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Short communication

Bull shark *Carcharhinus leucas* recruitment into the St Lucia Estuary, South Africa, after prolonged mouth closure, and the first observation of a neonate bull shark preyed on by a Nile crocodile *Crocodylus niloticus*

R Daly^{1,2*} , P Le Noury³, TN Hempson^{4,5} , M Ziembicki⁴, JM Olbers⁶ , GM Brokensha⁷ and BQ Mann¹ 

¹ Oceanographic Research Institute (ORI), Durban, South Africa

² South African Institute for Aquatic Biodiversity (SAIAB), Makhanda, South Africa

³ Noble Caledonia, London, United Kingdom

⁴ Oceans Without Borders, Vamizi Island, Quirimbas Archipelago, Cabo Delgado, Mozambique

⁵ ARC Centre of Excellence for Coral Reef Studies, James Cook University, Douglas, Queensland, Australia

⁶ Wildlands Conservation Trust, Pietermaritzburg, South Africa

⁷ The Bigger Picture Films, Durban, South Africa

* Corresponding author, e-mail: ryandaly.mail@gmail.com

Estuaries provide critical nursery habitat for juvenile bull sharks *Carcharhinus leucas*, as they have the ability to withstand a wide range of salinities. St Lucia is the largest estuarine lake in Africa and was once a key nursery for bull sharks until a prolonged and near-continuous period of mouth closure and drought between 2002 and 2021. The estuary mouth was opened for the first time in 13 years on 6 January 2021, and, within 10 days, bull shark pups recruited into the estuary. On 16 January, an adult Nile crocodile *Crocodylus niloticus* was observed preying on a live neonate bull shark which it swallowed whole. This observation provided the first photographic evidence in Africa and highlighted a unique interaction between these species, which are top predators in the freshwater and coastal environments, respectively. Estuaries remain important nursery habitats for bull sharks in the region and we assembled the known records of bull shark occurrence in all South African estuaries. In summary, the rapid recruitment of bull shark pups into St Lucia Estuary is notable for the management and conservation implications for this important estuarine system, as well as for regional bull shark populations.

Keywords: acoustic tagging, coastal wetland management, estuarine biological response, juveniles, shark nursery, World Heritage Site

Introduction

The St Lucia Estuary, located on the east coast of South Africa, is the largest estuarine lake system in Africa and has been part of a UNESCO-designated World Heritage Site since 1999. Its surface area of 300–350 km² makes up almost 80% of the total estuarine area in KwaZulu-Natal Province (KZN) and is the largest nursery habitat for estuarine fish species in South Africa (Mann et al. 2002; Whitfield 2005; Forbes et al. 2020). However, since 2002, increasing water extraction for irrigation upstream, compounded by a period of prolonged drought in the region, meant the mouth did not connect with the sea, except for a short period in 2007 following a big-sea event (Cyrus and Vivier 2006; Taylor 2006; Cyrus et al. 2010, 2020; Schutte et al. 2020). This, and the historic separation of the Mfolozi River from the St Lucia Estuary in 1953 and various management interventions over decades, led to low lake levels and extreme hypersalinity (up to 200 in parts of the lake), causing most of the marine-dependent ichthyofaunal biodiversity to die out (Taylor 2006; Mann and Pradervand 2007; Whitfield and Taylor 2009; Carrasco and Perissinotto 2012; Whitfield

2021). Subsequently, on 6 January 2021, the beach berm separating the St Lucia Estuary from the sea was artificially breached, allowing the system to reconnect with the sea—in anticipation that it would restore some of the estuarine ecological functioning of the system and in response to ongoing concerns from the public relating to the accumulation of sediment, the continued closed mouth, the freshwater state of the entire St Lucia system, the growth of reeds choking part of the estuary, and the back-flooding of sugarcane fields in the Mfolozi floodplain, among other concerns (AK Whitfield, South African Institute for Aquatic Biodiversity, pers. comm.).

Bull sharks *Carcharhinus leucas* are one of the few elasmobranchs able to tolerate a wide range of salinities (Pillans et al. 2008) and they typically use estuaries for nursery habitat as these environments provide reduced risk of predation and competition (Heupel and Simpfendorfer 2011). Bull sharks have been recorded in 12 of the 76 estuaries in KwaZulu-Natal, South Africa (see Table 1). Bass et al. (1973) reported that adult bull sharks pupped near the mouth of St Lucia, with the size

Table 1: Records of bull shark *Carcharhinus leucas* occurrence within estuaries, rivers and lakes in South Africa, listed from north to south. Distance from sea shows the distance at which the shark was recorded up the estuary, with NA reflecting records where such data were not available. Note that the Pongola River mouth is in Mozambique and is technically not a South African estuary, but bull sharks have been recorded in the South African section of this river. The Oceanographic Research Institute Cooperative Fish Tagging Project (ORI-CFTP) and the National Marine Linefish System (NMLS) databases are housed at the Oceanographic Research Institute in Durban, South Africa. EC = Eastern Cape; KZN = KwaZulu-Natal; WC = Western Cape

Estuary or River	Province	Distance from sea	Source of data
Pongola River	KZN	Up to 160 km	Bass et al. 1973; Kyle 2002; I Player, Ezemvelo KZN Wildlife (retired), pers. comm.
Kosi Bay	KZN	Up to 2 km	Bass et al. 1973; S Kyle, Ezemvelo KZN Wildlife (retired), pers. comm.; ORI-CFTP unpublished data
St Lucia Lake System	KZN	Up to 29 km	Bass et al. 1973; Vivier et al. 2010a; NMLS unpublished data; ORI-CFTP unpublished data
iMfolozi	KZN	Up to 70 km	Bass et al. 1973; Vivier et al. 2010b; Olbers 2012; S Kyle, pers. comm.; ORI-CFTP unpublished data
Richards Bay	KZN	Up to 2 km	Bass et al. 1973; Everett and Fennessy 2007; NMLS unpublished data; ORI-CFTP unpublished data
uMlalazi	KZN	Up to 7 km	Hemens et al. 1971; Bass et al. 1973; NMLS unpublished data
aMatigulu/iNyoni	KZN	NA	Hemens et al. 1972
uThukela	KZN	Up to 13 km	Bass et al. 1973; NMLS unpublished data; ORI-CFTP unpublished data
uMngeni	KZN	NA	Ezemvelo KZN Wildlife Honorary Officers (Beachwood, Durban)
Durban Bay	KZN	NA	Bass et al. 1973; NMLS unpublished data
uMkhomazi	KZN	NA	D Nieuwoudt, F Pretorius and R Da Rosa, competitive anglers, pers. comm.; ORI-CFTP unpublished data
uMzimkhulu	KZN	NA	F Pretorius and R Da Rosa, pers. comm.
uMthamvuna	KZN/EC	Up to 4.5 km	Karssing 2011; F Pretorius and R Da Rosa, pers. comm.; ORI-CFTP unpublished data
Mtentu	EC	Up to 4 km	RD pers. obs.
Msikaba	EC	NA	BQM pers. obs.
Mzimvubu	EC	>2 km	P Cowley, South African Institute for Aquatic Biodiversity (SAIAB), pers. comm.
Mtakatyi Estuary	EC	NA	C Thomassen and M Nothard, competitive anglers, pers. comm.
Mthatha	EC	NA	Plumstead et al. 1989a
Xhora Estuary	EC	NA	V Driesel, competitive angler, pers. comm.
Mbashe	EC	4 km	Plumstead et al. 1989b.
Nqabara River	EC	NA	V Driesel, pers. comm.
Kei River	EC	>1 km	Video evidence, P Cowley, pers. comm.
Nahoon River	EC	NA	https://www.iol.co.za/news/south-africa/canoelist-survives-zambezi-shark-attack-303482
Great Fish River	EC	>1 km	Compagno and Smale 1986
Swartkops River	EC	Up to 9 km	<i>Eastern Province Herald</i> , 10 July 1982
Knysna Estuary	WC	>1 km	Acoustic telemetry tag detection 2020, Acoustic Tracking Array Platform
Breede River	WC	Up to 28 km	J Filmlalter, SAIAB, unpublished data; RD pers. obs.; McCord and Lamberth 2009

range of sharks within the lower reaches of the system in the 1960s mostly smaller than 90 cm TL but with some adolescents (90–180 cm TL) observed farther upstream in the main lake. Historically, bull sharks appeared to tolerate salinities up to approximately 50 in St Lucia (Bass et al. 1973). However, since the mouth closure in 2002, followed by periods of low water levels that led to prolonged hypersalinity, it is presumed that many sharks perished after the peak in the drought in 2015, and it is uncertain whether any sharks remained in St Lucia thereafter (G Cliff, KwaZulu-Natal Sharks Board, pers. comm.).

The St Lucia Estuary is also home to one of the greatest concentrations of Nile crocodiles *Crocodylus niloticus* in South Africa, and these play an important ecological role in the system as top keystone predators (Whitfield and Blaber 1979; Combrink 2014; Somaweera et al. 2020).

Crocodiles in St Lucia are known to have a broad diet, which may include mullet *Mugil cephalus*, sharptooth catfish *Clarias gariepinus* and bull sharks (Pooley 1967; Whitfield and Blaber 1979). The average size of crocodiles in the lower reaches of St Lucia is 2.5 m and they have a mean daily intake of 1.1 kg of fish (Whitfield and Blaber 1979). Their diet may vary according to prey availability, and they are known to scavenge from fishers (Combrink 2014; Warner et al. 2016a).

This study had three primary objectives, namely to: (i) document the rapid recruitment of bull sharks into the St Lucia Estuary and highlight the importance of the system as a nursery for bull sharks in the region; (ii) report on the first observed predation of a neonate bull shark by an adult Nile crocodile; and (iii) collate a list of bull shark occurrences in all South African estuaries.

Methods and results

Within days of the St Lucia Estuary opening to the sea on 6 January 2021, Nile crocodiles were seen moving in and out of the mouth foraging on prey washing out of the estuary into the sea, including many sharptooth catfish. Additionally, adult bull sharks were observed by the authors at the estuary mouth on 9 and 10 January and were reported to have been seen at the mouth since the opening on 6 January (R Penn Sawers, Ezemvelo KZN Wildlife, pers. comm.). The presence of adult bull sharks at the mouth and adjacent coastline was observed sporadically for at least three months after the mouth was opened, with the peak in adult bull shark abundance noted within the first three weeks of the mouth opening.

On 16 January 2021, between 15:18 and 15:28, an adult Nile crocodile with a neonate bull shark in its jaws (Figure 1a) was observed and photographed (by GB, PL, MZ and RD) immediately inside the open mouth of the estuary (28°23.259' S, 032°25.572' E). When first observed,

the juvenile shark was still alive with its tail beating strongly (Figure 1b). The crocodile held the shark out of the water, firmly gripped in its jaws while periodically tossing and crushing the shark (Figure 1c). During this time many tooth puncture wounds were observed on the shark's body and later internal body tissue emerged from the shark's mouth (Figure 1d). The shark went limp before the crocodile swallowed it headfirst. At the time of the predation, the rising tide (there was a 2-m high tide at 17:54) was pushing seawater into the estuary mouth. Upon closer inspection of the images, the shark appeared to have a nylon fishing trace and sinker protruding from its mouth. Presumably, a recreational angler had hooked the shark and the shark most likely bit through the nylon fishing line. The trace may have become snagged on nearby reeds, leading to the crocodile responding to the struggling shark.

Soon after the predation event, the authors captured another neonate bull shark, measuring 81 cm total length and having an open umbilical slit, and tagged it with a coded acoustic tag (VEMCO V13). Subsequently,



Figure 1: An adult Nile crocodile *Crocodylus niloticus* killing and eating a neonate bull shark *Carcharhinus leucas* at St Lucia Estuary mouth, on 16 January 2021, 10 days after the system was reconnected to the sea after a prolonged period of closure. After the crocodile took the shark in its jaws it proceeded to bite and toss the shark while above water (a–c) before the shark died and was apparently pulverised (d) and then swallowed headfirst by the crocodile

the authors tagged another eight neonate bull sharks with acoustic tags at the St Lucia mouth, ranging between 67 and 85 cm TL, all with open umbilical slits which confirmed that they were neonates (Chin et al. 2015). The shark that fell prey to the crocodile was presumed to be part of this same cohort of neonates that were pupped at St Lucia mouth after it opened on 6 January. The crocodile that preyed on the shark had previously been tagged (X Combrink, Tshwane University of Technology, pers. comm.) and could be identified by one metal bolt on a caudal scute and three holes on the three subsequent caudal scutes near the terminus of the tail (not visible in the photographs provided). The total length of the crocodile was estimated to be 2.5 m.

In addition to making the observations recorded above, we compiled a list of all known records of bull sharks in South African estuaries (Table 1).

Discussion

Since the mouth closure and habitat change within St Lucia over the past two decades, it has been unclear whether any bull sharks survived in the system. However, the observations made during this study confirm that bull sharks were able to respond almost immediately to the opening of the estuary to the sea and to pup within the first week of the reconnection between estuary and sea. Indeed, four of the neonate bull sharks fitted with acoustic tags were recorded over 3 km from the mouth in the St Lucia estuary, providing evidence to suggest these pups recruited into the St Lucia estuarine system. Such a rapid biological response and recruitment into the system highlights the resilience of bull sharks and the importance of St Lucia to this and many other estuarine-dependent fish species. Additionally, this highlights how important the remaining estuaries in South Africa are to bull sharks (see Table 1). As bull sharks are known to exhibit natal philopatry, it is also possible that adult sharks born at St Lucia returned to their natal estuary to pup, guided by specific environmental cues in similar manner to other estuarine-associated fish species (James et al. 2008; Tillet et al. 2012).

There are records of saltwater crocodiles *Crocodylus porosus* preying on elasmobranchs in Australia, which, based on the infrequency of reports, appears to be a rare occurrence (Doody 2009; Sun 2014; Khan 2017). Additionally, there are records of the American alligator *Alligator mississippiensis* preying on several elasmobranch species in Florida, USA (Nifong and Lowers 2017). In Africa, there are previous reports of Nile crocodiles preying on bull sharks in St Lucia (Pooley 1967; Whitfield and Blaber 1979), with the present study providing the first photographic evidence. This is a notable observation as it confirms Nile crocodiles are indeed capable of preying on bull shark neonates in the St Lucia system, which is historically South Africa's largest bull shark nursery and home to one of the country's largest populations of Nile crocodiles (Bass et al. 1973; Warner et al. 2016b). Although bull sharks may not represent an important component of the diet of the Nile crocodile at St Lucia year-round, a single neonate shark weighing approximately 2.5 kg may constitute a large portion of a crocodile's daily ration and may be an important opportunistic source of food (Whitfield and Blaber

1979). Crocodiles have been documented to respond opportunistically to prey availability at St Lucia, as observed, for example, during the historic mullet run (Whitfield and Blaber 1979; Whitfield 2021). In this study, crocodiles were observed foraging at the mouth, where they were regularly seen preying on sharptooth catfish that had succumbed to the increased salinity and were being washed out to sea.

Although it remains unclear how the St Lucia ecosystem will respond over time to the artificial breaching of the mouth, this study provides evidence to suggest that recruitment of a top marine predator back into the system may be rapid. Despite decades of management effort to restore the ecological functioning of St Lucia, its resilience remains in the balance (Taylor 2006; Whitfield and Taylor 2009; Everett et al. 2015; Cyrus et al. 2020; Forbes et al. 2020; Whitfield 2021). St Lucia warrants the World Heritage Site status conferred upon it for its natural beauty and biodiversity, and we hope that unique observations such as reported here will further motivate the need to conserve and manage this system in a way that promotes its ecological functioning and protects its unique biodiversity.

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ORCID

Ryan Daly: <http://orcid.org/0000-0002-4409-6951>

Tessa Hempson: <http://orcid.org/0000-0002-1486-2635>

Bruce Mann: <http://orcid.org/0000-0002-7130-6301>

Jennifer Olbers: <http://orcid.org/0000-0001-8357-5157>

References

- Bass J, D'Aubrey JD, Kistnasamy N. 1973. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). *Investigational Report No. 33*. Durban, South Africa: Oceanographic Research Institute.
- Carrasco NK, Perissinotto R. 2012. Development of a halotolerant community in the St Lucia Estuary (South Africa) during a hypersaline phase. *PLoS ONE* 7: e29927.
- Chin A, Mourier J, Rummer JL. 2015. Blacktip reef sharks (*Carcharhinus melanopterus*) show high capacity for wound healing and recovery following injury. *Conservation Physiology* 3: cov062.
- Combrink AS. 2014. Spatial and reproductive ecology and population status of the Nile crocodile (*Crocodylus niloticus*) in the Lake St Lucia Estuarine System, South Africa. PhD thesis, University of KwaZulu-Natal, South Africa.
- Compagno LJV, Smale MJ. 1986. Recent records of four warm-water elasmobranchs from the Eastern Cape Province, South Africa. *South African Journal of Marine Science* 4: 11–15.
- Cyrus D, Vivier L. 2006. Fish breeding in, and juvenile recruitment to, the St Lucia Estuarine System under conditions of extended mouth closure and low lake levels. *African Journal of Aquatic Science* 31: 83–87.
- Cyrus DP, Vivier L, Owen RK, Jerling HL. 2010. Ecological status

- and role of the Mfolozi–Msunduzi estuarine system within the iSimangaliso Wetland Park, a World Heritage Site on the south-east coast of South Africa. *African Journal of Aquatic Science* 35: 109–116.
- Cyrus D, Schutte Q, Vivier L. 2020. The influence of prolonged drought and anthropogenic impact reversal on fish community structure and ecosystem state cycling of Lake St Lucia, Africa's largest estuarine lake. *African Journal of Aquatic Science* 45: 167–182.
- Doody JS. 2009. Eyes bigger than stomach: prey caching and retrieval in the saltwater crocodile, *Crocodylus porosus*. *Herpetological Review* 40: 26–29.
- Everett BI, Fennessy S. 2007. Assessment of recreational boat-angling in a large estuarine embayment in KwaZulu-Natal, South Africa. *African Journal of Marine Science* 29: 411–422.
- Everett BI, Cliff G, Dudley SFJ, Wintner SP, van der Elst RP. 2015. Do sawfish *Pristis* spp. represent South Africa's first local extirpation of marine elasmobranchs in the modern era? *African Journal of Marine Science* 37: 275–284.
- Forbes NT, Forbes AT, James B. 2020. Restoration of Lake St Lucia, the largest estuary in South Africa: historical perceptions, exploitation, management and recent policies. *African Journal of Aquatic Science* 45: 183–197.
- Hemens J, Metz H, Simpson DE, Coetzee OJ. 1971. Natal coast estuaries: environmental surveys; survey no. 2 – the Mlalazi Estuary. Steering Committee for Natal Rivers Research Fellowships: 37th Meeting, 30th August 1971. Steering Committee Report No. 37. Durban, South Africa: Research Group for Natal, National Institute for Water Research, Council for Scientific and Industrial Research. pp 7–20.
- Hemens J, Metz H, Simpson DE, Warwick RJ. 1972. Natal coast estuaries: environmental surveys; survey no. 4 – the Amatikulu Estuary. Twenty-Fifth Steering Committee Meeting: Marine Disposal of Effluents, 17th October 1972. Progress Report No. 24. Durban, South Africa: Natal Regional Laboratories, National Institute for Water Research, Council for Scientific and Industrial Research.
- Heupel MR, Simpfendorfer CA. 2011. Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus leucas*. *Marine Ecology Progress Series* 433: 237–244.
- James NC, Cowley PD, Whitfield AK, Kaiser H. 2008. Choice chamber experiments to test the attraction of postflexion *Rhabdosargus holubi* larvae to water of estuarine and riverine origin. *Estuarine, Coastal and Shelf Science* 77: 143–149.
- Karssing RJ. 2011. Fish survey of the Mtamvuna Estuary (26–30 September 2011). Internal report. Pietermaritzburg, South Africa: Ezemvelo KwaZulu-Natal Wildlife.
- Khan J. 2017. April 13. Endangered sawfish battle crocodiles and sharks. *Australian Geographic*. Available at <https://www.australiangeographic.com.au/news/2017/04/endangered-sawfish-battle-crocodiles-and-sharks/> [accessed 23 March 2021].
- Kyle R. 2002. Interesting new record and further notes on the occurrence of marine fish in Nyamithi Pan, Ndumo Game Reserve, South Africa. *Koedoe* 45: article 29.
- Mann BQ, Pradervand P. 2007. Declining catch per unit effort of an estuarine-dependent fish, *Rhabdosargus sarba* (Teleostei: Sparidae), in the marine environment following closure of the St Lucia estuarine system, South Africa. *African Journal of Aquatic Science* 32: 133–138.
- Mann BQ, James NC, Beckley LE. 2002. An assessment of the recreational fishery in the St Lucia estuarine system, KwaZulu-Natal, South Africa. *South African Journal of Marine Science* 24: 263–279.
- McCord ME, Lamberth SJ. 2009. Catching and tracking the world's largest Zambezi (bull) shark *Carcharhinus leucas* in the Breede Estuary, South Africa: the first 43 hours. *African Journal of Marine Science* 31: 107–111.
- Nifong JC, Lowers RH. 2017. Reciprocal intraguild predation between *Alligator mississippiensis* (American alligator) and Elasmobranchii in the southeastern United States. *Southeastern Naturalist* 16: 383–396.
- Olbens JM. 2012. Is that a shark in the watering hole? Zambezi sharks in Ezemvelo KZN Wildlife protected areas. Internal report. Pietermaritzburg, South Africa: Ezemvelo KwaZulu-Natal Wildlife.
- Pillans RD, Good JP, Anderson WG, Hazon N, Franklin CE. 2008. Rectal gland morphology of freshwater and seawater acclimated bull sharks *Carcharhinus leucas*. *Journal of Fish Biology* 72: 1559–1571.
- Plumstead EE, Prinsloo JF, Schoonbee HJ. 1989a. A survey of the fish fauna of Transkei estuaries. Part Three: The Mtata River estuary. *South African Journal of Zoology* 24: 282–289.
- Plumstead EE, Prinsloo JF, Schoonbee HJ. 1989b. A survey of the fish fauna of Transkei estuaries. Part Two: The Mbashe Estuary. *South African Journal of Zoology* 24: 273–281.
- Pooley AC. 1967. Observations on the Lake St Lucia crocodile population. In: Proceedings of the St Lucia Scientific Advisory Council Workshop: Charter's Creek, South Africa, February 1976. Paper 19. Durban, South Africa: Natal Parks Board.
- Schutte Q, Vivier L, Cyrus DP. 2020. Changes in the fish community of the St Lucia estuarine system (South Africa) following Cyclone Gamede, an episodic cyclonic event. *Estuarine, Coastal and Shelf Science* 243: article 106855.
- Somaweera R, Nifong J, Rosenblatt A, Brien ML, Combrink X, Eley RM et al. 2020. The ecological importance of crocodylians: towards evidence-based justification for their conservation. *Biological Reviews* 95: 936–959.
- Sun Y. 2014. 6 August. Croc takes on shark during epic battle. *ABC News*. Available at <https://abcnews.go.com/International/croc-takes-shark-wins/story?id=24862582> [accessed 23 March 2021].
- Taylor RH. 2006. Ecological responses to changes in the physical environment of the St Lucia Estuary. PhD thesis, Norwegian University of Life Sciences, Norway.
- Tillett BJ, Meekan MG, Field IC, Thorburn DC, Ovenden JR. 2012. Evidence for reproductive philopatry in the bull shark *Carcharhinus leucas*. *Journal of Fish Biology* 80: 2140–2158.
- Vivier L, Cyrus DP, Jerling HL. 2010a. Fish community structure of the St Lucia estuarine system under prolonged drought conditions and its potential for recovery after mouth breaching. *Estuarine, Coastal and Shelf Science* 86: 568–579.
- Vivier L, Cyrus DP, Owen RK, Jerling HL. 2010b. Fish assemblages in the Mfolozi–Msunduzi estuarine system, KwaZulu-Natal, South Africa, when not linked to the St Lucia mouth. *African Journal of Aquatic Science* 35: 141–154.
- Warner JK, Combrink X, Myburgh JG, Downs CT. 2016a. Blood lead concentrations in free-ranging Nile crocodiles (*Crocodylus niloticus*) from South Africa. *Ecotoxicology* 25: 950–958.
- Warner JK, Combrink X, Warner JK, Downs CT. 2016b. Nest predation and maternal care in the Nile crocodile (*Crocodylus niloticus*) at Lake St Lucia, South Africa. *Behavioral Processes* 133: 31–36.
- Whitfield AK. 2005. Preliminary documentation and assessment of fish diversity in sub-Saharan African estuaries. *African Journal of Marine Science* 27: 307–324.
- Whitfield AK. 2021. When the flathead mullet left St Lucia. *African Journal of Marine Science* 43: 161–169.
- Whitfield AK, Blaber SJM. 1979. Predation on striped mullet (*Mugil cephalus*) by *Crocodylus niloticus* at St Lucia, South Africa. *Copeia* 1979: 266–269.
- Whitfield AK, Taylor RH. 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 838–848.