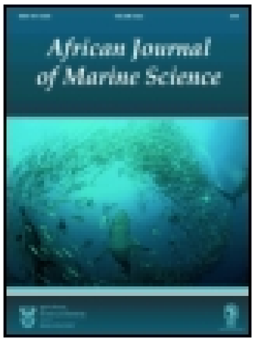

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Critical review

When the flathead mullet left St Lucia

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The St Lucia estuarine system on the east coast of South Africa is a declared World Heritage Site and Ramsar Site of International Importance. A major ecological feature of St Lucia during the last century was the annual spawning migration of the flathead mullet *Mugil cephalus* down the system in the first half of each year. Top predators, such as the African fish eagle *Haliaeetus vocifer*, white pelican *Pelecanus onocrotalus*, Nile crocodile *Crocodylus niloticus* and Zambezi shark *Carcharhinus leucas*, have made extensive use of adult *M. cephalus* as a food resource. With the advent of prolonged closure of the St Lucia mouth in the first decade of the 21st century, caused by the lack of St Lucia system connectivity with the Mfolozi River and a prolonged drought, this spawning migration has ceased to exist. The almost complete disappearance of *M. cephalus* was reinforced in the second decade of this century by a continued lack of any estuarine–marine connectivity. This loss of connectivity between Lake St Lucia and the sea for more than 12 years is longer than the normal life cycle of *M. cephalus*, and the possibility exists that the putative subpopulation of this species that occupied the system prior to the turn of the century may have been rendered locally extinct. In January 2021, the berm at the mouth of the estuary was artificially breached and the outflow of St Lucia estuarine waters into the sea occurred for the first time since 2002. However, it remains to be seen whether the recovery of the *M. cephalus* population to pre-2000 levels will occur over the short term (year) or longer term (decade). It is strongly recommended that an adaptive management strategy, rather than a fixed management approach, be adopted for the sake of future connectivity of the St Lucia system to the marine environment.

Keywords: ecosystem connectivity, Lake St Lucia, Mfolozi River, *Mugil cephalus*, piscivorous predators, population status, spawning migration

Introduction

The flathead mullet *Mugil cephalus* has a life-history cycle that encompasses mainly marine and estuarine environments but can also extend into fresh waters (Whitfield et al. 2012) (Figure 1). In most parts of the world *M. cephalus* spawns in the nearshore marine environment, the egg and embryo stages drift passively in ocean currents, and there is an onshore migration at the postflexion larval stage and first entry into estuaries at about 10 mm standard length (Wallace 1975a, 1975b). Some of these 0+ juveniles move up into the headwater region of certain estuaries, sometimes extending into adjoining river catchments (Bok 1979). Juvenile and subadult life stages mainly occupy estuarine waters, with adults then migrating to the sea to spawn (Wallace 1975b). Some adults return to estuaries following breeding (Whitfield and Blaber 1978a), but others may remain within the marine environment for most of their life cycle.

In the first half of the last century there was a popular article published in the *South African Angler* magazine entitled "When the pelicans come to St Lucia" (Tooth 1946). This article described the annual spawning migration of *M. cephalus* down the Narrows (Figure 2) and into the St Lucia Estuary. These pre-spawning mullet shoals were preyed upon by a variety of large piscivores, including the white pelican *Pelecanus onocrotalus*. To quote from Tooth (1946, p 9):

> By some instinct all of their own, the pelicans know when the mullet are to arrive, and a few days before this, thousands of pelicans are to be seen waiting at the mouth of the estuary. And so from now, the pelicans will be followed by anglers in their hundreds who know that this is the time of the year to get the best results. It is usually about the beginning to the middle of May that the mullet arrive; thousands and thousands of them in great shoals milling and jumping out of the water, being chivvied and harried by large dusky kob and blackfin sharks. The mullet, in their efforts to escape, make for shallow water where the pelicans await them. Indeed, many a boat from which anglers have been fishing has been known to be swamped by hundreds of these mullets leaping out of the water.

In this review, the life cycle and annual spawning migration of *M. cephalus* in the St Lucia system is described using the published literature. The scientific basis for the annual occurrence of the above event, its importance to the ecological functioning of the system, and the reasons for its disappearance from St Lucia over the past two decades

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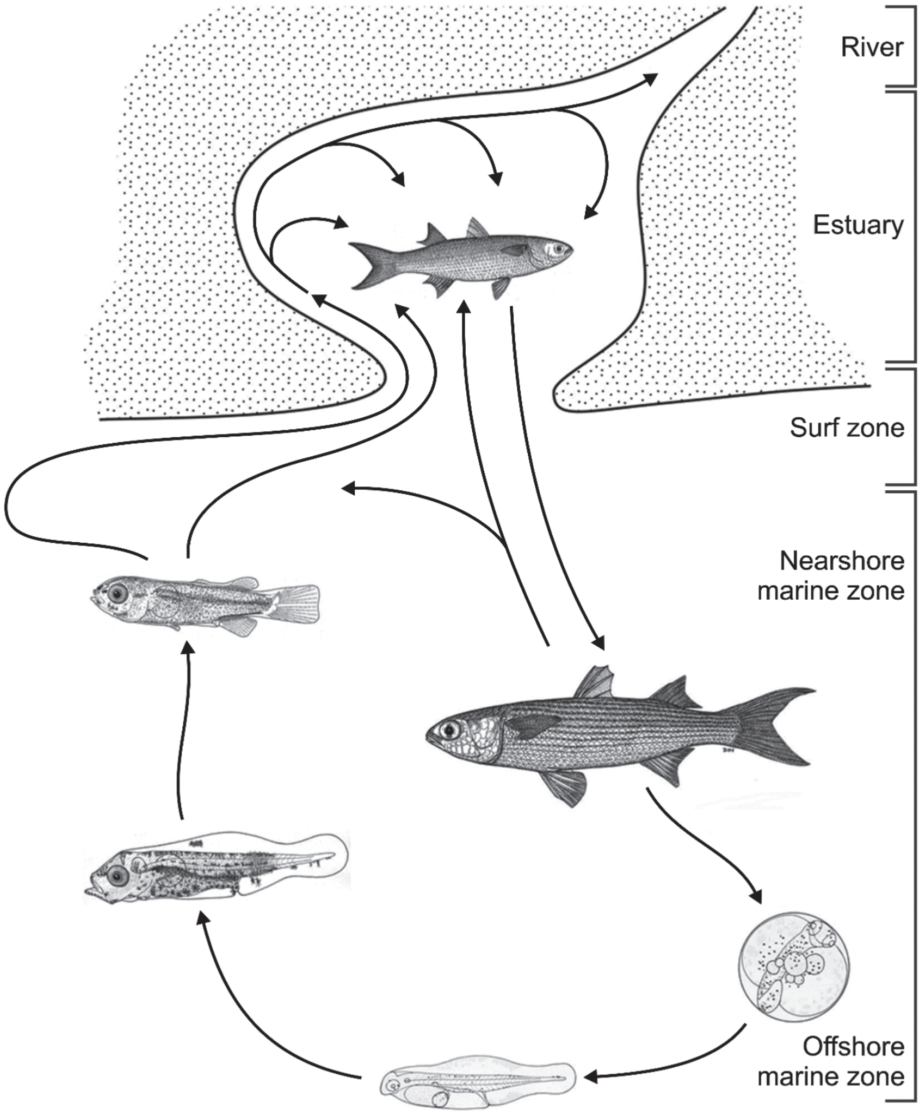

Figure 1: Generalised life cycle of the flathead mullet *Mugil cephalus* (after Whitfield et al. 2012)

are the subjects of the discussion below. I also explore the possibility that the putative St Lucia subpopulation of *M. cephalus* has now disappeared and is unlikely to return in the future. Finally, the implications of a proposed change towards a more adaptive management approach for the St Lucia ecosystem are discussed, as well as the benefits that could accrue in terms of the nursery function of the system for both marine fishes and invertebrates.

Biology and ecology of* M. cephalus *in the St Lucia system

Mugil cephalus was formerly a dominant marine fish species in the St Lucia system (Wallace 1975a, 1975b; Wallace and van der Elst 1975), initially spending approximately 3 years in the lakes (Figure 2) while growing from newly recruited 0+ juveniles to mature adults (Whitfield and Blaber 1978a). *Mugil cephalus* is not only representative of the migratory life cycles undertaken by a wide variety of mullet species that inhabit the lake, but the species also reflects the life histories of other marine fish taxa that utilise the St Lucia system as a nursery area (Wallace and van der Elst 1975). In addition, a proportion of spent *M. cephalus* used to return to the lake system following spawning (Wallace 1975b), thus reinforcing the importance of marine/estuarine connectivity for this species (Whitfield 2019).

Mugil cephalus can be regarded as a keystone species in the Lake St Lucia food web. This is because of its numerical abundance and biomass dominance in the trophic functioning of both the lake and the estuary (Wallace 1975a; Whitfield and Blaber 1978a). As a detritivore and primary consumer of particulate organic matter and benthic microalgae in the lake (Blaber 1976; Whitfield and Blaber 1978b), *M. cephalus* utilises the base of the trophic pyramid, from where it transfers energy to a variety of large piscivorous predators (see next section).

The annual spawning migration of *M. cephalus* from False Bay and North Lake, through South Lake, down the Narrows and then into the St Lucia Estuary (Figure 2) has been described by Wallace (1975a, 1975b) and confirmed

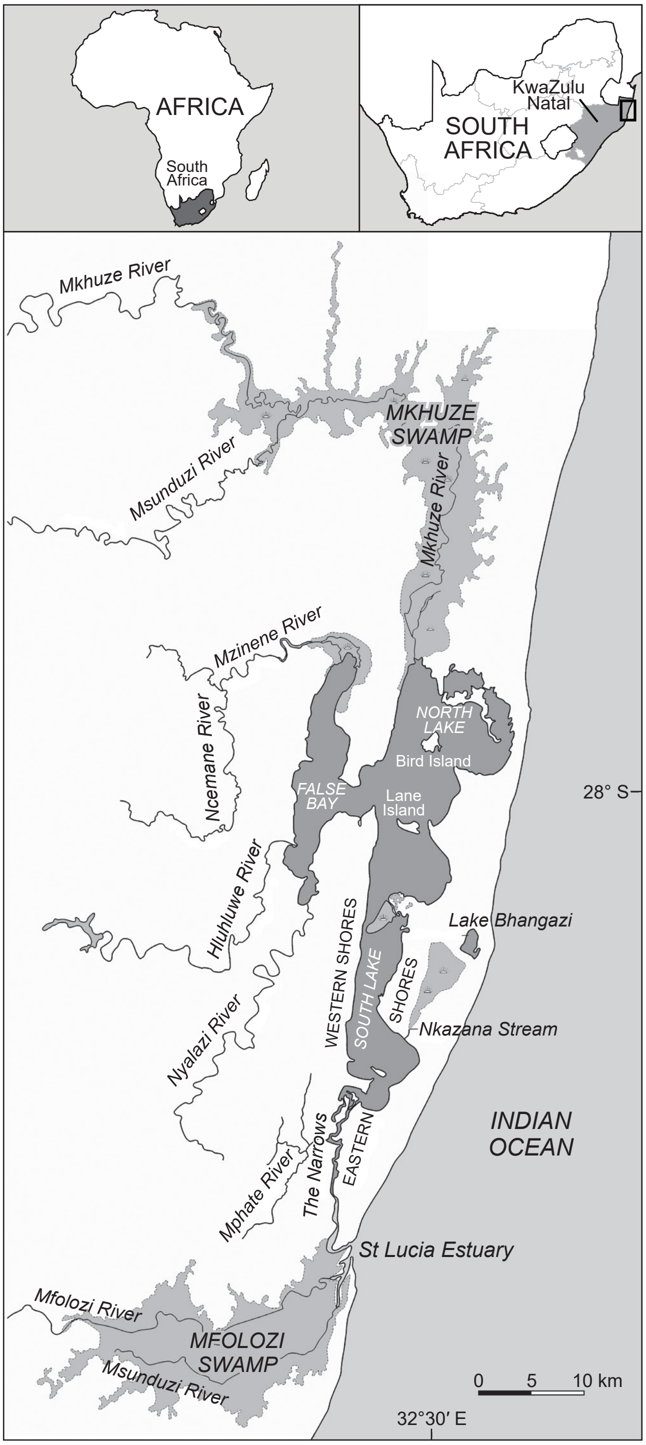

Figure 2: Map of the St Lucia system (KwaZulu-Natal, South Africa) showing localities mentioned in the text. Grey shading represents historic swamp areas associated with the system

by Whitfield and Blaber (1978a). During the late summer months (January–March), shoaling activity by adult and subadult *M. cephalus* occurred in North Lake, and a general southward movement of shoals several kilometres in length took place towards South Lake. However, the migratory urge of the sexually immature individuals was not as strong as that in the adults, and the subadults did not follow the shoals moving into South Lake.

The sizes of the shoals could be gauged by the jumping activity of the fish, with several hundred sometimes leaping into the air at the same time. Jumping activity occurred during the day and night but the exact cause of this behaviour has not been determined. Disturbance by sharks, crocodiles and boating activities always generated a spike in fish jumping behaviour but it also appeared to occur when no predatory or boat activity was recorded (personal observation). Apart from evading predators, the jumping behaviour might also be: (i) a function of increasing oxygen uptake in the pharyngobranchial organ (Hoese 1985); (ii) a means of dislodging external parasites (Atkinson et al. 2018); or (iii) a mechanism to communicate with adult conspecifics in terms of the direction and progression of these large aggregations towards the sea (Whitfield and Blaber 1978a).

Catches of adult *M. cephalus* in South Lake remained high between February and early May and the adults then moved into the Narrows and down into the St Lucia Estuary. Records kept by conservation staff at the St Lucia Estuary indicate that the mullet shoals were remarkably consistent in their dates of arrival, which event occurred between 12 April and 12 May for every year between 1968 and 1974 (Wallace 1975a). Similar dates of arrival were recorded in 1975 and 1976 by the author. In the estuary, the lake shoals appeared to be joined by marine *M. cephalus* adults to form massive shoals prior to spawning and were pursued by sharks from the sea, and pelicans and crocodiles in the estuary.

The annual reproductive cycle for *M. cephalus* in Lake St Lucia and the St Lucia Estuary is depicted in Figure 3. These data show that gonad development in adult fish, mostly 3–4 years in age, commences in March and April, with the majority reaching an active-ripe and ripe stage of development by May and June when most marine spawning occurs (Wallace 1975b). A proportion of spent individuals have been recorded returning to St Lucia between June and December following spawning (Figure 3). Unfortunately, the St Lucia Estuary mouth became constricted between June and August 1970 and this resulted in adult *M. cephalus* in the estuary and lake resorbing their gonads (Figure 3) due to an inability to access the marine environment where spawning usually occurs (Wallace 1975b). Large adult female *M. cephalus* from St Lucia produce proportionally more ova than smaller individuals, with a female of 54 cm SL producing approximately 2 632 000 ova in a single spawning season, whereas an adult female of 34 cm SL produced only about 861 000 ova (Whitfield and Blaber 1978a).

The *M. cephalus* participating in the 1976 spawning migration were estimated to be between 3 and 7 years of age (Whitfield and Blaber 1978a). In addition, the oligohaline waters flowing down the Narrows and into the sea during that year precluded inshore marine spawning that may have occurred during previous years when ripe running *M. cephalus* were captured within 150 m of the St Lucia Estuary mouth (Wallace 1975b). During April and May 1976 heavy catchment rain resulted in turbid, silt-laden water entering the coastal zone, and shoals of adult *M. cephalus* were observed congregating on the outskirts

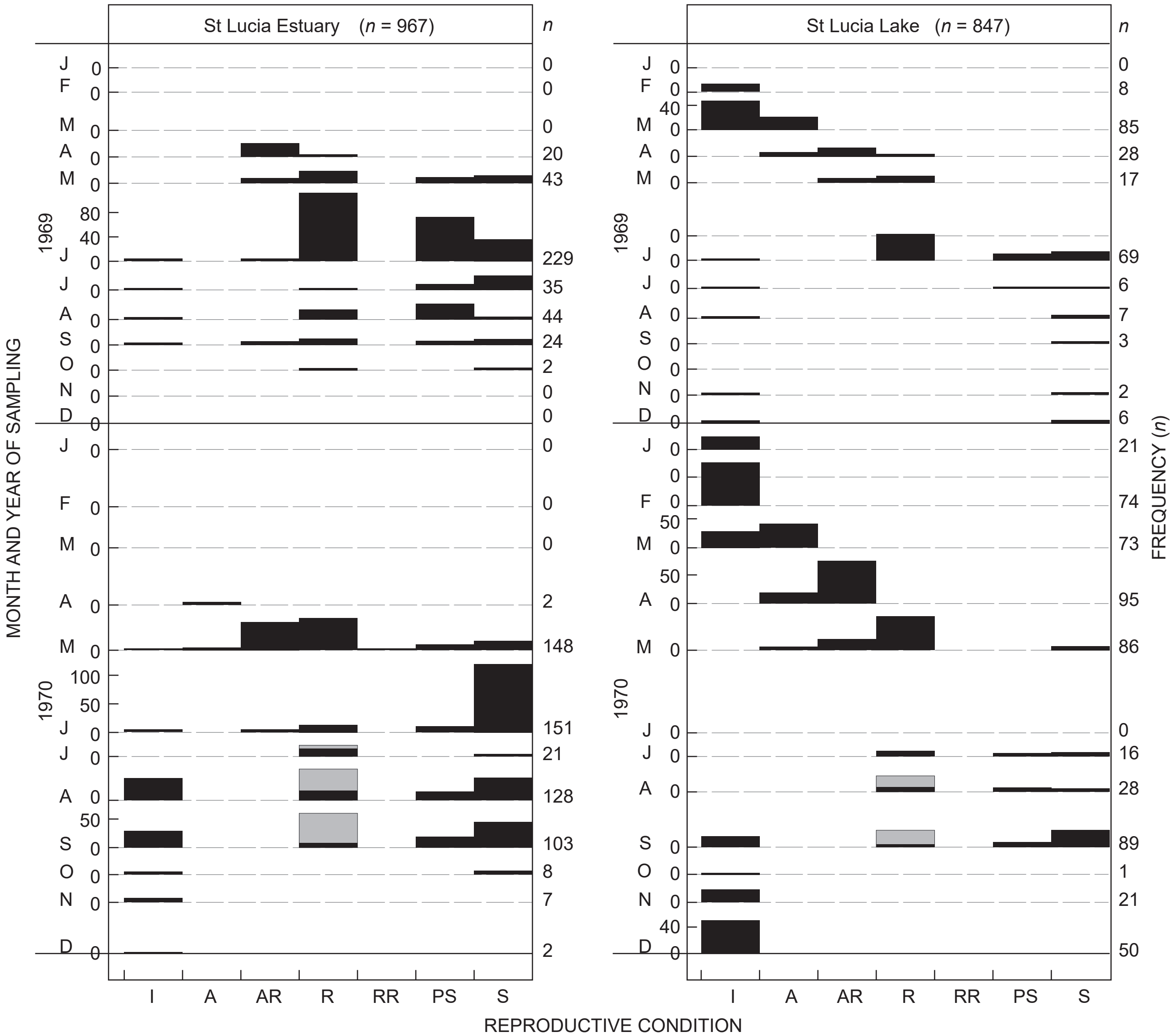

Figure 3: Numbers of adult *Mugil cephalus* from the St Lucia system, South Africa, in various stages of gonadal development in the different months during 1969 and 1970 (adapted from Wallace 1975b). The lightly shaded blocks indicate fish that were in the process of resorbing their gonads due to the lack of access to the sea. Fish reproductive condition: I = inactive; A = active; AR = active ripe; R = ripe; RR = ripe running; PS = partially spawned; S = spent

of the floodwaters and did not enter the St Lucia Estuary. According to Sylvester et al. (1975), only 10% of fertilised *M. cephalus* eggs survive a salinity of 26 over 24 hours, whereas 91% survive a salinity of 32 over 24 h.

Not all the adult *M. cephalus* spawn at the same time since both ripe and spent individuals have been simultaneously recorded in the St Lucia system (Wallace 1975b) (Figure 3). In addition, the recording of partially spawned individuals in the system (Figure 3) strongly suggests that this species is a serial spawner. Both of the above strategies ensure that a protracted spawning season occurs, which gives rise to an extended recruitment period into estuaries, thus safeguarding against temporary adverse environmental conditions in either the sea or in estuarine nursery habitats. Fortunately, May to September is a relatively stable period in most KwaZulu-Natal estuaries, as river flooding is usually confined to the summer months.

Recruitment of 0+ juveniles into the St Lucia system occurs mainly in the 10–20 mm size class, with most early juveniles entering the system from June to September (Wallace and van der Elst 1975). Movement of *M. cephalus* of 10–30 mm SL up into the northern lakes can be quite rapid and can average as much as 0.8 km per day (Whitfield and Blaber 1978a). Growth of juveniles in food-rich subtropical estuaries such as St Lucia is rapid, with fish attaining a growth rate of as much as 17 mm per month in the first year. Sexual maturity begins at about 35 cm TL for both males and females, with at least 80% of the sampled population being sexually mature at about 45 cm TL for males and 49 cm TL for females (Wallace 1975b).

Natural predation on M. cephalus *in the St Lucia system*

There is strong evidence to suggest that *M. cephalus* was an important prey item for natural apex predators such as the African fish eagle *Haliaeetus vocifer*, white pelican, Zambezi shark *Carcharhinus leucas* and Nile crocodile *Crocodylus niloticus* (Whitfield 1980). Indeed, loss of *M. cephalus* from the St Lucia ecosystem would be expected to have a material impact on the ecology of these top predators and therefore the functioning of the entire ecosystem. In addition, extensive illegal gillnetting in the northern lake compartments were an additional heavy mortality factor for *M. cephalus* in the St Lucia system (Mann 1995).

Scores of large Nile crocodiles gathered along the length of the Narrows each year to prey on the migrating mullet (Whitfield and Blaber 1979a) (Figure 4). It is probable that the crocodiles followed the mullet shoals down the lake and into the Narrows but that those from the Mfolozi River were not able to join the St Lucia crocodiles as there was no connection between the St Lucia and Mfolozi systems at the time of the Whitfield and Blaber (1979a) study. The Narrows ensured that the shoals of migrating *M. cephalus* were densely packed and therefore the fish were extremely vulnerable to capture by crocodiles, most of which were 2–3 m in length (Whitfield and Blaber 1979a). *Mugil cephalus* were captured underwater and then carried to the shore where the grip on the fish was altered before the fish was swallowed headfirst. Decline in the daily numbers of crocodiles in the St Lucia Narrows after the departure of the *M. cephalus* shoals to the sea to spawn (Figure 4) may be linked to most of the crocodiles returning to the lake until the cycle repeated itself the following year.

A similar pattern of white pelican numbers in the St Lucia Estuary and Narrows was recorded by Whitfield and Blaber (1979b). However, the numbers of pelicans following the *M. cephalus* shoals down the Narrows in 1976 (Figure 5) was considerably less than in previous years and may have been linked to the near-absence of marine *M. cephalus* shoals entering the estuary from the sea in this particular year (Whitfield and Blaber 1979b). During April 1957 and 1958, large shoals of adult *M. cephalus* entered the St Lucia Estuary from the sea and moved north up the Narrows, being followed by large flocks of foraging white pelicans (Feely 1962). When preying on the migrating fish, a flock of pelicans would form an arc and herd part of a shoal into the shallows where the mullet were then captured and swallowed. The breeding of white pelicans on islands in North Lake (Figure 2) commences soon after the conclusion of the annual *M. cephalus* spawning migration in May.

The African fish eagle at Lake St Lucia preyed predominantly on Mugilidae, especially *M. cephalus*, during 1975/1976 (Whitfield and Blaber 1978c). This is because the mugilids forage benthically but form shoals at the water surface when not feeding, thus becoming vulnerable to fish eagle predation. The sizes of *M. cephalus* being recorded as prey of fish eagles at Lake St Lucia in relation to the size composition of *M. cephalus* in gillnet catches from the lake during 1975 and 1976 are shown in Figure 6 (Whitfield and Blaber 1978c). The *M. cephalus* captured by fish eagles ranged in size from 25 to 55 cm SL, with most of them being adult fish. It is perhaps significant that the start of the fish eagle breeding season in the St Lucia system (May) coincides with the annual spawning migration of *M. cephalus*.

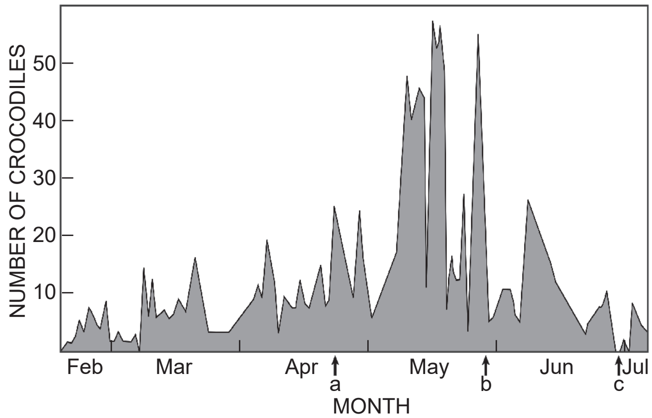

Figure 4: Numbers of Nile crocodiles *Crocodylus niloticus* observed by a tour boat operator in the St Lucia Narrows during 1976. Point 'a' represents the date of arrival of flathead mullet *Mugil cephalus* in the Narrows; point 'b' indicates the arrival of mullet shoals in the St Lucia Estuary; and point 'c' indicates when the first spent *M. cephalus* were recorded in South Lake upon their return to the system following spawning in the sea (after Whitfield and Blaber 1979a)

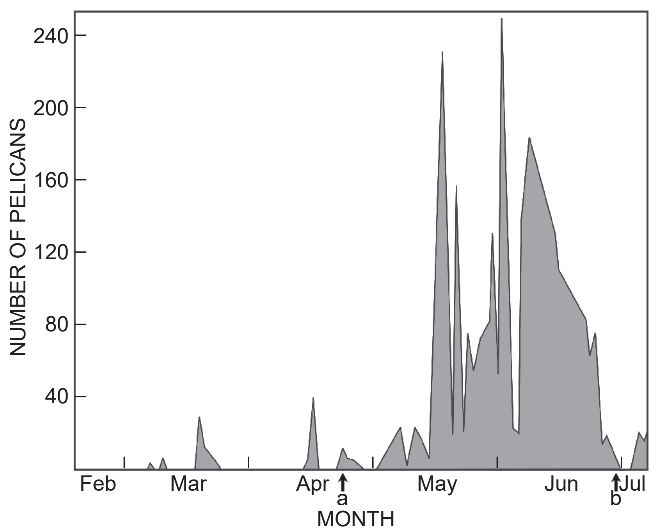

Figure 5: Ground-level counts of white pelicans *Pelecanus onocrotalus* in the St Lucia Narrows made by a boat-launch operator in 1976. Point 'a' is the date of arrival of *Mugil cephalus* shoals in the Narrows; point 'b' is the date when the first spent *M. cephalus* were recorded in South Lake following spawning in the sea (after Whitfield and Blaber 1979b)

Prolonged estuary mouth closure and the status of M. cephalus *in the St Lucia system*

During most of the second half of the last century the St Lucia Estuary was artificially maintained in an open-mouth state using a dredger, and several periods of extreme hypersalinity (>80) were recorded during prolonged drought periods. A salinity of 60 is tolerated easily by *M. cephalus* in the lake but the numbers of mullet decline

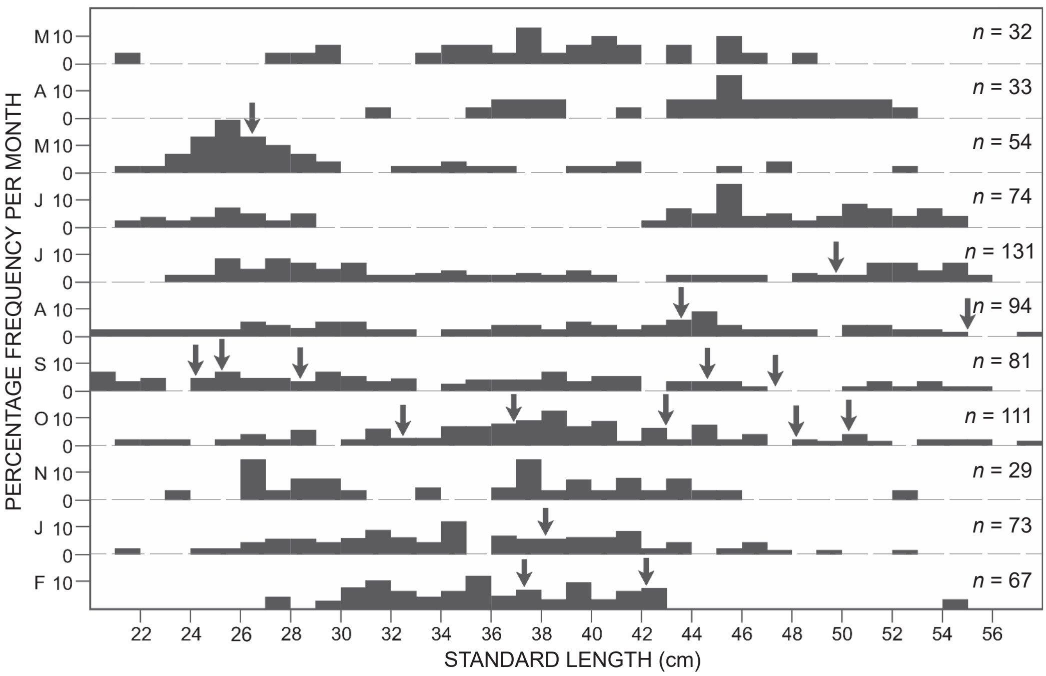

Figure 6: Size frequencies of *Mugil cephalus* in gillnet catches from Lake St Lucia, South Africa, during the period March 1975 to February 1976, in relation to the confirmed sizes (arrows) of individual *M. cephalus* in the lake that had been preyed on by African fish eagles *Haliaeetus vocifer* (after Whitfield and Blaber 1978c)

rapidly between salinities of 70 and 80, with this species being either dead or absent from areas of St Lucia where salinities rise above 80 (Wallace 1975a). Modelling has shown that although lake salinities as high as 70 would have sometimes been recorded under the natural dry cycle at St Lucia, salinities above 80 would not have occurred, yet have been a frequent occurrence during the last 70 years. These extreme hypersaline conditions, under both open and closed estuary-mouth conditions, have led to major fish kills within the St Lucia system, including of *M. cephalus* (Whitfield et al. 2006).

During the first drought decade of this century (2000–2009), when the connectivity between Lake St Lucia and the sea was severely restricted or lost altogether (Cyrus and Vivier 2006a) and Mfolozi River water was unavailable to the lake, extreme hypersaline conditions were recorded. In addition, prolonged evaporation with little freshwater input to the lakes resulted in up to 90% of the water surface area being lost for extended periods (Cyrus et al. 2010a). Under these conditions, the annual *M. cephalus* spawning migration did not take place and the available fish catch data suggest that most of the *M. cephalus* present within the system perished during the time of mouth closure.

A breaching of the St Lucia Estuary mouth by overwash waves generated by an offshore cyclone, Cyclone Gamede, in May 2007 resulted in the mouth remaining open for 4 months (Schutte et al. 2020). Recruitment of juvenile and adult *M. cephalus* into the St Lucia system would have been possible, but seine-net and gillnet catch per unit effort (CPUE) for this species during 2006–2008 remained low at a combined total of only 1.15 (a dimensionless index obtained by combining the CPUE values from the different gear types) (Vivier et al. 2010a). Of the three most-abundant fish species in the St Lucia littoral during this period (i.e. Mozambique tilapia *Oreochromis mossambicus*, longspine glassy *Ambassis ambassis* and Cape halfbeak *Hyporhamphus capensis*), only the freshwater *O. mossambicus* was consistently abundant during the last century.

Salinity was the most important factor structuring the ichthyofaunal fish assemblage, and the abundance of estuary-associated marine fish species during this decade (2000–2009) declined by 75% as the system became progressively more saline following isolation from the sea (Schutte et al. 2020). In 2008 there were 51 estuary-associated marine fish species recorded and this declined to 37 species in 2011, with 2 estuarine and 22 marine species being lost to the system altogether.

A question then arose: Could the Mfolozi/Msunduzi Estuary, which had been separated from the St Lucia system in the 1950s and still opened to the sea on a regular basis, act as an alternative refuge for estuary-associated marine fish species that normally recruited into the adjacent St Lucia system? A study by Vivier and Cyrus (2009), again using both seine-nets and gillnets, indicated that although a large number of estuary-associated marine fish species were recorded in the Mfolozi/Msunduzi Estuary, the numbers of fish involved were relatively low since the estuarine area of the Mfolozi is only 1.8 km^2 compared with the area of the St Lucia system at 300–350 km^2. Furthermore, the CPUE of *M. cephalus*, a numerically and biomass dominant species in the St Lucia system, was only 0.23 in the Mfolozi arm of the estuary and 0.09 in the Msunduzi arm of the estuary, where CPUE is again a dimensionless index obtained by combining the values from the different gear types (Vivier and Cyrus 2009).

Although some of the *M. cephalus* stock that would have recruited into the St Lucia system if it had been available may have found refuge in the Mfolozi/Msunduzi Estuary, the numbers of fish involved would have been comparatively small. It is perhaps also notable that none of the top-four littoral estuary-associated species in the Mfolozi/Msunduzi Estuary, namely the bald glassy *Ambassis dussumieri*, slender glassy *Ambassis natalensis*, slimy *Leiognathus equula* and longarm mullet *Moolgarda cunnesius* (Vivier et al. 2010b), were in the top-four species that occurred in the Lake St Lucia littoral during the last century (Whitfield 1977).

The ecological importance of the relinkage of the Mfolozi/Msunduzi river systems to the St Lucia system has been clearly spelt out by Cyrus et al. (2010b). In January 2004, the Mfolozi River was in flood and waters from this system actually spilled into the St Lucia Estuary and Narrows, bringing with it some estuary-associated marine species that were in the Mfolozi/Msunduzi Estuary at the time. Nine estuary-associated marine fish species were subsequently recorded in the St Lucia system by Cyrus and Vivier (2006b), but in low numbers. *Mugil cephalus* were only recorded from South Lake, and all were in the 290–350 mm SL size range, thus indicating that adults predominated. Cyrus and Vivier (2006b) warned that if the St Lucia mouth remained closed to the sea in the following years, these potential first-time spawners would not be able to join breeding populations in the marine environment.

In January 2005, another Mfolozi River flooding event spilled into the St Lucia Estuary and Narrows, but recruitment of estuary-associated marine fishes appeared to be minimal, and those recruits that did enter the St Lucia system were unable to move north of South Lake because of the compartmentalisation of the system brought about by low lake-water levels (Cyrus and Vivier 2006b).

The progressive demise of *M. cephalus* in the St Lucia system is well documented by Schutte et al. (2020) and Cyrus et al. (2020). Fish sampling of the entire St Lucia system between May 2008 and November 2011 revealed that *M. cephalus* comprised a mere 0.05% of the total number of fishes captured (Schutte et al. 2020). Based on four system-wide fish sampling surveys between May 2010 and November 2012, before the Mfolozi Spillway between the Mfolozi and St Lucia Estuary was opened in July 2012, the CPUE of *M. cephalus* was only 0.12 ind. m-netting^{-1} haul^{-1} (0.03% of the total St Lucia fish catch). This CPUE then declined further over the subsequent four sampling occasions from November 2012 until May 2015 to 0.03 ind. m-netting^{-1} haul^{-1} and 0.02% of the total St Lucia fish catch (Cyrus et al. 2020). Thus, the abundance and contribution of the St Lucia *M. cephalus* to the overall fish population has changed dramatically, from being a dominant fish species in the system during the past century to an insignificant component of the ichthyofauna in this century. Indeed, unpublished fish netting data from the entire St Lucia system revealed that no *M. cephalus* were captured during sampling expeditions between the beginning of 2016 and the end of 2019 (Q Schutte, University of Zululand, pers. comm.).

The full reconnection of the Mfolozi River to the St Lucia system in 2012 was primarily responsible for the filling up of the lakes and, towards the end of this decade (2010–2019), oligohaline conditions prevailed in the St Lucia Estuary, Narrows and South Lake (Jones et al. 2020). Unfortunately, semi-drought conditions continued to persist, and summer river flows from the Mfolozi were insufficient to naturally breach the St Lucia Estuary berm. Hence, any possibility of early juvenile recruitment of *M. cephalus* into the St Lucia system was effectively prevented, and *M. cephalus* has almost disappeared from the entire system in recent years (Schutte et al. 2020). It is possible that the deteriorating situation could begin to reverse as a consequence of the assisted breaching of the St Lucia mouth in January 2021 (St Lucia Scientific Technical Advisory Group 2021). Since most *M. cephalus* recruitment into KwaZulu-Natal estuaries occurs between June and September (Wallace and van der Elst 1975), the mouth will need to remain open until at least June for full replenishment of this species into Lake St Lucia to commence. However, the possibility exists that previous *M. cephalus* populations from this region are now depleted and that recruitment will be poor even if the estuary mouth remains open during winter.

Future status of M. cephalus *in the St Lucia system*

Fortunately, the iSimangaliso Wetland Park Authority accepted that the relinkage of the Mfolozi River to the St Lucia Estuary was a high priority for the future ecology of the St Lucia system (Cyrus et al. 2010a; Whitfield et al. 2013). Unfortunately, the Mfolozi fresh water introduced large loads of suspended sediment, which has predictably settled in the St Lucia Estuary and Narrows, causing channel constrictions and a shallowing of both the estuary and the Narrows, and altering the normal particle-size composition of the substratum (Jones et al. 2020). The silt and mud that is deposited as a thick layer over the sand in the lower reaches of the St Lucia system is cause for concern since the particle sizes of these fine sediments is below the mean sand particle size usually ingested by mullet species such as *M. cephalus* (Blaber 1976).

During the past decade, the Mfolozi River flows have been unable to both fill up the St Lucia system and facilitate a natural breaching of the berm at the estuary mouth. This has had dire consequences for the future of estuary-associated marine fish species in the St Lucia system, and *M. cephalus* in particular. However, now that the Mfolozi River is reconnected to the St Lucia system (St Lucia Scientific Technical Advisory Group 2021), and the lake level exceeded mean sea level during February, March and April in 2021 (C Fox, Ezemvelo KwaZulu-Natal Wildlife, pers. comm.), future mouth breaching opportunities are likely to occur more frequently and the drying out of the lake compartments will be much less of a threat than was the case during the past two decades.

Mugil cephalus that occurs in the St Lucia system is part of a cryptic species complex (Whitfield et al. 2012), with fish from this system being part of the southern African clade of *M. cephalus* (Durand and Whitfield 2016). In addition, there is a possibility that this clade is subdivided, like the southern African dusky kob *Argyrosomus japonicus*, into estuarine and more marine subpopulations (Childs et al. 2015). Furthermore, the southern African *A. japonicus*, like *M. cephalus*, is now regarded as a cryptic species and endemic to the region (Barnes et al. 2016).

A major concern is that the putative St Lucia subpopulation of *M. cephalus* has been decimated or possibly eliminated altogether. Although some 'St Lucia' individuals may have survived by using the Mfolozi Estuary during the first decade of this century, the prolonged closure of the joint Mfolozi/St Lucia mouth for most of the second decade may well have been too long to ensure the survival of this putative genetic subpopulation. Assuming there are still some 'St Lucia' *M. cephalus* in existence, it is likely that full recovery to the previous huge shoals that participated in the annual spawning migration down the system will require many years and perhaps even decades of good connectivity between the St Lucia Estuary and the marine environment.

The maximum age recorded for *M. cephalus* in Australia is 11 years (Smith and Deguara 2003), and specimens up to age 10 years have been recorded from a large artificial impoundment in the Eastern Cape Province (Ellender et al. 2012). Globally, it appears that *M. cephalus* can attain a maximum age of 13 years (Thomson 1966). The above information suggests that *M. cephalus* in the St Lucia system may have become temporarily extinct by the time the estuary mouth was artificially breached in January 2021 after having been closed for 12.5 years since August 2008. Clearly there are consequences for *M. cephalus* because of this extremely prolonged closed-mouth phase.

Lake St Lucia is naturally characterised by continual and sometimes large changes in physico-chemical conditions, but during the past century the 'pendulum' has been reaching new and unsustainable extremes because of human activities and interference in the ecology of the system. Indeed, the St Lucia pendulum of ecological states has undergone five extreme-scale swings over the past 100 years, all of which would not have occurred in the pristine state:

- The first unnatural extreme was triggered by the canalisation of the Mfolozi Swamps, with consequent major sedimentation of both the St Lucia Estuary and Narrows.
- The second was the creation of a separate mouth for the Mfolozi River to the south of the St Lucia Estuary and the resultant loss of Mfolozi water to the St Lucia system.
- The third was the artificial maintenance of a permanently open estuary mouth using dredgers in the Narrows and estuary, and the resultant extreme hypersalinity in the upper lakes during drought conditions.
- The fourth was the natural closure of the St Lucia Estuary without a freshwater supply from the Mfolozi River, which resulted in the almost complete evaporation of the lakes during prolonged drought conditions.
- The fifth was the prolonged closure of the system such that ecological connectivity between the estuarine system and the sea threatened the nursery function of St Lucia for marine fish and invertebrate species. Linked to this state was the progressive loss of habitat diversity and the gradual conversion of St Lucia into a coastal lake as opposed to an estuarine lake due to the increased prevalence of fresh water and oligohaline conditions, as well as the loss of all connectivity with the marine environment.

All the above 'states,' which are not equal in their impact on the natural functioning of the system, represent ecological tipping points that would not have occurred in the pristine St Lucia system. Therefore, management of the system needs to avoid tipping points if possible, and the extreme pendulum swings need to be restrained within more-normal ranges of estuarine ecological functionality.

From the above it is apparent that we are at a critical juncture in planning the ongoing management of the St Lucia Estuary in terms of both sediment scouring and biological connectivity. While natural breaching of the St Lucia Estuary is ideal for the ecology of the system, prolonged closed phases of more than a decade are unnatural and push the system into states that would not have occurred in the pristine state. The suggestion is therefore made that we have now entered an era of adaptive management whereby mouth management decisions need to be prioritised according to estuarine ecological principles, considering that the system is operating under major constraints of water-supply reduction and sediment-supply overload.

A final consideration is the size of the St Lucia system relative to all other estuaries in South Africa. When full of water, the St Lucia system covers an area of approximately 35 000 ha compared with a total South African estuarine area of approximately 70 000 ha, constituting approximately 50% of the nursery habitat for estuary-associated fish species in the country (Whitfield et al. 2006). Within KwaZulu-Natal, St Lucia accounts for about 80% of the estuarine area in the province. The loss of St Lucia as a nursery for southern African mugilids, including *M. cephalus*, cannot be overemphasised. In addition, there are some overexploited estuary-associated fish species such as *A. japonicus* that are now down to less than 3% of the original spawner stock biomass (Whitfield et al. 2020). Clearly, the future of many estuary-associated marine fish species, including *M. cephalus* and *A. japonicus*, is closely tied to the estuarine health of the St Lucia system.

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