can survive in hypersaline waters, thus implying that "negative" estuaries may also serve as a suitable nursery habitat. What is not clear, however, is how salinity affects *Elops* growth and mortality in "positive" versus "negative" estuaries.

Food chains and fish abundance

Salinity change affects not only the physiology of fishes; it also impacts on the food resources for all

aquatic biota. The major autochthonous primary producers in Lake St Lucia include phytoplankton, microphytobenthos and macrophytes, all of which are affected by the prevailing salinity regime. Under low salinity conditions (< 15 ‰) the important submerged aquatic macrophyte *Potamogeton pectinatus* tends to be well established within the system (Ward 1976). If low salinities persist for a prolonged period (>6 months) then the macrophyte beds become very extensive and attain a high biomass.

Salinities above 20 ‰ lead to the replacement of *P. pectinatus*, with *Ruppia cirrhosa* and *Zostera capensis*. All macrophytes tend to disappear once salinities rise above 50 ‰ (Ward 1976). It has been suggested that the cyclical senescence of aquatic macrophytes in the lake during high salinity regimes may increase the amount of detritus available, and is therefore beneficial to the fauna (Hutchison 1977). Although the detritus pool may be temporarily increased by the decomposition of large plant beds, the more long-term effects on detritivorous invertebrates and fishes are negative because growing plants are absent during hypersaline conditions.

Salinities above 55 ‰ result in the disappearance of much of the zoobenthos and only chironomids and ostracods remain (Boltt 1975). Many zoobenthic feeding fishes are capable of surviving in salinities above this level but the absence of suitable prey will lead to a change in diet or having to move to areas of the lake where salinities are less than 55 ‰. Evidence to support this view is provided by Wallace (1975) who found that the few specimens of smallspotted grunter (*Pomadasys commersonnii*) and goldlined seabream (*Rhabdosargus sarba*) recorded in areas of the lake where salinities were >70 ‰ were no longer able to feed on their normal molluscan and crustacean prey items but were consuming mainly filamentous and cynophytic algae. In addition, hypersaline conditions may also affect food conversion by fishes in the same way that oligohaline conditions can result in reduced growth, condition and food conversion efficiencies in juvenile *P. commersonnii* (Deacon and Hecht 1999).

The five penaeid prawn species that dominate the St Lucia hyperbenthos appear unable to survive in salinities above 65 ‰ (Champion 1976). Catch per unit effort declines of more than 99% occurred for all these species when lake salinities rose above 40 ‰. Since penaeid prawns are an important prey item of

large predatory fish in Lake St Lucia (Whitfield and Blaber 1978a), any decline in the abundance of these invertebrates is likely to have an effect on the condition, distribution and abundance of fish species such as *A. japonicus* and *E. machnata*. The most common swimming prawn, *Fenneropenaeus indicus*, showed a 93% decline in the northern parts of Lake St Lucia between 1966 and 1968 due to the onset of hypersaline conditions (>50 ‰) in this region (Champion 1976). *Fenneropenaeus indicus* numbers declined by only 15% in the southern parts of the system, where salinities were similar between 1966 and 1968.

The movement of predatory fish away from North Lake in response to the hypersaline conditions and declining food resources would be expected to increase fish abundance in South Lake. In the case of *A. japonicus*, Wallace (1975) was able to discern an increase in the gill net catch in the south during periods of very high salinity in the north, and a tendency for the fish to redistribute towards the north (causing catch rates to decline in the south) when salinities became less extreme (Fig. 8). This trend was not reflected in catches in the St Lucia Estuary, where changes in abundance occurred annually and seemed to be related to cyclical events in the biology of *A. japonicus* rather than salinities in the lake (Wallace 1975).

There is much evidence in support of the hypothesis that increasing salinities (>50 ‰) cause a decline in large fish abundance in Lake St Lucia. According to van der Elst et al. (1976) gill net catch rates at salinities of < 20 ‰ were double those when salinities exceeded 50 ‰. Although more recent gill net catch data indicates that low fish catches can occur under all salinity regimes, it is noteworthy that the three highest CPUEs were recorded at salinities of between 10 ‰ and 20 ‰ (Fig. 9). These fish abundance trends are also supported by Mann et al. (2002) who found an inverse relationship between anglers CPUE and increasing lake salinities (Fig. 10).

Phytoplankton is present during both high and low salinity regimes (Johnson 1977), but this food resource is not consumed directly by any fish species within the lake (Whitfield 1980). However, phytoplankton is utilized by zooplankton which is, in turn, preyed upon by zooplanktivorous fishes within the system (Blaber 1979). Most of the zooplankton species in Lake St Lucia were found to tolerate salinities
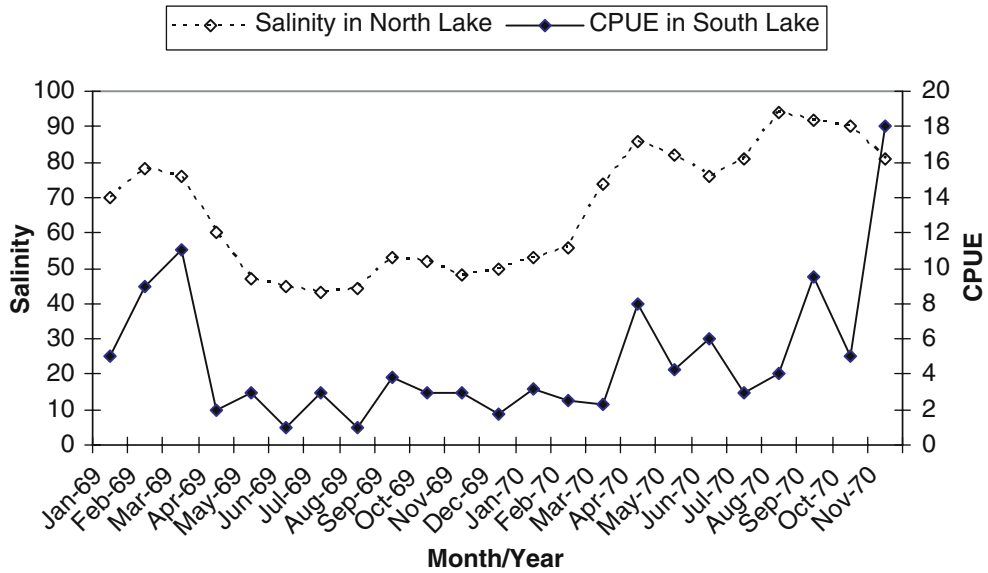
Fig. 8 Relationship between salinity (‰) in St Lucia's North Lake and the abundance (gill net catch per 24 h) of *Argyrosomus japonicus* in South Lake (after Wallace 1975)
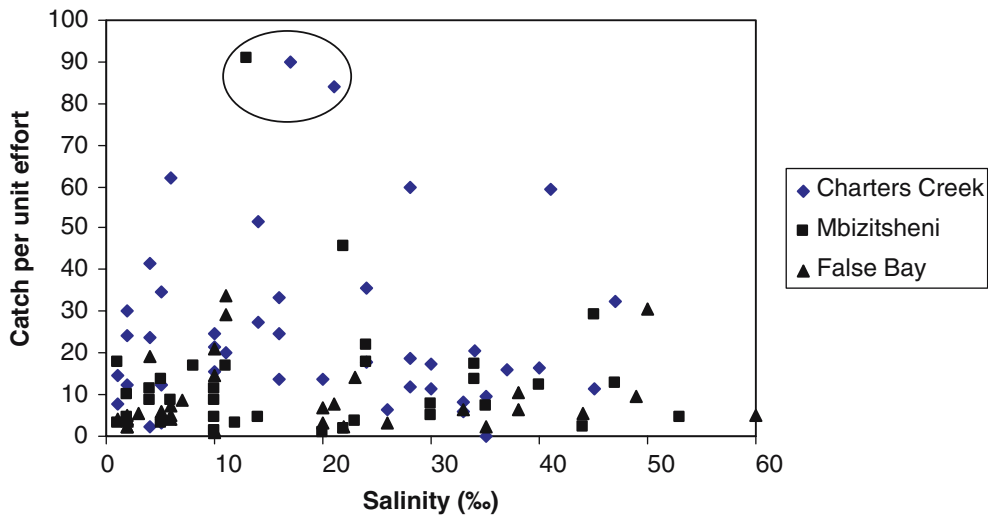

Fig. 9 Individual gill net catch per unit effort data collected by Ezemvelo KwaZulu-Natal Wildlife at three sites under different salinity conditions in Lake St Lucia, with the three highest catches encircled

above 40 ‰, with many of the dominant taxa capable of breeding in 60 ‰ (Grindley 1976). Unfortunately most of these species disappear from the plankton once salinities rise above 70 ‰ which will have major consequences for the feeding ecology of zooplanktivorous fishes that can tolerate hypersaline conditions.

Microphytobenthos is also present under a range of salinity regimes although the tolerances of individual taxa differ considerably (Cholnoky 1968). Most

species that are found in Lake St Lucia have a wide salinity tolerance, e.g. the diatom *Coscinodiscus granii* was abundant between 10 ‰ and 50 ‰ (Johnson 1977) and probably has an even wider tolerance range. Mugilids are a dominant group of fishes in Lake St Lucia (Whitfield and Blaber 1978b) and their dependence on detritus and microphytobenthos (Blaber 1976) will enable them to survive prolonged hypersaline conditions when compared to invertebrate feeding fish species whose prey has succumbed
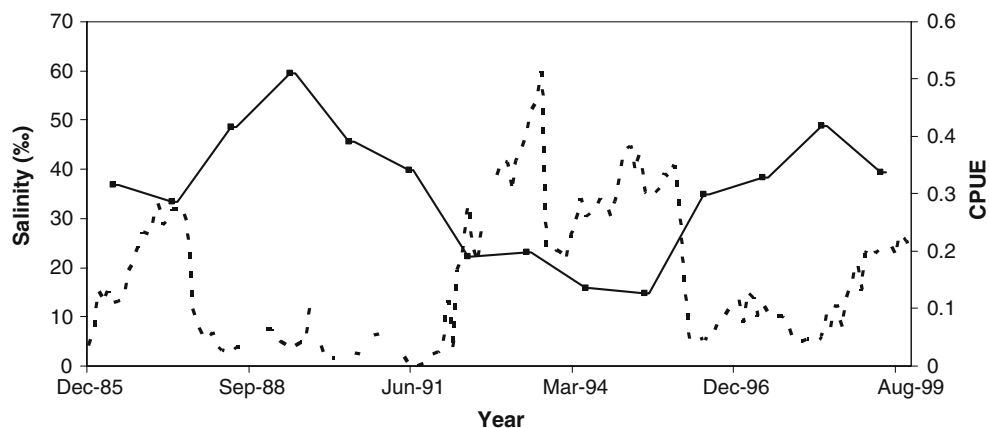
Fig. 10 Total catch per unit effort (fish per angler per hour) of all angling fish species in South and North lake combined (solid line) versus the average salinity (dashed line) measured in these compartments (data from Mann et al. 2002)

to the adverse salinity regime. Evidence to support this view is provided by Wallace (1975) who found that *O. mossambicus*, *M. cephalus* and milkfish (*Chanos chanos*), all of which are primarily detritivorous feeders (Whitfield and Blaber 1978c), remained abundant in North Lake when salinities were in excess of 70 ‰.

It is important to note that when salinities exceed 110 ‰, *O. mossambicus* appears to be the only fish species capable of surviving under such conditions (van der Elst 1972). Indeed, as salinities in Lake St Lucia declined during 2004 following renewed freshwater inputs, *O. mossambicus* proliferated and comprised almost half of all fishes captured in December 2004 (Cyrus et al. 2005). This was primarily due to very successful breeding in the spring and summer of 2004 under conditions of reduced competition and limited piscivorous predation from depleted marine fish populations. However, the abundant *O. mossambicus* populations soon attracted the attention of pelicans, with increasing numbers of these birds preying on this favoured food item (Whitfield and Blaber 1979b) during the latter half of 2004 and early 2005 (Fig. 11, M. Bowker, pers. comm.).

Mass mortalities of fishes

Most observations on the impacts of salinity changes on fishes in southern African estuaries are derived from extreme salinity events (Whitfield 1995). In this context Lake St Lucia has proven to be an ideal field laboratory for the recording of fish responses to extreme salinities under natural conditions. During June 1976, when salinities throughout Lake St Lucia were <3 ‰, a minimum of 100,000 fish of marine origin, belonging to at least seven species, died when water temperatures suddenly declined to 12°C (Blaber and Whitfield 1976). A temperature-induced fish kill involving an estimated 250,000 individuals comprising at least 21 species was noted in the winter of 1987 (Cyrus and McLean 1996) but salinities on that occasion were much higher than those recorded in June 1976. Low temperatures are not always necessary to trigger a fish kill in oligohaline waters. Bennett (1985) documented how marine fishes in the Bot River estuarine lake survived low winter emperatures (<14°C) and salinities (<8 ‰), only to undergo a mass mortality during spring (October) when water temperatures had increased to 18°C and salinities declined further to 2–3 ‰.

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 a lethal combination of low salinities and sudden low temperature leading to osmoregulatory failure, with fungal infection of the skin lesions
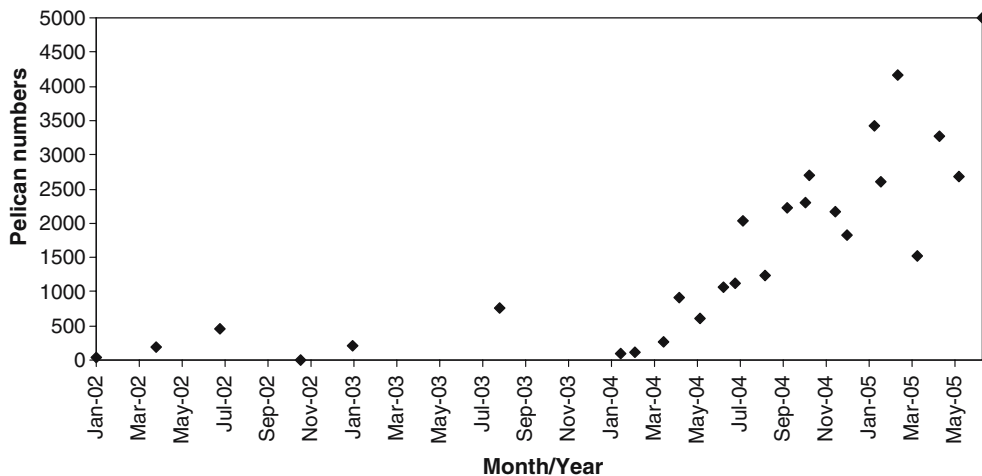
Fig. 11 Pelican counts from the Lake St Lucia system between January 2002 and May 2005 (data provided by M. Bowker)

hastening the death process. The disorientation behaviour shown by dying fish in the lake is symptomatic of osmoregulatory failure recorded in *R. holubi* (Blaber 1974), and the development of skin lesions under freshwater conditions has also been documented in osmoregulatory stressed white steenbras (*Lithognathus lithognathus*) (Mehl 1973).

The cichlid *O. mossambicus* is abundant in Lake St Lucia but was not recorded dying in the 1976 mass mortality (Blaber and Whitfield 1976). Experimental work conducted by Allanson et al. (1971) has shown that osmoregulation by *O. mossambicus* breaks down at 11°C in salinities below 5 ‰. Therefore, the survival of this freshwater species in St Lucia during the 1976 winter may have been partially facilitated by the brackish water conditions prevailing within the lake. In contrast, large numbers of *O. mossambicus* were recorded dying during July 1978 in Lake Bhangazi, a freshwater system on the eastern shores of St Lucia (Bruton and Taylor 1979). This mass mortality coincided with low winter water temperatures (<13°C) whereas no *O. mossambicus* were recorded dying in the adjacent Lake St Lucia over the same period. A similar mortality of *O. mossambicus* was recorded in the Kasouga Estuary during July 1979 when winter water temperatures coincided with salinities declining from 30 ‰ to <3 ‰ as a result of river flooding (Jubb 1979).

Mass fish mortalities during high salinity regimes in Lake St Lucia have also been recorded. When the estuary mouth was open during 1969/70 and all the hypersaline lake compartments were linked, fish

mortalities, as evidenced by sightings of dead specimens, were rare. According to Wallace (1975) this was because the fish population tended to move southwards to alleviate stress before conditions in North Lake and False Bay became lethal. However, mortalities during 1969/70 did occur and generally followed sudden periods of cold weather.

The physiological explanation for fish mortalities under low temperatures at both extremes of the salinity continuum can be attributed to the reduction in enzymatic rates which result in a lowering of ionic efflux and an increase in the osmotic concentration of the body fluids (Maetz and Evans 1972). Thus when a fish is already close to its upper or lower limit of salinity tolerance, a temperature-induced reduction in osmoregulatory efficiency can result in internal ionic concentrations reaching lethal levels for that species. This effect has been experimentally demonstrated by Blaber (1973) for one of the common marine fish species in Lake St Lucia, viz. the sparid *R. holubi*. Temperature and salinity tolerance experiments indicated that salinity tolerance decreased as temperatures decreased beyond certain levels. Thus a drop in temperature from 18°C to 12°C would not have caused a mortality at a salinity of 30 ‰, but it would have resulted in 100% mortality at 60 ‰ and 50% mortality at 1 ‰.

When the St Lucia Estuary mouth closed in June 2002, salinities throughout the system were below 35 ‰, with South Lake at 30 ‰ and False Bay at 10 ‰. Overall, an estimated five million tons of salt was trapped within the system and, as evaporation exceeded freshwater

inflow over the succeeding months, water volume decreased and salinities rose. Between March and December 2003 the lake became compartmentalized due to low lake levels, with the total water surface area declining to 25% of normal. Hypersaline conditions prevailed in most areas, with parts of False Bay having salinities in excess of 150 ‰ before drying up and those in South Lake rising above 70 ‰ in places. Isolation of the lake compartments meant that fish species were trapped and could not escape to areas of lower salinity. During the summer of 2003/04 a minimum of eight fish mortality events were recorded, most of which were dominated by two to three species. Since different fish taxa dominated on each occasion, this mortality pattern indicates species specific impacts (Cyrus et al. 2005).

In contrast to the above hypersaline conditions and lake compartmentalization, during the 1969/70 hypersalinities fish from False Bay and North Lake were able to move to South Lake where salinities were lower, or even out to sea via the Narrows (Wallace 1975). Fish movement between the lake compartments was possible because the mouth remained open and lake levels did not show significant declines due to the inflow of sea water into the system to compensate for evaporation.

The impact of the 2003/04 hypersaline conditions at St Lucia on certain estuary-associated marine fish species may be large, especially as Cyrus et al. (2005) have estimated that as many as 40% of species may have disappeared from the system and overall stock abundance may be as much as 50% below 'normal' levels. If the surface area of St Lucia (35,000 ha) is compared to the total surface area of all South African estuaries (approximately 70,000 ha), then the possibility exists that the loss of the Lake St Lucia nursery area for estuary-associated marine fish species over the past few years may cause significant short-term declines in the future abundance of these taxa on both a local and regional scale.

Fish mortalities that are indirectly linked to hypersalinity have also been recorded at St Lucia. During July and August 1969 the protozoan *Noctiluca scintillans* underwent a massive proliferation following a period of hypersalinity in North Lake and False Bay. The 'red water' was associated with a minor fish mortality, mostly mugilids, that were washed up along with the decaying masses of plankton (Grindley and Heydorn 1970). Salinities in these lake compartments had declined from more than 80 ‰ in March 1969 to 40–50 ‰ during the red water events. No occurrences of red water were noted during the most recent hypersaline conditions in North Lake and False Bay (Cyrus et al. 2005).

Some global comparisons

Salinity is an important driving force that influences the structuring of estuarine fish assemblages around the world (e.g. Raseira et al. 2002; Jaureguizar et al. 2003; Albaret et al. 2004a; Barletta et al. 2005). Salinity also has both a direct and indirect influence on food availability (Forbes and Cyrus 1993), as well as influencing the physiology of individual species (Moser and Gerry 1989; Comyns et al. 2004). The ability of many estuarine residents to spawn under varying salinities is seen as an advantage for those taxa (Strydom et al. 2002), whereas the marine migrants tend to breed either at sea or on the ebb tide in the lower reaches of estuaries so that the fertilized eggs hatch in coastal waters where the salinity is approximately 35 ‰ (Hesp et al. 2004). Those taxa that are best adapted to cope with wide salinity fluctuations have access to productive estuarine environments and are at a competitive advantage over those species that are less euryhaline. Optimum salinity conditions will obviously vary between species and within individual taxa depending on developmental stage (Davenport 1985; Boltachev and Valovaya 1994).

There are very few estuarine or coastal lakes that exhibit similar salinity characteristics to St Lucia. The Laguna Madre of Texas, located in the Gulf of Mexico, is one of the few systems where comparable information is available. This large (>100,000 ha), shallow (mean depth=<1 m) system with limited river inflow also has widely fluctuating salinities, ranging from more than 100 ‰ in some years to 2 ‰ following major rainfall events (Hedgpeth 1967). As is the case at Lake St Lucia, major fish mortalities are recorded during winter when abnormally cold temperatures occur and during summer when high salinities coincide with high water temperatures. According to Hedgpeth (1967) almost double the number of fish species are found in low salinities (<10 ‰) when compared to high salinity (>60 ‰) regimes, a situation that is very similar to fish species responses in Lake St Lucia (Fig. 6).

The normally closed Wellstead Estuary (Australia) is also subjected to salinity fluctuations on the scale of Lake St Lucia. Between October 1993 and September 1997 the estuary remained closed and salinities rose above 110 ‰ in March 1997 (Young and Potter 2002). Although species such as *M. cephalus* and yellow-eye mullet (*Aldrichetta forsteri*) were able to survive the highly variable salinities, others such as western hardyhead *Leptatherina wallacei* and bridled goby *Acentrogobius bifrenatus* perished. The atherinid *Atherinosoma elongata* was the only species caught in March 1997 at the lower estuary site when the salinity reached 122 ‰. Other species moved from the lower to the upper reaches of the estuary where salinities did not rise to such high levels (Young and Potter 2002). The increased densities of fishes in the upper reaches of the Wellstead Estuary indicated a salinity response that can be equated to the movement of *A. japonicus* from North Lake to South Lake in the St Lucia situation (Fig. 8).

The permanently open Sine Saloum Estuary (Senegal) is also characterized by prolonged periods of zero river flow, with hypersaline conditions (mean=45–50 ‰) prevailing in most parts of the system and salinities reaching >100 ‰ in the upper reaches. As expected, salinity is a strong driver of fish assemblage structure within this estuary (Simier et al. 2004), with the highest species diversity being associated with a station in the middle reaches where aquifers reduce the salinity to 25 ‰ (Vidy 2000). Also of interest is the fact that both the bonga shad *Ethmalosa fimbriata* and blackchin tilapia *Sarotherodon melanotheron* have slower growth rates and reduced size-at-maturity in the hypersaline parts of this estuary (Albaret et al. 2004b; Diop et al. 2004). The extent to which these fish responses can be attributed to reduced food resources, high osmoregulatory demands and increased energy expenditure in a hypersaline environment is unknown.

At the other extreme, low salinities (< 5 ‰) can also result in marked changes in the fish species composition of estuaries. High rainfall associated with El Niño events cause salinities in the Patos Estuary lagoon (Brazil) to decline, thus facilitating the invasion of this system by additional freshwater species (Garcia et al. 2003); a situation reminiscent to that recorded in Lake St Lucia. Within 3–6 months of the end of the El Niño period, large seawater inputs to

the lagoon give rise to increased densities of estuary-associated marine taxa and the fish assemblage returned to its pre-El Niño state (Garcia and Vieira 2002). Similar changes in species composition have been documented in the St Lucia system, with the diversity and abundance of freshwater taxa increasing following river flooding and lowered lake salinities (van der Elst et al. 1976). Although most marine species can tolerate oligohaline conditions (Fig. 6), these salinities are not optimal for the feeding, growth and survival of large numbers of this dominant group. Indeed, it could be argued that osmotically the optimum salinity for most fishes in Lake St Lucia is between 10 ‰ and 20 ‰, since the three highest catches were recorded within this range (Fig. 9), and it also happens to encompass the isosmotic state for many marine and estuarine fish species (Blaber 1974; Martin 1990; Helfman et al. 1997).

Prolonged lowered salinities resulting mainly from freshwater sewage spills or winter rains into the Tijuana Estuary and Los Peñasquitos Lagoon (California) caused the loss of most marine fish species from the channels of these two systems (Nordby and Zedler 1991). Similarly, low salinities prevailing in the middle and upper reaches of the Gambia Estuary (West Africa) meant that the juveniles of most marine fish species were confined to the higher salinity lower reaches of this system during the rainy season (Darboe et al. 2004). Further evidence of marine fish responses to low salinity can be found in the Gulf of Finland (Baltic Sea) where salinities declined from 6 ‰ to < 1 ‰ along a transect and was an important factor influencing fish species richness, with marine taxa gradually disappearing as salinities declined towards the less haline eastern areas (Lappalainen et al. 2000). Detailed information on the responses of marine fishes to low salinities in the St Lucia system are more limited than equivalent data collected during high salinity regimes, especially how the recruitment of the larvae and juveniles of marine taxa are influenced by widespread oligohaline conditions. In this context Darboe et al. (2004) suggested that river flooding in certain West African tropical estuaries may temporarily reduce the nursery ground value of these systems to juvenile marine recruits.

In the Kosi estuarine system (South Africa) the diversity of marine fishes declines between the northern, more saline lakes, and the southern oligohaline Lake Nhlange (Blaber 1978). During the

late 1970s, increased rainfall and run-off into Lake Nhlange resulted in further salinity declines to below 1 ‰ and certain predatory marine species such as great barracuda *Sphyraena barracuda* and double-spotted queenfish *Scomberoides lysan* moved away from this lake to the more saline northern compartments (Blaber and Cyrus 1981). There was a corresponding increase in the numbers of the freshwater predator *C. gariepinus* and cichlids such as *O. mossambicus* in Lake Nhlange (Blaber 2000), a situation very similar to that recorded in Lake St Lucia under oligohaline conditions. As was the case in Lake St Lucia when salinities were < 3 ‰, at least 22 marine taxa were still present within Lake Nhlange when salinities were < 1 ‰ (Blaber 2000). However, some of these marine species (e.g. *P. commersonnii*) in Lake Nhlange suffered mass mortalities during July 1975 due to a combination of low salinities (1 ‰) and low temperatures (Blaber 1978).

A reverse trend to that described in Lake Nhlange above was recorded in Ébrié Lagoon (Ivory Coast), where an artificial opening of the lagoon resulted in salinities increasing from almost freshwater to at least 20 ‰ (Albaret and Ecoutin 1989). In response, the numbers of freshwater fish in the system decreased and marine taxa became dominant.

The relationship between salinity and the presence of marine fish species in estuarine lakes can be complicated by the segmented nature of certain systems. For example, Hill et al. (1975) found that the fish community of Lagoa Poelela (Mozambique) was dominated by freshwater species (mainly *O. mossambicus* and redbreast tilapia *Tilapia rendalli*), despite the fact that salinities in the lake were 8 ‰. The low representation of marine taxa in Lagoa Poelela was attributed to the 75 km long channel and lagoonal systems connecting Poelela to the sea. Marine species that were not recorded in Lagoa Poelela were found in Lagoa Massava and Quissico which were closer to the sea (Hill et al. 1975).

Young et al. (1997) found that the ichthyofaunal composition in the Moore Estuary (Australia) changed progressively in an upstream direction, reflecting a decline in marine species and an increase in the density of estuarine species along this salinity axis. Fish species distributions during a normal horizontal salinity gradient period within the St Lucia system indicated a similar longitudinal distribution pattern for marine and estuarine species, with many marine species extending into South Lake but not the northern parts of the system, and certain estuarine species being more abundant in the northern lake compartments (Millard and Broekhuysen 1970). Further support for salinity being a primary influence on the balance between marine and estuarine fishes in estuaries is provided by the work of Griffiths (2001). He found that in Shellharbour Lagoon (Australia) the salinity during both the open and closed phases was maintained at a level intermediate of the tolerances of both marine and estuarine species, thus conferring stability on the system with respect to changes in fish assemblage composition.

Conclusions

The unique features of Lake St Lucia have provided an ideal opportunity to examine the impact of short-, medium- and long-term salinity changes on the ichthyofauna of this estuarine system. Overall, it would appear that the different fish groupings have differential salinity range preferences (Table 1). Although freshwater species have a definite preference for oligohaline conditions, *O. mossambicus* was common under all five major salinity regimes. Both the marine and estuarine fish groups are well represented under low (1–10 ‰) and medium (11–40 ‰) salinity regimes. Most marine species are still common under high salinity conditions (41–70 ‰) but many of these taxa are absent under extreme hypersalinity (71–110 ‰).

The ability of the estuarine and marine fish groups to cope with changing salinity regimes at St Lucia is very apparent. However, certain primary and secondary food sources (e.g. aquatic macrophytes, zoobenthos) are less able to tolerate hypersaline conditions. Therefore the abundance of particular fish taxa in a lake compartment may decline long before the limits of that species' salinity tolerance is attained. In this context, the absence of a fish taxon from a particular area cannot be presumed to be because the salinity tolerance of that species has been exceeded; the cause may be indirect and related to the loss of an important food source and structural changes in the habitat. Whitfield (1986) has shown major changes in fish species composition in the Swartvlei estuarine system as a result of the loss of aquatic macrophyte beds and associated invertebrate prey.

Short-, medium- and long-term salinity fluctuations have always been a natural feature of the St Lucia

Table 1 Relative diversity and abundance of the three major fish groups in Lake St Lucia under five different salinity regimes

Fish group	Salinity regime (‰)				
	1–10	11–40	41–70	71–110	111–120
Freshwater	++++	++	+	+	+
Estuarine	++++	++++	++	+	
Marine	+++	++++	+++	+	

system (Hutchison 1976). However the salinity fluctuations have changed considerably over the past century as the quantity of fresh water entering the lake has been reduced. Studies have been initiated to investigate various management options that could rectify this situation and return the lake to more natural regimes. The current review and interpretation of information about fish responses to changing salinities provides insights that will need to be considered when deciding on future management options.

References

Albaret JJ, Ecoutin JM (1989) Communication mer-lagune: impact d'une reouverture sur l'ictyofaune de la lagune Ébrié (Côte d'Ivoire). Rev d'Hydrobiol Trop 21:71–88

Albaret JJ, Darboe FS, Dé Morais LT, Ecoutin JM, Raffray J, Simier M (2004a) Fish diversity and distribution in the Gambia Estuary, West Africa, in relation to environmental variables. Aquat Living Resour 17(1):35–46

Albaret JJ, Diop K, Durand JD, Guinand B, Kantoussan J, Lae R, Mbow A, Panfili J, Thiaw OT, Thior D (2004b) Influence of salinity on life history traits of the bonga shad Ethmalosa fimbriata (Pisces, Clupeidae): comparison between the Gambia and Saloum estuaries. Mar Ecol Prog Ser 270:241–257

Allanson BR, Bok A, van Wyk NI (1971) The influence of exposure to low temperature on Tilapia mossambica II: change in serum osmolarity, sodium and chloride ion concentration. J Fish Biol 3:181–185

Barletta M, Barletta-Bergan A, Saint-Paul U, Hubold G (2005) The role of salinity in structuring the fish assemblages in a tropical estuary. J Fish Biol 66:45–72

Benfield MC, Bosschieter JR, Forbes AT (1990) Growth and emigration of Penaeus indicus H. Milne-Edwards (Crustacea: Decapoda: Penaeidae) in the St Lucia estuary, southern Africa. Fish Bull 88:21–28

Bennett BA (1985) A mass mortality of fish associated with low salinity conditions in the Bot River estuary. Trans R Soc S Afr 45:437–448

Berruti A (1983) The biomass, energy consumption and breeding of waterbirds relative to hydrological conditions at Lake St Lucia. Ostrich 54:65–82

Bickerton IB (1989) Aspects of the biology of the genus Macrobrachium (Decapoda: Caridea: Palaemonidae) in the St Lucia system. MSc dissertation, University of Natal, Durban

Blaber SJM (1973) Temperature and salinity tolerance of juvenile Rhabdosargus holubi (Steindachner) (Teleostei: Sparidae). J Fish Biol 5:593–598

Blaber SJM (1974) Osmoregulation in juvenile Rhabdosargus holubi (Steindachner) (Teleostei: Sparidae). J Fish Biol 6:797–800

Blaber SJM (1976) The food and feeding ecology of Mugilidae in the St Lucia lake system. Biol J Linn Soc 8:267–277

Blaber SJM (1978) Fishes of the Kosi system. Lammergeyer 24:28–41

Blaber SJM (1979) The biology of filter feeding teleosts in Lake St Lucia, Zululand. J Fish Biol 15:37–59

Blaber SJM (2000) Tropical estuarine fishes. Ecology, exploitation and conservation. Blackwell Science, Oxford, 372 pp

Blaber SJM, Cyrus DP (1981) A revised checklist and further notes on the fishes of the Kosi system. Lammergeyer 31:5–14

Blaber SJM, Whitfield AK (1976) Large scale mortality of fish at St Lucia. S Afr J Sci 72:218

Blaber SJM, Kure NF, Jackson S, Cyrus DP (1983) The benthos of South Lake, St Lucia following a period of stable salinities. S Afr J Zool 18:311–319

Bok AH (1979) The distribution and ecology of two mullet species in some freshwater rivers in the eastern Cape, South Africa. J Limnol Soc S Afr 5:97–102

Boltachev AR, Valovaya NA (1994) Aspects of the ecology of aquatic animals in mixohaline estuaries of Guinea. Hydrobiol J 30(4):68–78

Boltt RE (1975) The benthos of some southern African lakes. Part 5: the recovery of the benthic fauna of St Lucia following a period of excessively high salinity. Trans R Soc S Afr 41:295–323

Bruton MN, Taylor RH (1979) Cichlid fish mortality in a freshwater lake in Natal. Lammergeyer 27:1–4

Champion HFB (1976). Recent prawn research at St Lucia with notes on the bait fishery. In: Heydorn AEF (ed) St Lucia scientific advisory council workshop meeting at Charters Creek 15–17 February 1976. Natal Parks, Game and Fish Preservation Board, Pietermaritzburg, pp 1–20

Chiappa-Carrara X, Sanvicente-Añorve L, Monreal-Gómez A, Salas de León D (2003) Ichthyoplankton distribution as an indicator of hydrodynamic conditions of a lagoon system in the Mexican Caribbean. J Plank Res 25:687–696

Cholnoky BJ (1968) Die diatomeen assoziationen der Santa Lucia Lagune in Natal (Süd Afrika). Bot Mar 11(Suppl.):1–121

Comyns BH, Fulling GL, Peterson MS, Rakocinski CF (2004) Defining the fundamental physiological niche of estuarine fishes and its relationship in understanding distribution, vital metrics, and optimal nursery conditions. Environ Biol Fish 71(2):143–149

Connell AD (1996) Sea fishes spawning pelagic eggs in the St Lucia estuary. S Afr J Zool 31:37–41

Cyrus DP (1988) Turbidity and other physical factors in Natal estuarine systems Part 2: estuarine lakes. J Limnol Soc S Afr 14:72–81

Cyrus DP (1989) The Lake St Lucia system. A research assessment. S Afr J Aquat Sci 15:3–27

Cyrus DP (1991) The biology of *Solea bleekeri* (Teleostei) in Lake St Lucia on the south east coast of Africa. Neth J Sea Res 27:209–216

Cyrus DP, McLean S. (1996) Water temperature and the 1987 fish kill at Lake St Lucia on the south eastern coast of Africa. S Afr J Aquat Sci 22:105–110

Cyrus DP, Vivier L, Mackay CF (2005) Lake St Lucia fish survey – December 2004. Coast Res Unit Zululand Invest Rep 118:1–27

Darboe FS, Mbye EM, Vidy G (2004) Juvenile fish assemblages in the creeks of the Gambia estuary. Aquat Living Resour 17(1):56–64

Davenport J (1985) Osmotic control in marine animals. Soc Exp Biol 39:207–244

Day JH (1981) Summaries of current knowledge of 43 estuaries in southern Africa. In: Day JH (ed) Estuarine ecology with particular reference to southern Africa. A.A. Balkema, Cape Town, pp 251–330

Day JH, Millard NAH, Broekhuysen GJ (1954) The ecology of South African estuaries. Part 4: the St Lucia system. Trans R Soc S Afr 34:129–156

Deacon N, Hecht T (1999) The effect of reduced salinity on growth, food conversion and protein efficiency ratio in juvenile spotted grunter, *Pomadasys commersonnii* (Lacépède) (Teleostei: Haemulidae). Aquacult Res 30:13–20

Diop K, Diouf K, Durand JD, Lae R, Mbow A, Ndiaye P, Panfili J, Thior D (2004) Influence of salinity on the life-history traits of the West African black-chinned tilapia (*Sarotherodon melanotheron*): comparison between the Gambia and Saloum estuaries. Aquat Living Resour 17(1):65–74

Drinkwater KF, Frank KT (1994) Effects of river regulation and diversion on marine fish and invertebrates. Aquat Conserv 4:135–151

Fielding PJ, Forbes AT, Demetriades NT (1991) Chlorophyll concentrations and suspended particulate loads in St Lucia, a turbid estuary on the east coast of South Africa. S Afr J Mar Sci 11:491–498

Forbes AT, Benfield MC (1986) Tidal behaviour of postlarval penaeid prawns (Crustacea: Decapoda: Penaeidae) in a southeast African estuary. J Exp Mar Biol Ecol 102:23–34

Forbes AT, Cyrus DP (1992) Impact of a major cyclone on a southeast African estuarine lake system. Neth J Sea Res 30:265–272

Forbes AT, Cyrus DP (1993) Biological effects of salinity gradient reversals in a southeast African estuarine lake. Neth J Aquat Ecol 27:265–272

Garcia AM, Vieira JP (2002) The link between El Niño freshwater outflow and the dynamics of an estuarine fish assemblage in South Brazil. J Fish Biol 61(Suppl A):275–276

Garcia AM, Vieira JP, Winemiller KO (2003) Effects of the 1997–1998 El Niño on the dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). Estuar Coast Shelf Sci 57:489–500

Gillanders BM, Kingsford MJ (2002) Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. Oceanogr Mar Biol 40:233–309

Griffiths SP (2001) Factors influencing fish composition in an Australian intermittently open estuary. Is stability salinity dependent? Estuar Coast Shelf Sci 52(6):739–751

Grindley JR (1976) Zooplankton of St Lucia. In: Heydorn AEF (ed) St Lucia scientific advisory council workshop meeting at Charters Creek 15–17 February 1976. Natal Parks, Game and Fish Preservation Board, Pietermaritzburg, pp 1–8

Grindley JR, Heydorn AEF (1970) Red water and associated phenomena in St Lucia. S Afr J Sci 67:210–213

Harris SA, Cyrus DP (1995) Occurrence of fish larvae in the St Lucia Estuary, KwaZulu-Natal, South Africa. S Afr J Mar Sci 16:333–350

Hedgpeth JW (1967). Ecological aspects of the Laguna Madre, a hypersaline estuary. In: Lauff GH (ed) Estuaries. American Association for the Advancement of Science, Washington, D.C., pp 408–419

Helfman GS, Collette BB, Facey DE (1997) The diversity of fishes. Blackwell Science, Malden

Hesp SA, Potter IC, Schubert SRM (2004) Factors influencing the timing and frequency of spawning and fecundity of the goldlined seabream (*Rhabdosargus sarba*) (Sparidae) in the lower reaches of an estuary. Fish Bull 102(4):648–660

Hill BJ (1979) Biology of the crab *Scylla serrata* (Forskål) in the St Lucia system. Trans R Soc S Afr 44:55–62

Hill BJ, Blaber SJM, Boltt RE (1975) The limnology of Lagoa Poelela. Trans R Soc S Afr 41:263–271

Hobday DK (1975) Quaternary sedimentation and development of the lagoonal complex, Lake St Lucia, Zululand. Ann S Afr Mus 71:93–113

Hutchison IPG (1974) Lake St Lucia research report, vol. 2: St Lucia lake and estuary hydrographic data. Hydrological Research Unit, University of the Witwatersrand, Johannesburg

Hutchison IPG (1976) The hydrology of the St Lucia system. In: Heydorn AEF (ed) St Lucia scientific advisory council workshop meeting at Charters Creek 15–17 February 1976. Natal Parks, Game and Fish Preservation Board, Pietermaritzburg, pp 1–15

Hutchison IPG (1977) Lake St Lucia – the computer points the way. Afr Wildlife 31(2):25–27

Hutchison IPG, Midgley DC (1978) Modelling the water and salt balance in a shallow lake. Ecol Model 4:211–235

Hutchison IPG, Pitman WV (1977) Lake St Lucia: mathematical modelling and evaluation of ameliorative measures. Civil Eng S Afr 19:75–82

Jaureguizar AJ, Menni R, Bremec C, Mianzan H, Lasta C (2003) Fish assemblage and environmental patterns in the Rio de la Plata estuary. Estuar Coast Shelf Sci 56:921–933

Johnson IM (1977) A study of the phytoplankton of the St Lucia system. MSc dissertation, University of Natal, Pietermaritzburg

Joubert, LS, Davies DH (1966) The penaeid prawns of the St Lucia lake system. Invest Rep Oceanogr Res Inst 13:1–40

Jubb RA (1979) Cichlid fish mortality: Kasouga River estuary. Lammergeyer 27:51

Lappalainen A, Shurukhin A, Alekseev G, Rinne J (2000) Coastal fish communities along the northern coast of the Gulf of Finland, Baltic Sea: responses to salinity and eutrophication. Int Rev Hydrobiol 85:687–696

Lee C-S, Tamaru CS, Kelley CD, Moriwake A, Miyamoto GT (1992) The effect of salinity on the induction of spawning and fertilization in the striped mullet, Mugil cephalus. Aquaculture 102:289–296

Maetz J, Evans DH (1972) Effects of temperature and branchial sodium exchange and extrusion mechanisms in seawater-adapted flounder Platichthys flesus L. J Exp Biol 56:565–585

Mann BQ, James NC, Beckley LE (2002) An assessment of the recreational fishery in the St Lucia estuarine system, KwaZulu-Natal, South Africa. S Afr J Mar Sci 24:263–279

Martin TJ (1988) Interaction of salinity and temperature as a mechanism for spatial separation of three co-existing species of Ambassidae (Cuvier) (Teleostei) in estuaries on the south-east coast of Africa. J Fish Biol 33(Suppl A): 9–15

Martin TJ (1990) Osmoregulation in three species of Ambassidae (Osteichthyes: Perciformes) from estuaries in Natal. S Afr J Zool 25:229–234

Martin TJ, Cyrus DP, Forbes AT (1992) Episodic events: the effects of cyclonic flushing on the ichthyoplankton of St Lucia estuary on the southeast coast of Africa. Neth J Sea Res 30:273–278

McBride RS, MacDonald TC, Matheson RE, Rydene DA, Hood PB (2001) Nursery habitats for ladyfish, Elops saurus, along salinity gradients in two Florida estuaries. Fish Bull 99(3):443–458

Mehl JAP (1973) Ecology, osmoregulation and reproductive biology of the white steenbras Lithognathus lithognathus (Teleostei: Sparidae). Zool Afr 8:157–230

Millard NAH, Broekhuysen GJ (1970) The ecology of South African estuaries. Part 10. St Lucia. A second report. Zool Afr 5:277–307

Mires D, Shak Y, Shilo S (1974) Further observations on the effect of salinity and temperature changes on Mugil capito and Mugil cephalus fry. Bamidgeh 26:104–109

Moser ML, Gerry LR (1989) Differential effects of salinity changes on two estuarine fishes, Leiostomus xanthurus and Micropogonias undulatus. Estuaries 12(1):35–41

Nordby SN, Zedler JB (1991) Responses of fish and macrobenthic assemblages to hydrologic disturbances in Tijuana Estuary and Los Peñasquitos Lagoon, California. Estuaries 14(1):80–93

Owen RK, Forbes AT (1997) Salinity, floods and the infaunal macrobenthic community of the St Lucia estuary, KwaZulu-Natal, South Africa. S Afr J Aquat Sci 23:14–30

Pooley AC (1973) Notes on the ecology of the Lake St Lucia crocodile population. IUCN Suppl Paper 41:81–89

Raseira MB, Vieira JP, Garcia AM (2002) The beach seine fish assemblage of the Patos Lagoon and marine adjacent areas, Brasil: from the ocean to the limnic. J Fish Biol 61(Suppl A):279

Simier M, Blanc L, Aliaume C, Diouf PS, Albarat JJ (2004) Spatial and temporal structure of fish assemblages in an "inverse estuary", the Sine Saloum system (Senegal). Estuar Coast Shelf Sci 59(1):69–86

Skelton PH (1993) A complete guide to the freshwater fishes of southern Africa. Southern Book Publishers, Halfway House, South Africa, 388 pp

Smith MM, Heemstra PC (1986) Smiths' sea fishes. Macmillan South Africa, Johannesburg, 1047 pp

Steinke TD, Ward CJ (1988) Litter production by mangroves. II St Lucia estuary and Richards Bay. S Afr J Bot 54:445–454

Strydom NA (2000) Possible de-lousing behaviour by the dusky kob. Ichthos 64:9

Strydom NA, Whitfield AK, Paterson AW (2002) The influence of altered freshwater flow regimes on larval and juvenile Gilchristella aestuaria (Pisces: Clupeidae) abundance in the upper reaches of two South African estuaries. Mar Freshwater Res 53:431–438

Strydom NA, Whitfield AK, Wooldridge T (2003) The role of estuarine type in characterizing early stage fish assemblages in warm temperate estuaries, South Africa. Afr Zool 38(1):28–43

Sylvestor JR, Nash CE, Emberson CR (1975) Salinity and oxygen tolerances of egg and larvae of Hawaiian striped mullet, Mugil cephalus L. J Fish Biol 7:621–629

Taylor RH (1991) The greater St Lucia wetland park. Parke-Davis for Natal Parks Board, Pietermaritzburg

Taylor RH (1993) Proceedings of the workshop on water requirements for Lake St Lucia. Department of Environment Affairs, Pretoria, ISBN 0-620-17459-5, pp 1–83

Taylor R, Kelbe B, Haldorsen S, Botha GA, Været L, Wejden B, Bjørkenes MS (in press) Groundwater-dependent ecology of the shoreline of the subtropical Lake St Lucia estuary. Environ Geol

van der Elst RP (1972) Fresh water fish in super saline waters. Natal Wildlife 13(3):13

van der Elst RP, Blaber SJM., Wallace JH, Whitfield AK (1976) The fish fauna of Lake St Lucia under different salinity regimes. In: Heydorn AEF (ed) St Lucia scientific advisory council workshop meeting at Charters Creek 15–17 February 1976. Natal Parks, Game and Fish Preservation Board, Pietermaritzburg, pp 1–20

Vidy G (2000) Estuarine and mangrove systems and the nursery concept: which is which? The case of the Sine Saloum system (Senegal). Wetlands Ecol Manage 8:37–51

Vrdoljak SM (2004) Spatial and temporal dynamics of freshwater wetlands on the Eastern Shores of St Lucia, as reflected by their macrofaunal composition and distribution. MSc dissertation, University of KwaZulu-Natal, Durban

Wallace JH (1975) The estuarine fishes of the east coast of South Africa. Part 1. Species composition and length distribution in the estuarine and marine environments. Part 2. Seasonal abundance and migrations. Invest Rep Oceanogr Res Inst 40:1–72

Wallace JH, van der Elst RP (1975) The estuarine fishes of the east coast of South Africa. Part 4. Occurrence of juveniles in estuaries. Part 5. Ecology, estuarine dependence and status. Invest Rep Oceanogr Res Inst 42:1–63

Ward CJ (1976). Aspects of the ecology and distribution of submerged macrophytes and shoreline vegetation of Lake St Lucia. In: Heydorn AEF (ed) St Lucia scientific advisory council workshop meeting at Charters Creek 15–17 February 1976. Natal Parks, Game and Fish Preservation Board, Pietermaritzburg, pp 1–12

Whitfield AK (1977) Predation of fish in Lake St Lucia, Zululand. MSc dissertation, University of Natal, Pietermaritzburg

Whitfield AK (1980) Food chains in Lake St Lucia. In: Bruton MN, Cooper KH (eds) Studies on the ecology of Maputaland. Wildlife Society, Durban and Rhodes University, Grahamstown, pp 427–431

Whitfield AK (1986) Fish community structure response to major habitat changes within the littoral zone of an estuarine coastal lake. Environ Biol Fish 17:41–51

Whitfield AK (1994) An estuary-association classification for the fishes of southern Africa. S Afr J Sci 90:411–417

Whitfield AK (1995) Mass mortalities of fish in South African estuaries. S Afr J Aquat Sci 21:29–34

Whitfield AK (1998) Biology and ecology of fishes in southern African estuaries. Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology No. 2, 1–223

Whitfield AK (1999) Ichthyofaunal assemblages in estuaries: a South African case study. Rev Fish Biol Fisheries 9:151–186

Whitfield AK, Blaber SJM (1978a) Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. J Fish Biol 13:675–691

Whitfield AK, Blaber SJM (1978b) Distribution, movements and fecundity of Mugilidae at Lake St Lucia. Lammergeyer 26:53–63

Whitfield AK, Blaber SJM (1978c) Resource segregation among iliophagus fish in Lake St Lucia, Zululand. Environ Biol Fish 3:293–296

Whitfield AK, Blaber SJM (1979a) The distribution of the freshwater cichlid *Sarotherodon mossambicus* in estuarine systems. Environ Biol Fish 4:77–81

Whitfield AK, Blaber SJM (1979b) Feeding ecology of piscivorous birds at Lake St Lucia. Part 3: swimming birds. Ostrich 50:10–20

Whitfield AK, Blaber SJM (1980) The diet of *Atilax paludinosus* (water mongoose) at St Lucia, South Africa. Mammalia 44:315–318

Whitfield AK, Heeg J (1977) On the life cycles of the cestode *Ptychobothrium belones* and nematodes of the genus *Contracaecum* from Lake St Lucia, Zululand. S Afr J Sci 73:121–122

Whitfield AK, Wooldridge TH (1994) Changes in freshwater supplies to southern African estuaries: some theoretical and practical considerations. In: Dyer KR, Orth RJ (eds) Changes in fluxes in estuaries: implications from science to management. Olsen and Olsen, Fredensborg, pp 41–50

Whitfield AK, Blaber SJM, Cyrus DP (1981) Salinity ranges of some southern African fish species occurring in estuaries. S Afr J Zool 16:151–155

Wright CI, Mason TR (1990) Sedimentary environment and facies of St Lucia estuary mouth, Zululand, South Africa. J Afr Earth Sci 11:411–420

Young GC, Potter IC (2002) Influence of exceptionally high salinities, marked variations in freshwater discharge and opening of estuary mouth on the characteristics of the ichthyofauna of a normally-closed estuary. Estuar Coast Shelf Sci 55:223–246

Young GC, Potter IC, Hyndes GA, de Lestang S (1997) The ichthyofauna of an intermittently open estuary: implications of bar breaching and low salinities on faunal composition. Estuar Coast Shelf Sci 45:53–68