# The demise of the Nile crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in South Africa: The case of the Olifants River

PETER J. ASHTON<sup>1</sup>

Natural Resources and the Environment, CSIR, P.O. Box 395, Pretoria 0001, South Africa

#### INTRODUCTION

The water quality of almost all of South Africa's river systems has worsened progressively as a result of increasing urbanization and industrialization; the adverse effects of poor water quality have been compounded by the operation of water storage reservoirs and abstraction of increased volumes of water for human uses (Ashton, 2007). This has resulted in a progressive – and sometimes dramatic – reduction in the numbers and abundance of several sensitive species of insects, amphibians, fish and aquatic mammals in the worst-affected river systems (O'Keeffe et al., 1989; Darwall et al., 2009). More recently, public attention has been caught by the deaths of large numbers of Nile crocodiles (*Crocodylus niloticus*) at several points along the Olifants River, the largest of several rivers flowing through South Africa's renowned Kruger National Park (Steyn, 2008; Van Vuuren, 2009). While people's attitudes towards crocodiles range from reverence to revulsion (Graham and Beard, 1973), the Nile crocodile is a keystone species for the Olifants River (Joubert, 2007) and the recent crocodile deaths have caused serious concern. Unfortunately, the Olifants River situation reflects the cumulative effects of slightly more than a century of ecosystem stress as a result of human activities in the catchment (Oberholster et al., 2010). How did the situation arise and what are the future prospects for this river system?

#### THE OLIFANTS RIVER SYSTEM

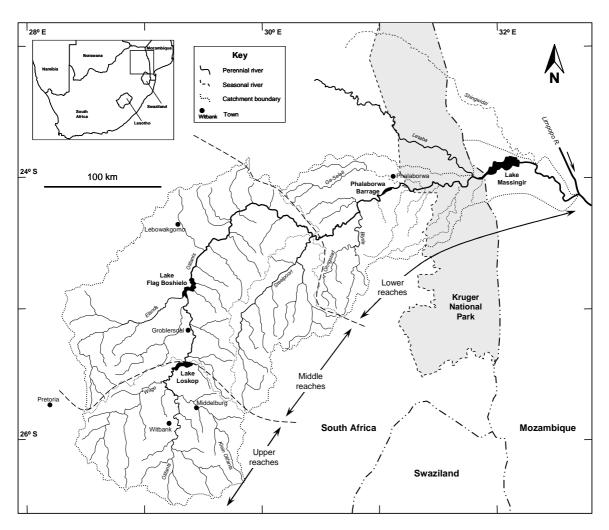
The Olifants River rises in the Highveld region of South Africa, flowing north-north-eastwards towards Mozambique, where it is joined by the Letaba River immediately before flowing into Mozambique, and by the ephemeral Shingwidzi River downstream of Lake Massingir (Figure 1). The South African portion of the Olifants catchment covers an area of some 74,500 km², and is home to some 4 million people (approximately 8% of the South African population; Van Vuuren, 2009). The South African portion of the Olifants catchment contains 201 water storage dams (38 of which have volumes larger than 1 Mm³), while the huge Massingir Dam (capacity = 2,844 Mm³) commands the lower reaches of the Olifants River in Mozambique. The combined capacity of all the dams (4,688 Mm³) exceeds the mean annual runoff of the catchment (Middleton and Bailey, 2009).

The upper reaches of the Olifants catchment (Figure 1) are characterized by large-scale coal mining, coal-fired power generation plants, irrigated agriculture and a diverse array of heavy and light industries as well as several towns and smaller urban centres (Driescher, 2008). The middle reaches of the catchment contain extensive areas of irrigated agriculture as well as several platinum, chrome and vanadium mines, two ferro-chrome refineries and numerous smaller urban centres (Ashton *et al.*, 2001). A large proportion of the population is rural in character, occupying former Apartheid "homelands". The lower reaches of the catchment contain several small mines and the important copper and phosphate mining complex around the town of Phalaborwa, and the Olifants River flows through the Kruger National Park (KNP) before entering Lake Massingir in Mozambique (Mussagy, 2008). Key water supply reservoirs located along the length of the Olifants River include the Phalaborwa Barrage and lakes Loskop, Flag Boshielo and Massingir (Figure 1). The main stem of the Olifants River and several of its larger tributaries (e.g. the Wilge, Elands, Steelpoort, Blyde and Ga-Selati rivers) are important sources of water for intensive irrigated agriculture (Joubert, 2007). The growing demands for water have progressively reduced flows in the lower reaches of the Olifants River within the KNP and surface flows have ceased for short periods during recent dry periods (Biggs

-

<sup>&</sup>lt;sup>1</sup> Correspondence to: Peter J. Ashton, Natural Resources and the Environment, CSIR, PO Box 395, Pretoria 0001, South Africa. E-mail: <a href="mailto:pashton@csir.co.za">pashton@csir.co.za</a>.

and Rogers, 2003). Water released from Lake Massingir is used for the large Chokwe irrigation scheme located along the banks of the Limpopo River, downstream of its confluence with the Olifants River.



**Figure 1**. Sketch map of the Olifants River catchment showing major tributaries, towns, key water storage reservoirs and the approximate extents of the upper, middle and lower river reaches. The inset shows the position of the mapped area within southern Africa.

Treated, partly treated and untreated effluents from mines, industries and sewage treatment plants – particularly in the upper reaches of the Olifants River – combined with seepage of acidic mine drainage from several active and abandoned coal mines in the upper reaches, contribute an "unusual cocktail" of nutrients, salts and metal ions to the river system (Driescher, 2008; Steyn, 2008). A large proportion of these substances accumulate in the sediments and water column of the water storage reservoirs located along the Olifants River and its tributaries. Nutrient concentrations (total nitrogen = 2.67 mg L<sup>-1</sup>; total phosphorus = 0.7 mg L<sup>-1</sup>; Oberholster *et al.*, 2010) indicate that Lake Loskop is hypertrophic, while the concentrations of aluminium and iron in Lake Loskop (Al = 1.56 mg L<sup>-1</sup>; Fe = 1.2 mg L<sup>-1</sup>; Oberholster *et al.*, 2010) are well above those suggested in national water quality guidelines (Al < 5 μg L<sup>-1</sup>; Fe < 0.1 mg L<sup>-1</sup>; DWAF, 1996). Blooms of the toxic cyanobacterium *Microcystis aeruginosa* in Lake Loskop are thought to be responsible for recent fish kills and it is clear that human users of water from this reservoir also face risks to health (Oberholster *et al.*, 2010).

In the middle reaches of the catchment, extensive soil erosion in densely populated areas and return flows from irrigated agriculture contribute large quantities of suspended sediments and agricultural chemicals to the Olifants River (Ashton *et al.*, 2001). Water released from the Phalaborwa Barrage can contain suspended sediment concentrations as high as 60,000 to 70,000 mg L<sup>-1</sup>, while

concentrations of metal ions and total dissolved salts are also high (Ashton *et al.*, 2001). The substances present in these discharges have been recorded downstream into Lake Massingir (Mussagy, 2008).

Despite the availability of national water quality guidelines (DWAF, 2006) and regular monitoring of water quality at over 35 sites in the Olifants catchment, there appears to have been little official reaction to the steady deterioration in water quality (De Villiers and Mkwelo, 2009). The accumulation of dangerously high levels of metal ions in fish species along the entire length of the Olifants River render these unfit for human consumption (Seymore *et al.*, 1995; Du Preez *et al.*, 1997; Avenant-Oldewage and Marx, 2000; Coetzee *et al.*, 2002). Other studies have shown that the water in key water storage reservoirs contains dangerously high concentrations of trace metals and nutrients (Driescher, 2008; Oberholster *et al.*, 2010), posing potential problems for irrigated crops and domestic use of water from these reservoirs.

## **CHANGES IN NILE CROCODILE POPULATIONS**

The Nile crocodile (*Crocodylus niloticus*) is the largest and best-known of the three crocodile species in Africa and has been recorded in several types of fresh and brackish water habitats in over 20 African countries (Cott and Pooley, 1971). Earlier, deliberate eradication programmes resulted in a sharp drop in numbers, particularly of larger specimens, greatly reducing the distribution of crocodiles in many countries (Pooley, 1982; Jacobsen, 1984; Swanepoel, 2001; Botha, 2010a). For over three decades, the Nile crocodile has been regarded as endangered or vulnerable and all trade in crocodile products is subject to Appendix I of the CITES Convention (Groombridge, 1982).

Prior to the promulgation of South African reptile protection legislation in 1969, Nile crocodiles were regarded as vermin, to be shot on sight (Pooley, 1969). However, despite the relief afforded by legislation, crocodile numbers have continued to decline and their distribution has shrunk as a result of continuing habitat destruction and incidents of water pollution (Jacobsen, 1984; Swanepoel, 1999, 2001; Botha, 2005, 2006, 2010a). Nile crocodile populations in South Africa are now restricted to the northern and eastern portions of the country, occupying rivers and reservoirs along the middle and lower reaches of the Incomati, Limpopo, Olifants, Maputo and Usutu basins as well as lakes Kosi, Sibaya and St Lucia (Tinley, 1976; Jacobsen, 1984; Branch, 1998). The largest populations and highest population densities exist in river reaches located within formally conserved areas such as the Kruger National Park (KNP), where they are regarded as tourist attractions (Joubert, 2007). Outside of protected areas, rural communities see crocodiles as a threat to their livelihoods and livestock, and destroy their nests and eggs whenever possible (Musambachime, 1987; McGregor, 2005).

From an ecological perspective, the Nile crocodile has long been considered an iconic or keystone species for aquatic biodiversity in many African rivers and lakes (Pooley, 1969; Tinley, 1976). However, despite this recognition of their importance, crocodiles are often omitted from regional studies of aquatic biodiversity (e.g. O'Keeffe *et al.*, 1989; Darwall *et al.*, 2009). In recent years the crocodile populations in several South African rivers and lakes have undergone severe setbacks (Branch, 1998) with particularly dramatic declines recorded for different sections of the Olifants River (Jacobsen, 1984; Swanepoel, 1999, 2001; Botha, 2006; Van Vuuren, 2009; Botha, 2010a, 2010b). Recent surveys have shown that Nile crocodile populations have reached alarmingly low levels in Lakes Loskop and Flag Boshielo and the lower reaches of the Olifants River, with far fewer large individuals of reproductive age recorded (Botha, 2006, 2010a, 2010b). The available evidence suggests that habitat alteration and adverse water quality are responsible for these changes (Botha, 2010a, 2010b).

Over the past 15 years isolated incidents of large-scale fish mortality have been recorded at different times in Lake Loskop, accompanied by occasional deaths of soft-shelled terrapins (*Pelusios sinuatus*). These incidents have become more frequent since 2003 and have coincided with Nile crocodile mortalities (Botha, 2006; Driescher, 2008). The most recent crocodile survey on Lake Loskop suggests that the crocodile population has declined from approximately 30 animals in 1984 to a total of 8 in 2009, with no individuals of reproductive age present (Botha, 2010a). Histopathological examinations of Nile crocodile and terrapin carcasses from Lake Loskop indicated that their deaths could be ascribed to pansteatitis, which is associated with the intake of rancid fish after a fish die-off. In turn, the massive fish kills (each comprising several tonnes) in Lake Loskop appear to have resulted

from sporadic incidents of acid mine drainage flowing into the lake (Driescher, 2008; Oberholster et al., 2010).

The dam wall of Lake Flag Boshielo, located downstream of Lake Loskop (Figure 1), was raised by 5 metres in 2005. When the reservoir filled after good rains, rising water flooded extensive areas of marginal vegetation that had not been cleared from the dam basin during construction, eliminating most of the basking sites used by large crocodiles. In the absence of suitable shoreline sites, three large crocodiles attempted to bask on the crest of the dam's main spillway and fell to their deaths (DWAF, 2006). Since the raising of the dam wall, Flag Boshielo's Nile crocodile population has declined from approximately 135 individuals in 2005 to 98 in 2009, with many individuals retreating to refuges in tributary rivers (Botha, 2010a). Importantly, the numbers of large individuals of reproductive age were also greatly reduced.

The largest recorded mortalities of Nile crocodiles along the lower reaches of the Olifants River and its gorge section inside the KNP, with 170 carcasses recorded in 2008 and a further 28 carcasses in 2009. Expert opinion suggests that some crocodile carcasses may have sunk and not been recorded (Danny Govender: Disease Ecologist, South African National Parks, personal communication). Histopathological investigations revealed the presence of pansteatitis and the carcasses were burnt. Aerial counts suggest that Nile crocodile numbers in the Olifants River gorge section in KNP have dropped from 760 to 480, though it is unclear whether this is due to mortality or to emigration (Danny Govender, personal communication). Intensive studies on the water chemistry and sediment quality in areas where dead Nile crocodiles were found revealed elevated concentrations of aluminium and iron in the sediments, though no evidence was found for the presence of possible toxicants.

#### IMPLICATIONS FOR CONSERVATION OF THE OLIFANTS RIVER

Against this background, it is pertinent to ask the question: what do the Nile crocodile mortalities in the Olifants River indicate and what can be done about the situation?

The answer to this seemingly straightforward question is neither explicit nor simple. The Nile crocodile is an apex predator that occupies the top of the aquatic food chain, feeding predominantly on fish and, less frequently, on unwary mammals that drink from the rivers and lakes that it occupies. The presence of a healthy Nile crocodile population is seen to indicate that the ecosystem in question is also healthy (Pooley, 1969; Joubert, 2007). In this sense, the Nile crocodile is a keystone species (Simberloff, 1998). If this situation were as simple as it sounds, then it would be relatively straightforward to implement management actions that would ensure the ecosystem remained "healthy", based on the relative abundance and vitality of its crocodile population. Theoretically, if appropriate monitoring and management responses were closely linked, the ecosystem could then be managed in a way that would ensure society continued to derive the required array of goods and services (Grumbine, 1994).

However, several authors have pointed out the difficulty of managing ecosystems on the basis of their perceived "health" because so little is known about the processes and functions that characterise a "healthy" ecosystem (e.g. Rogers and Biggs, 1999). This complexity increases in aquatic ecosystems where catchment land uses must be carefully managed to achieve a specific desired state in the aquatic ecosystem (Davies and Wishart, 2000; Wishart and Davies, 2003); this becomes particularly difficult when the catchment is controlled by different authorities, each with differing or competing mandates (Ashton, 2007). Theoretically, the inherent difficulty of managing entire catchments or ecosystems can be reduced through adaptive management approaches, where management goals and procedures are changed in response to observed ecosystem responses (Walters and Holling, 1990). Despite suggestions that adaptive management approaches have seldom enhanced understanding of the system being managed (Simberloff, 1998), this has been applied successfully throughout the KNP as the basis for all ecosystem management (Biggs and Rogers, 2003). However, despite the successes achieved within the KNP savannah systems, the application of adaptive management to the rivers flowing through the KNP remains problematic because the upper catchments of all these rivers are outside the park boundaries (Roux et al., 2008).

While it may be relatively straightforward to identify a keystone species in a particular ecosystem, it is seldom as easy to identify the ecosystem functions of the species or the mechanisms by which it

exerts influence on that ecosystem (Simberloff, 1998). An important issue is that when the population of a keystone species such as the Nile crocodile declines, it is seldom a simple matter to identify the precise cause. In the Olifants River, the available evidence suggests that there is a link between the already high and steadily increasing levels of water pollution and the sporadic fish kills that occur mainly during the winter months. In turn, the presence of pansteatitis in dead Nile crocodiles and terrapins suggests that this has been caused by the consumption of rancid fish (Oberholster *et al.*, 2010). In combination, therefore, the evidence implicates sources of water pollution (excessively high concentrations of nutrients, organic compounds, metal ions and dissolved salts) as the most likely root cause for the Nile crocodile deaths.

The Olifants River situation highlights the problem that arises when a single keystone species such as the Nile crocodile is used as the sole indicator of aquatic ecosystem health. Because of their stealthy nature and tendency to avoid interactions with humans, crocodiles are difficult to monitor accurately (Botha, 2010a). By the time that the death or one or more crocodiles indicates an adverse effect has occurred, other harmful effects must have already happened at lower trophic levels. It is then difficult to collect, disentangle and interpret the evidence to identify the original source of the problem.

#### PROSPECTS FOR THE FUTURE

If the continued decline in the Nile crocodile population of the Olifants River and its water storage reservoirs signals a situation similar to that which has happened in the Yangtze River in China (Dudgeon, 2010), it will be extremely difficult to reverse the situation. The problem will likely be even more difficult if the anticipated adverse effects of changing climate – increased temperatures and altered rainfall patterns – also occur (De Wit and Stankiewitz, 2006). Aquatic biodiversity in South African river ecosystems has already been shown to be severely depleted and threatened; climatic changes would increase this vulnerability (Driver *et al.*, 2005).

In the upper Olifants River catchment, several new coal mining leases have been granted (DME, 2004) and, if unchecked, the already high levels of acidic mine drainage will likely increase in future. The progressive urbanization, industrialization and changes in habitat along the length of the Olifants River, combined with the adverse effects of water pollution, have already placed enormous strains on the aquatic ecosystems (Swanepoel, 1999; Steyn, 2008; Oberholster *et al.*, 2010). Anticipated future growth in demands for water and electricity plus the generation of increased quantities of effluents from towns, farms and industries (DWAF, 2004) suggest that the Olifants River and its reservoirs will receive even larger volumes of wastes in future. Unless remedial actions are implemented now and stricter statutory effluent controls are enforced – both now and in the future – the Olifants River aquatic ecosystem and its Nile crocodiles face a bleak prospect.

#### **ACKNOWLEDGEMENTS**

I am particularly grateful to my colleagues Jan Myburgh, Hannes Botha, Abré Steyn, Jannie Coetzee and André Hoffman for providing me with references and with current and historical data on crocodile populations in the Olifants River. I thank Danny Govender and Danie Pienaar of the South African National Parks in Kruger National Park for details of crocodile mortalities in the lower Olifants River section within the Kruger National Park.

## **REFERENCES**

Ashton PJ. 2007. Riverine biodiversity conservation in South Africa: current situation and future prospects. *Aquatic Conservation: Marine and Freshwater Ecosystems* **17**: 41-445.

Ashton PJ, Love D, Mahachi H, Dirks PGH. 2001. *Impacts of Mining and Mineral Processing Activities on Water Resources and Water Quality in the Zambezi, Limpopo and Olifants Basins in Southern Africa*. Mining, Minerals and Sustainable Development Project Report. IIED: Johannesburg.

Avenant-Oldewage A, Marx HM. 2000. Bioaccumulation of chromium, copper and iron in the organs and tissues of *Clarias gariepinus* in the Olifants River, Kruger National Park. *Water SA* **26**: 569-581.

Biggs HC, Rogers KH. 2003. An adaptive system to link science, monitoring and management in practice. In *The Kruger Experience: Ecology and management of savanna heterogeneity*, Du Toit JT, Rogers KH, Biggs HC (eds). Island Press: Washington; 59-80.

Botha PJ. 2005. *The Ecology and Population Dynamics of the Nile Crocodile* (Crocodylus niloticus) *in the Flag Boshielo Dam, Mpumalanga Province, South Africa*. Unpublished MSc thesis, University of Pretoria: Pretoria, South Africa.

Botha PJ, 2006. *The Current Nile Crocodile Population in the Loskop Dam*. Mpumalanga Tourism and Parks Agency: Nelspruit, South Africa.

Botha PJ. 2010a. *Monitoring the Nile Crocodile Population in the Olifants River and Selected Tributaries During 2005 and 2009.* Report on the Co-operative Project between the Department of Water Affairs and Mpumalanga Tourism and Parks Agency, South Africa.

Botha PJ. 2010b. *The Distribution, Conservation Status and Blood Biochemistry of Nile Crocodiles in the Olifants River System, Mpumalanga, South Africa*. Unpublished PhD thesis, University of Pretoria: Pretoria, South Africa.

Branch WR (ed.). 1998. South African Red Data Book – Reptiles and Amphibians. South African National Scientific Programmes Report No. 151. CSIR: Pretoria, South Africa.

Coetzee L, Du Preez HH, van Vuren JHJ. 2002. Metal concentrations in *Clarias Gariepinus* and *Labeo umbratus* from the Olifants and Klein Olifants River, Mpumalanga, South Africa: Zinc, copper, manganese, lead, chromium, nickel, aluminium and iron. *Water SA* **28**: 433-448.

Cott HB, Pooley AC. 1971. The status of crocodiles in Africa. *Proceedings of the First Working Group of the Crocodile Specialist Group*. IUCN: New York.

Darwall WRT, Smith KG, Tweddle D, Skelton PH (eds). 2009. *The Status and Distribution of Freshwater Biodiversity in Southern Africa*. IUCN: Gland, Switzerland, and South African Institute for Aquatic Biodiversity: Grahamstown, South Africa.

Davies BR, Wishart MJ. 2000. River conservation in the countries of the Southern African Development Community (SADC). In *Global perspectives on River Conservation: Science, Policy and Practice,* Boon PJ, Davies BR, Petts GE, (eds). John Wiley & Sons Ltd: Chichester; 179-204.

Department of Minerals and Energy (DME). 2004. *Operating and Developing Coal Mines in the Republic of South Africa*. Directory, D2/2004. Department of Minerals and Energy: Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF) 1996. South African Water Quality Guidelines. Volume 7: Aquatic Ecosystems. Department of Water Affairs and Forestry: Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF). 2004. *Olifants Water Management Area: Internal Strategic Perspective*. Report PWMA 04/000/00/0304. Department of Water Affairs and Forestry: Pretoria, South Africa.

Department of Water Affairs and Forestry (DWAF). 2006. Raising of Flag Boshielo Dam: Observations on Nile Crocodile Deaths at Main Spillway. Olifants River Water Resources Development Project Phase 1. Report No. 20/2/B501-11/G/1/29. Directorate Civil Design, Department of Water Affairs and Forestry: Pretoria, South Africa.

De Villiers S, Mkwelo ST. 2009. Has monitoring failed the Olifants River? Water SA 35: 671-676.

De Wit M, Stankiewicz J. 2006. Changes in surface water supply across Africa with predicted climate change. *Science Express*, 2 March 2006, 10.1126.

Driescher AC. 2008. A water quality study of Loskop Dam and the upper catchment of the Olifants River. Unpublished MSc thesis, University of the Free State: Bloemfontein, South Africa.

Driver A, Maze K, Rouget M, Lombard AT, Nel JL, Turpie JK, Cowling RM, Desmet P, Goodman P, Harris J, et al. 2005. National spatial biodiversity assessment 2004: priorities for biodiversity conservation in South Africa. *Strelitzia* **17**: 1-45.

Dudgeon D. 2010. Requiem for a river: extinctions, climate change and the last of the Yangtze. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**: 127-131.

Du Preez HH, Van Der Merwe M, Van Vuren JHJ. 1997. Bioaccumulation of selected metals in African catfish, *Clarias gariepinus* from the lower Olifants River, Mpumalanga, South Africa. *Koedoe* **40**: 77-90.

Graham A, Beard P. 1973. *Eyelids of Morning: The Mingled Destinies of Crocodiles and Men.* New York Graphic Society: New York.

Groombridge B (ed.). 1982. The IUCN Amphibia – Reptilia Red Data Book Part 1. Testudines, Crocodylia, Rhynchocephalia. IUCN: Gland, Switzerland.

Grumbine RE. 1994. What is ecosystem management? Conservation Biology 8: 27-38.

Jacobsen NHG. 1984. The distribution and status of crocodile populations in the Transvaal outside the Kruger National Park. *Biological Conservation* **29**: 191-200.

Joubert SCJ. 2007. *The Kruger National Park: A History*. 3 Volumes. High Branchings (Pty) Ltd.: Johannesburg, South Africa.

McGregor J-A. 2005. Crocodile crimes: people versus wildlife and the politics of post-colonial conservation on Lake Kariba, Zimbabwe. *Geoforum* **36**: 353-369.

Middleton BJ, Bailey AK. 2009. *Water Resources of South Africa, 2005 Study (WR2005)*. WRC Report No. TT 380/08. Water Research Commission: Pretoria, South Africa.

Musambachime MC. 1987. The fate of the Nile crocodile in African waterways. *African Affairs* **12**: 197-207.

Mussagy A. 2008. Massingir Dam and Smallholder Agricultural Rehabilitation Project – Plankton Monitoring Programme MDSAR DP04 – Annual Report (September 2006 to August 2007). Ministry of Public Works and Housing, National Directorate of Water: Maputo, Mozambique.

Oberholster PJ, Myburgh JG, Ashton PJ, Botha A-M. 2010. Responses of phytoplankton upon exposure to a mixture of acid mine drainage and high levels of nutrient pollution in Lake Loskop, South Africa. *Ecotoxicology and Environmental Safety* **73**: 326-335.

O'Keeffe JH, Davies BR, King JM, Skelton PH. 1989. The conservation status of southern African rivers. In *Biotic Diversity in Southern Africa: Concepts and Conservation*, Huntley BJ (ed.). Oxford University Press: Cape Town; 266-289.

Pooley AC. 1969. Conservation and management of crocodiles in Africa. *Journal of the South African Wildlife Management Association* **3**: 101-103.

Pooley AC. 1982. Discoveries of a Crocodile Man. William Collins Sons and Co Ltd: Johannesburg.

Rogers KH, Biggs HC. 1999. Integrating indicators, endpoints and value systems in strategic management of the rivers of the Kruger National park, South Africa. *Freshwater Biology* **41**: 439-452.

Roux DJ, Nel JL, Ashton PJ, Deacon AR, de Moor FC, Hardwick D, Hill L, Kleynhans CJ, Maree GA, Moolman J, Scholes RJ. 2008. Designing protected areas to conserve riverine biodiversity: Lessons from a hypothetical redesign of the Kruger National Park. *Biological Conservation* **141**: 100-117.

Seymore T, Du Preez HH, Van Vuren JHJ. 1995. Manganese, lead and strontium bioaccumulation in the tissues of the yellowfish, *Barbus marequensis* from the lower Olifants River, Eastern Transvaal. *Water SA* **21**: 159-172.

Simberloff D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biological Conservation* **83**: 247-257.

Steyn AJ. 2008. The dying river: Pollution killed the Olifants. Farmer's Weekly (22 August 2008).

Swanepoel DGJ. 1999. Movements, nesting and the effects of pollution on the Nile crocodile *Crocodylus niloticus* in the Olifants River, Kruger National Park. Unpublished MSc thesis, University of Natal: Pietermaritzburg, South Africa.

Swanepoel DGJ. 2001. The Raising of the Arabie Dam Wall and the Impacts on the Nile Crocodile Population. Unpublished Report No. P.RSA/00/0699. Department of Water Affairs and Forestry: Pretoria, South Africa.

Tinley KL. 1976. The Ecology of Tongaland. Report 1: Lake Sibayi; Report 2: Pongolo and Mkuze Floodplains; Report 3: Kosi Lake System. Natal Branch of the Wildlife Society of South Africa: Durban.

Van Vuuren L. 2009. Experts unite to save abused river from extinction. Water Wheel 8: 14-17.

Walters CJ, Holling CS. 1990. Large-scale management experiments and learning by doing. *Ecology* **71**: 2060-2068.

Wishart MJ, Davies BR. 2003. Beyond catchment considerations in the conservation of lotic biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**: 429-437.

# Full citation for the final published paper:

Ashton, P.J. (2010). The demise of the Nile crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in South Africa: The case of the Olifants River. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**: 489-493.