

# DYNAMICS OF THE SEASONAL FLOODPLAIN FISHERY OF THE OKAVANGO DELTA, BOTSWANA

---

Ketlhatlogile Mosepele

Thesis for the degree of Philosophiae Doctor (PhD)  
University of Bergen, Norway  
2019

UNIVERSITY OF BERGEN



# **DYNAMICS OF THE SEASONAL FLOODPLAIN FISHERY OF THE OKAVANGO DELTA, BOTSWANA**

Ketlhatlogile Mosepele



Thesis for the degree of Philosophiae Doctor (PhD)  
at the University of Bergen

Date of defense: 28.08.2019



© Copyright Ketlhatlogile Mosepele

The material in this publication is covered by the provisions of the Copyright Act.

Year: 2019

Title: DYNAMICS OF THE SEASONAL FLOODPLAIN FISHERY OF THE OKAVANGO  
DELTA, BOTSWANA

Name: Ketlhatlogile Mosepele

Print: Skipnes Kommunikasjon / University of Bergen

---

UIB

**DYNAMICS OF THE SEASONAL FLOODPLAIN FISHERY OF THE  
OKAVANGO DELTA, BOTSWANA**

---

**Ketlhatlogile Mosepele**

---

## **Scientific environment**

This thesis contributes knowledge in the management of floodplain fisheries in the developing world, through using the Okavango Delta (in Botswana) as a case study. The PhD work is registered in the faculty of Mathematics and Natural Sciences. It was fully funded by the University of Botswana, through the Okavango Research Institute (ORI), where I am employed as a fulltime academic staff member.

---

## Acknowledgements

I give my deepest gratitude to my supervisor, Prof. Kolding for his tireless guidance, his mentorship and his patience in turning my «flowery» prose into scientific language. Without you, this work would never have been completed. My deepest thanks also to all those colleagues who encouraged me in this journey, especially Dr Lesego Stone, Dr and Mrs Murray-Hudson, Dr and Mr Mogomotsi, Prof. G. Wilson and Prof. D.L. Kgathi. Kitso Carol Moetedi and Josepine Gopolang Makoba, thanks very much for your support. Prof. Masamba, you have always been a role model to me, my brother. Your words of encouragement gave me the fortitude to complete this journey.

I dedicate this work to the greatest love of my life, my dearest wife Belda Quetina Mosepele, and to my beloved son, Poloko João Mosepele. Your love and belief in me kept me going, and my love for you will remain forever. To you Quetina, «*Te amo muito, juntos, para sempre, mogatsaka*». Without you, this work would have been impossible, «*porque tu es minha vida*».

---

## Introduction

This thesis is the result of 20 years of work in the Okavango Delta, Botswana. I was employed as a Fisheries Research Officer in the Ministry of Agriculture the first 6 years of my professional career from 1996 to 2002. During that period I participated in several benchmark achievements, which included: (i) the first ever Frame Survey in the Okavango Delta; (ii) the first ever Catch Assessment Survey in the Okavango Delta; (iii) the initiation of the first long term monitoring of the Delta's fish stocks; and (iv) the first ever creel survey to assess the impact of traditional fishing gear on the Delta's fish stocks. Since mid-2002, I have been involved in fisheries research in the Okavango Delta as an academic staff member of the Okavango Research Institute (ORI), under the University of Botswana. Hence, this study is a culmination of over a decade of fisheries research in the Okavango Delta, alone or in collaboration with colleagues and students. It encompasses a broad range of topics from limnology to fisheries management of floodplain systems, using the Okavango Delta as a case study. During the past 16 years at ORI, I have supervised/ co-supervised six graduate students (three PhD and six MSc) and 13 undergraduate students. I have also contributed to a PhD work on the limnology and juvenile fish of the Okavango Delta; am currently co-supervising a PhD student on the fisheries dynamics of Cahorra Bassa Reservoir in Mozambique; and another PhD student on the aquatic fauna of a non-perennial river system in Zimbabwe. I have also written or co-authored 75 publications (32 peer reviewed journal articles, 31 peer reviewed book chapters and books, 6 papers in refereed conference proceedings, and 6 published technical reports) in various aspects of fisheries biology and management. I have also presented/ co-presented 55 papers in international conferences, symposia and workshops as part of my professional experience. This thesis however, contains eight selected published, peer-reviewed journal articles and one submitted manuscript.

The thesis covers the research that I have done on the Delta's fish stocks and its fishery, highlighting floodplain ecosystem dynamics and their role on fish production, and the management questions facing floodplain fisheries. The thesis is arranged thematically into four sections; (i) juvenile fish, (ii) adult fish, (iii) floodplain

---

dynamics and lastly (iv) an overall synthesis chapter. Table 1 summarizes the data that I have collected, or contributed in its collection, and used in this PhD work. The actual data collection protocols and materials are fully described in the respective publications. Some of the data were collected with other researchers and published with me as a co-author: (i) Papers I – III were other PhD studies done in the Delta where I was a key collaborator. More specifically papers I - II are from PhD work based at the Okavango Research Institute (ORI) where I was one of the supervisors. Paper III is also a PhD work based at ORI, but registered at the University of Oslo where I was a key research collaborator. Paper VI is an MSc work based at ORI, but with the student registered at Rhodes University where I was one of the supervisors. The lead author for paper VIII was a PhD student registered at the University of Florida based on data that I collected at ORI. The data for papers I – II are not summarized in Table 1 even though I participated in their collection. The data sampling protocols for these papers are described in the publications. The reason for including all nine papers in the present thesis is because they provide the most comprehensive available picture of the drivers and dynamics that determines the fish dynamics of the Okavango Delta.

### Data collection

Table 1 Summary of data sources used in this study

Data type	Data Source	Period	Mesh Size (mm)	No of records	No of species/ groups
Fishery Independent	Lundgren nets <sup>2</sup>	1999 - 2001	13 - 110	12559	43
	Namibian nets <sup>2</sup>	2001 - 2009	12 - 150	60398	51
	Botswana nets <sup>2</sup>	1999 - 2006	50 - 125	31160	43
Fishery Dependent	Subsistence Fisher's Nets <sup>2*</sup>	1999 - 2002	50 - 125	53579	36
	Commercial Fisher's Nets <sup>2*</sup>	1999 - 2002	50 - 125	35352	28
	Fishing Baskets	2001 - 2003	-	827	45
	Mosquito Nets	2001 - 2001	-	30	22
	Subsistence Hook and Line	2001 - 2003	-	761	25
	Commercial Hook and Line	2001 - 2002	-	1633	7
	Recreational Hook and Line	1970 - 1999	-	1264	19
	Fishing Traps	2002 - 2002	-	234	17
	Drive fishing nets	1999 - 2001	50 - 125	1047	12
	Total Yield <sup>1,3</sup>	1988 - 2008	-	1632	-
	Frame survey <sup>4</sup>	1998	-	3257	-
	Frame survey <sup>5</sup>	2005	-	2733	-
	Catch and effort <sup>1a</sup>	1999 - 2005	50 - 125	100931	5
	<b>TOTAL</b>	<b>1970 - 2008</b>	<b>12 - 150</b>	<b>301407</b>	<b>-</b>

<sup>1a</sup>Collected by Fisheries Division field staff from fishers' daily catch records. The fishers record fish caught in five major groups (Breams, Catfishes, Silver catfish, Tigerfish, Others)

<sup>2</sup>Collected by the first author

<sup>3</sup>Data from Catch Assessment Surveys by the Fisheries Division staff

\*While these data were collected several years ago, subsequent studies by Mosepele et al (2007) and Mmopelwa et al (2009) have shown that the fishing behavior of these fishers remains unchanged. Therefore, these data continue to reflect current conditions, except for drive fishing which was prohibited by the Fish Protection Regulations of 2008 (Botswana Government, 2008).

All the data collected from the Okavango Delta (Figure 1) and used in this study are summarized in Table 1. Two main types of data were used in this study: (i) Fishery independent and (ii) fishery dependent data.

**Fishery independent data:** These are research data collected by the Fisheries Division staff based at Ngarange, Mohembo, Seronga and Guma in the panhandle of the Delta (Figure 1). Research data from Nxaraga, Lake Ngami, Chanoga and Xakanaxa (Figure 1) were collected by technical staff from ORI. As shown in Table 1, several kinds of gear were used to collect these data. These included Lundgren, Namibian and Botswana nets, which cumulatively amounted to just over 104 000 individual fish records. Lundgren nets are nylon, monofilament multi-meshed, 12, 3-m long multi-panel nets made up of meshes of sizes ranging from 13 to 110 mm stretched meshes arranged geometrically (Mosepele, 2000). Both Botswana and Namibian nets are multi-filament multi-meshed nets. Botswana nets are made up of five mesh panels, each 5 meters long, of sizes 50 to 125 mm stretched mesh arranged geometrically (Mosepele, 2000) making them 25 m long. Namibia nets are longer as they are made up of 9 m long panels, made up of different meshes ranging from 12 to 150 mm stretched mesh (Mmopelwa et al 2009; Mosepele et al 2011), making them 90 m long.

The fish sampling protocol was similar in all the study sites. Soaking time for the research nets was 12 hours overnight, and nets were removed at 6 am the following day. After removal from the water, nets were placed in buckets, and then fish from each panel were placed in separate containers and processed separately. Each individual fish specimen was identified to species according to Skelton (2001) and total length (TL, cm) measurements taken. For selected species, maturity stage was determined according to Nikolsy (1969). Data were then captured in Pasgear 2 (Kolding and Skålevik, 2010), which is a customized database package for large fisheries datasets. Data were scrutinized and cleaned according to Mosepele (2000) before analysis.

**Fishery dependent data:** These data were collected by three major approaches; (i) fisher records, (ii) creel surveys, (iii) population surveys.



*Total yield* data were collected from Catch Assessment Surveys (CAS) conducted by the Fisheries Division. These surveys were conducted similar to van Zwieten et al. (2003) in fishing villages around the Okavango Delta by fisheries officers. In each village around the Delta, a fisheries officer will spend 2-3 days and measure the average catch per selected fishers once a quarter. This catch was then multiplied by the total number of fishers in each extension area to estimate the total catch by village (Fisheries Officer periodically conducted mini frame surveys in their extension areas so that they could have an estimate of the total number of fishers in their areas). Fisheries officers were encouraged to collect these CAS data across a broad spectrum of fisher types (i.e. active and not so active fishers). This estimated catch by village was then added for all the fishing villages in the Delta to generate total yield estimates for the Delta.

***Fisher records:*** Catch and effort data (Table 1) were collected from fisher records by the Fisheries Division officers from fishing villages around the Okavango Delta between 1995 and 2005. However, due to errors in data collection, data from 1995 – 1998 were not used in the analysis and were discarded. Just over 100000 daily catch and effort records between 1999 and 2005 were collected and used in this study. The fishing villages are located in both the Delta panhandle and other parts of the Delta (Paper IX). Data collection protocol followed a procedure where the Fisheries officers distribute data record forms to fishers in their duty station. This was an efficient data collection system from the fishery because Fisheries officers knew the fishers in their area very well. Fishers were required to record their daily catches according to five fish groups (i.e. Breams, Catfish, Silver catfish, Tiger-fish and an Others group) and effort used. Fisheries officers would periodically visit fishers in their extension area during the course of the month to monitor their daily records, teach those who were failing to record, and offer other extension activities. Data forms were then collected at the end of the month and new forms distributed. The Fisheries Officers then sent the daily catch and effort record forms to the District headquarters in Maun at the end of every quarter. These data were then captured into Pasgear 2 (Kolding and Skålevik, 2010) where they were also cleaned before analysis.

Recreational hook and line data were daily fish data recorded by commercial tour operators in the Delta's panhandle from their clients. These data, while not extensive (just over 1200 records over 38 years), were important in giving an over-view of the effort and catches of recreational fishing in the Delta. Data records included identification of each individual species caught, TL measurements, type of lure used, and the relative fishing effort (12 hours soaking time). Other data that were instrumental towards a full understanding of the overall fishing pattern (Paper IX) were commercial and subsistence fisher nets. Both these data sets were recorded by commercial and subsistence fishers in a procedure similar to what Ticheler et al (1998) implemented in Bangweulu, Zambia. For the Okavango, they are described in detail by Mosepele (2000).

***Creel surveys:*** Creel surveys were conducted by Fisheries Division officers around the Delta (Mosepele, 2001). Officers' recorded individual species caught, TL, fisher sex and age, and relative effort (12 hours soaking time) from randomly selected fishers in fishing villages. Data also covered catches from traditional fishing gear that were used in the Delta (Mmopelwa et al 2009). These data, used in conjunction with frame survey data, were instrumental in contributing to the fish stock assessment paper (Paper IX). Just over 1800 records were collected from creel surveys.

***Population surveys:*** These data were collected from around the Okavango Delta from two frame surveys conducted in 1998 and 2005. 3200 individual fishers records were collected in 1998 (Mosepele, 2001) while just over 2700 records were collected in 2005 (Bokhutlo et al. 2007). The basic data collection procedure involved a group of Fisheries officers conducting a population survey in each village around the Okavango Delta. Officers would visit every household in a village to determine and assess the profile of fishers in the household.

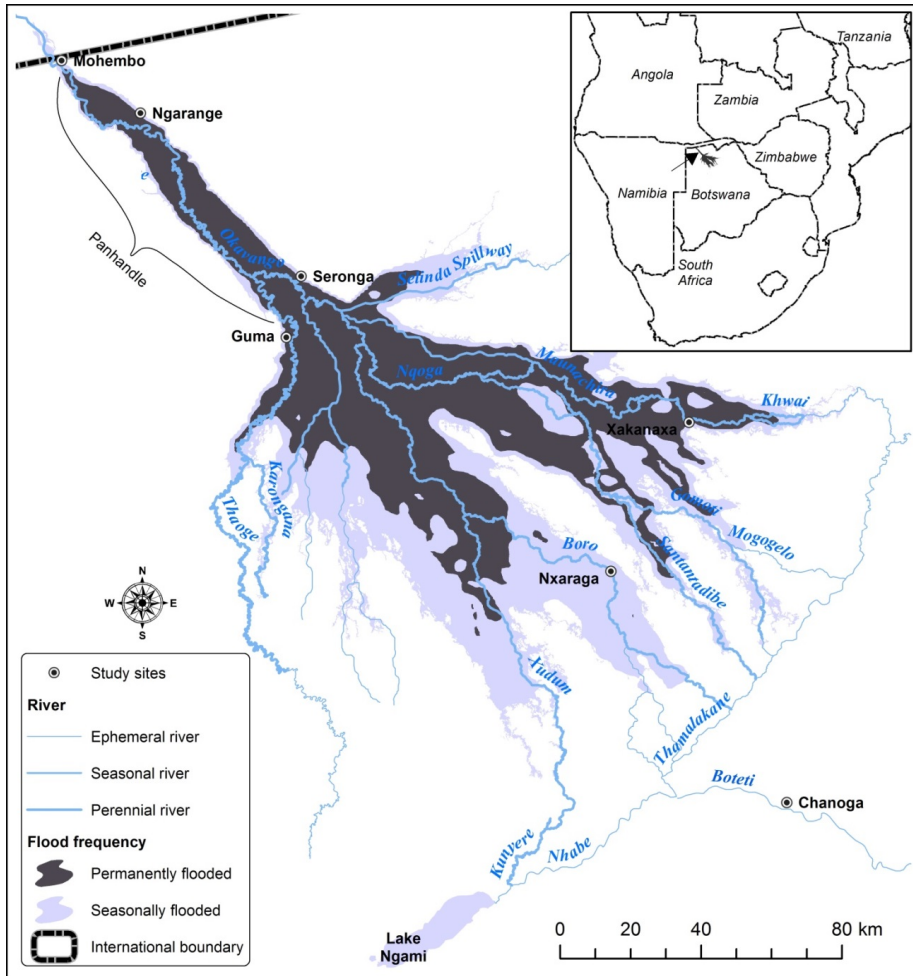


Figure 1 Key study sites for this PhD thesis (Map produced by the Okavango Research Institute GIS laboratory).

## Abstract

Inland fisheries provide vital proteins, jobs and income, for some of the most marginalized communities of the world. The role of inland fisheries in household food security is particularly important in Africa, where most of the world's poorest are found. Therefore, there is a compelling need to enhance our understanding of the dynamics of floodplain fisheries because of their intrinsic value to riparian communities. Understanding their importance will lead to their sustainable utilisation, which will contribute to the attainment of some of the 2030 Sustainable Development Goals. Therefore, this thesis examines the relationship between fish dynamics and environmental variability in flood-pulsed systems, by using the Okavango Delta as a case study. Establishing this relationship is important towards identifying the key drivers of change, restoration and persistence in floodplain fish communities. The thesis also highlights the dynamic interactions between seasonal hydrology and nutrient dynamics in floodplain systems. These dynamic processes, coupled with a heterogeneous system, sustain a diverse fish community that is a key source of livelihoods for the delta's riparian community. Dynamic processes within the fish community, such as distribution, feeding and growth are driven by the seasonal flood pulse. Currently, the Okavango Delta fishery is managed through a series of classical management approaches which are incompatible with the dynamic nature of flood-pulsed systems. The best management approach is through balanced harvesting, which has been inadvertently implemented by traditional exploitation practices.

Management interventions in floodplain fisheries should be adaptive, practical, realistic and implementable, which in particular means acceptable to the stakeholders. Most developing countries have limited resources, and these should be spent on achievable and practical activities. Informed management also necessitates continuous long-term monitoring of exploited fisheries to follow changes and to gradually improve our understanding fishing patterns and their impact on the fish communities. This involves the collection of fisheries related data across a broad spectrum of activities (e.g. fish consumption, employment creation, various kinds of biological data on species exploited, gear use and efficiencies, etc.) and associated factors/ variables (e.g. environmental factors, various land-use activities, etc.). Once

these have been documented and understood, they can be integrated into a flexible management system, which will allow for more adaptive management of these resources. Such integration is currently lacking in the Okavango Delta and also in floodplain fisheries in general.

## List of Publications

### (i) Juvenile fish

- Paper I:** Siziba, N., Chimbari, M.J., **Mosepele, K** and Masundire, H., 2011. Spatial and temporal variations in densities of small fishes across different temporary floodplain types of the lower Okavango Delta, Botswana. *African Journal of Aquatic Science*, 36(3):309-320.
- Paper II:** Siziba, N., Chimbari, M.J., Masundire, H., **Mosepele, K** and Ramberg, L., 2013. Variation in Assemblages of Small Fishes and Micro-crustaceans After Inundation of Rarely Flooded Wetlands of the Lower Okavango Delta, Botswana. *Environmental Management*. DOI 10.1007/s00267-013-0183-9
- Paper III:** Lindholm, M., Hessen, D.O., **Mosepele, K** and Wolski, P., 2007. Flooding size and energy pathways on a floodplain of the Okavango Delta. *Wetlands*, 27 (4): 775–784

### (ii) Adult fish

- Paper IV:** **Mosepele K.**, Mosepele B., Wolski P., Kolding J., 2012. Dynamics of the feeding ecology of selected fish species from the Okavango River delta, Botswana. *Acta Ichthyologica et Piscatoria*, 42 (4): 271 – 289. DOI: 10.3750/AIP2012.42.4.01
- Paper V:** **Mosepele, K.**, Kolding, J and Bokhutlo, T., 2017. Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. *Ecohydrology and Hydrobiology*. DOI: 10.1016/j.ecohyd.2017.01.005
- Paper VI:** Thethela, B., Weyl, O., **Mosepele, K** and Wilson, G., 2015. Age and growth of sharp-tooth catfish, *Clarias gariepinus* (Burchell 1822) (Clariidae), in the Lower Okavango Delta, Botswana. *Marine and Freshwater Research*, 66: 1-9

### (iii) Floodplain dynamics

- Paper VII:** **Mosepele, K.**, Moyle, P.B., Merron, G.S., Purkey, D and Mosepele, B., 2009. Fish, floods and ecosystem engineers; interactions and conservation in the Okavango Delta, Botswana. *Bioscience*, 59 (1): 53 – 64
- Paper VIII:** Linhoss, A.C., R. Muñoz-Carpena, M. Allen, G. Kiker, **K. Mosepele.**, 2012. A flood pulse driven fish population model for the Okavango Delta, Botswana. *Ecological Modelling*, 228: 27 – 38
- Paper IX:** **Mosepele, K.**, Kolding, J and Bokhutlo, T. Fish stock assessment in inland floodplain fisheries; the case of the Okavango Delta. *International Journal of Limnology* (Submitted)

## References

- Bokhuto, T, Kootsositse, M.V and Mosepele, K., 2007. Okavango Delta fishery frame survey. Department of Wildlife and National Parks, Gaborone. <http://www.scribd.com/doc/37412763/ODMP-Fishery-Frame-Survey-Draft-Report>
- Botswana Government., 2008. Fish protection regulations. Government Printing and Publishing Services, Gaborone.
- Kolding J., and Skaalevik A. 2010. Pasgear II. Version 2.1. A database program for experimental or artisanal fishery data. University of Bergen, Norway.  
Available at <http://>
- Mmopelwa, G., Mosepele, K., Mosepele, B., Moleele, N and Ngwenya, B., 2009. Environmental variability and the fishery dynamics of the Okavango Delta, Botswana: The case of subsistence fishing. *African Journal of Ecology*, 47 (Suppl. 1): 1–9
- Mosepele, K ., 2001. Description of the Okavango delta fishery. Technical Report to the Fisheries Section, Ministry of Agriculture, Gaborone, Botswana.
- Mosepele, K, Mmopelwa, T.G, and Mosepele, B., 2003. Characterization and monitoring of the Okavango delta artisanal fishery, pp 391 – 413. In Bernard, T, Mosepele, K and Ramberg, L (Editors). *Environmental Monitoring of Tropical and Subtropical Wetlands*. University of Botswana, Maun and University of Florida, Gainesville, FLA.
- Mosepele, K., 2000. Length based fish stock assessment of the main exploited fish stocks of the Okavango delta, Botswana. MPhil Thesis, University of Bergen, Bergen, Norway.
- Mosepele, K., Mmopelwa, G, Mosepele, B and Kgathi, D. L., 2007. Indigenous knowledge and fish utilization in the Okavango Delta, Botswana: Implications for food security, pages 292 - 302. In Ahmed, A (Editor). *Managing*

knowledge, technology and development in the era of information revolution.  
(Griffith University: Australia).

Mosepele, K., Mosepele, B., Bokhutlo, T and Amutenya, K., 2011. Spatial variability in fish species assemblage and community structure in four subtropical lagoons of the Okavango delta, Botswana. *Physics and Chemistry of the Earth*, 36(14-15): 910-917

Nikolsky, G.V., 1969. Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Olivier and Boyd: United Kingdom.

Skelton PH. 2001. A complete guide to freshwater fishes of southern Africa. Struik Publishers: Cape Town

Ticheler H.J., Kolding J., Chanda B. 1998. Participation of local fishermen in scientific fisheries data collection: a case study from the Bangweulu swamps, Zambia. *Fisheries Management and Ecology* 5: 81-92.

van Zwieten P.A.M., Goudswaard P.C., Kapasa C.K., 2003. Mweru-Luapula is an open exit fishery where a highly dynamic population of fishermen makes use of a resilient resource base. Pp 1 – 33. *In*: Jul-Larsen E., Kolding J., Overa R., Nielsen J.R., Zwieten P.A.M. (eds.) Management, Co-management or No Management? Major Dilemmas in Southern African Freshwater Fisheries, 2: Case Studies. FAO Fisheries Technical Paper 426/2, Rome.

[www.imr.no/forskning/utviklingssamarbeid/eaf\\_nansen\\_proprammet/nansi](http://www.imr.no/forskning/utviklingssamarbeid/eaf_nansen_proprammet/nansi)

*“The published papers are reprinted with permission from their publishers. All rights reserved.”*



# Contents

Scientific environment.....	0
Acknowledgements .....	2
Introduction .....	3
Abstract.....	10
List of Publications .....	12
Contents.....	15
1. Chapter 1.....	16
2. Chapter 2.....	44
3. Chapter 3.....	56
4. Chapter 4.....	70
5. Chapter 5.....	80
6. Chapter 6.....	99
7. Chapter 7.....	113
8. Chapter 8.....	122
9. Chapter 9.....	134
10. Chapter 10.....	146

# 1. Chapter 1

Tropical inland fisheries, while producing at least 15-20% of the global fish production, are based on the tiny fraction ( $\approx 0.04\%$ ) that tropical aquatic freshwater systems contribute to the world's freshwater resources (Kolding and Zwieter, 2006). Most importantly, inland fisheries provide vital proteins, jobs and income for some of the most marginalized communities of the world (Allan et al. 2005; Welcomme, 2011; HLPE 2014; Bene et al, 2015), but a growing global population, with a consequent increase in food demand, will place increased pressure on the global water resources (e.g. <http://www.waterforfood.org/>). According to Molden and de Fraiture (2004), this situation is of particular concern in Africa, where pressure on water resources is expected to increase rapidly within the next two decades. In addition climate change will increase water stress in southern Africa (Boko et al., 2007) because of reduced rainfall (Clark, 2006), which will likely decrease fish productivity (Magadza, 2011) and increase food insecurity. An increased pressure on resources has raised concerns of overexploitation exacerbated by lack of knowledge on ecosystem response to changes in species, size, and trophic composition of fish assemblages (Allan et al., 2005). There is a compelling need to understand the dynamics of floodplain fisheries better because of their prevalence, high productivity and intrinsic value to riparian communities in Africa.

Floodplain fisheries are generally considered among the most productive in the tropics (Junk, et al 1989; Welcomme, 2009), with an average potential fish production rate 2.5-4x that of tropical lakes and reservoirs on a water surface area basis ( Bayley, 1991). The Okavango Delta (Fig. 1) is one of the largest inland river deltas in the world (Allanson, et al 1990) with a fishery which is predominantly artisanal, combined with a small-scale commercial gill net fishery (Mosepele, et al 2003). Common with most African inland fisheries, the fishery is characterized by a multi-species, multi-gear fishery harvesting the fish community across different trophic levels (Paper X). Approximately 65 % of the 25,000 people (based on 1995 population estimates) who live within the periphery of the Delta depend on the fishery as a source of livelihood (Mosepele, 2001). Due to competing interests in the Delta's fish resources, particularly between the flourishing tourist industry and the

local people, there has been a long history of stakeholder conflicts and repeated allegations of over-exploitation of the fish resource and deterioration of the environment. However, apart from a preliminary analysis (Mosepele, 2000) there have been no informed assessment studies on the Okavango delta fishery. The underlying objective for this study was to provide an improved understanding of the dynamics of the fish productivity and its relationship with environmental and fisheries factors, in order to provide informed knowledge to aid in solving the recurrent conflicts and management questions. Because of the complex and dynamic nature of the fishery (approximately 71 species and high seasonal variability, Paper X), a conventional fish stock assessment, based on steady state assumptions, is considered only partly adequate for a comprehensive and accommodating evaluation of the fishery. The Okavango Delta is subject to seasonal flooding which, like elsewhere, seem to play a key role in determining the nature of its fishery (Paper VII). However, a comprehensive understanding of the relationship between the hydrological regime and the dynamics of the fishery, the productivity, and the trophic interrelationships has never been established.

The aim of this study was to examine the relationship between fish dynamics and environmental variability. Establishing this relationship is important towards identifying the key drivers of change and resilience in floodplain fish communities. Understanding this relationship will aid in floodplain fisheries and water management, as a step beyond prevailing management regimes based on steady state conditions (Mosepele, 2014). Tropical and sub-tropical floodplains are dynamic pulsating systems, which are constantly changing at various spatio-temporal scales, but where the fluctuations are also essential for regeneration and maintenance of the ecosystem. Proper understanding of floodplains is key towards their conservation under socio-economic development of riparian communities. The fundamental philosophy underpinning this thesis is that floodplains are dynamic, interconnected aquatic-terrestrial systems driven by seasonal flooding and drying that is mediated by a flood pulse at intra- and inter-annual scales and that management needs to be equally dynamic and adaptive.

### **1.3 Description of the study area**

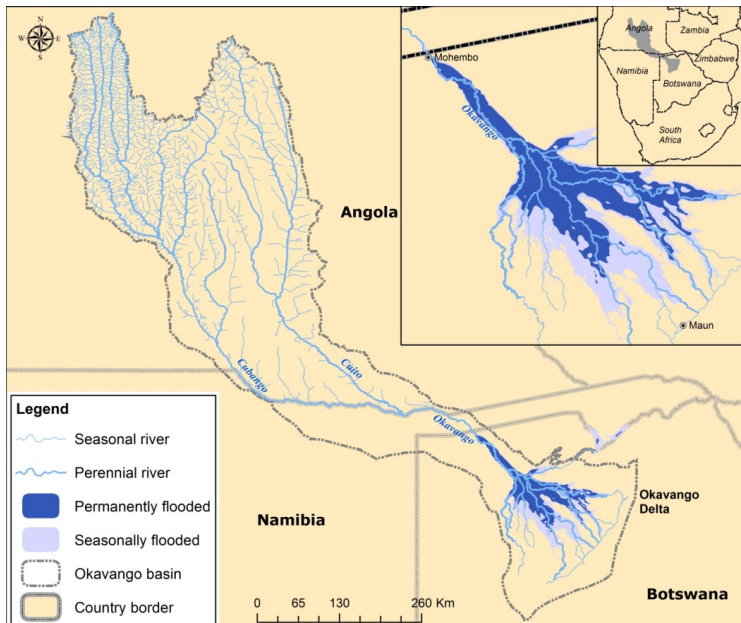


Figure 1 Map of the Okavango River basin in southern Africa, with the three countries sharing the drainage basin. The insert shows the Okavango Delta inside Botswana, which is the focus of this study. (Source: The ORI GIS Laboratory)

The Okavango river basin (Fig 1) is one of the driest and most sparsely populated basins in southern Africa. It is an endorheic (no outlet) system that spans three countries (Angola, Namibia and Botswana) (Ashton and Neal, 2003; McCarthy et al 2003).

The catchment of the Okavango River Basin is estimated to range in size from 429 000 km<sup>2</sup> (Ashton and Neal, 2003) to 530 000km<sup>2</sup> (Andersson et al., 2003). Due to the close direct connection between the Delta, situated in a dryland, and the upstream catchment area, where most of the water originates, development projects altering the Okavango River's flow are highly likely to impact the delta's ecological functioning and fisheries productivity. The basin is located in a water scarce area, and future planned water abstractions are projected to amount to about 3% of the mean annual runoff of the Okavango River when entering Botswana at Moheambo at the distant end of the so-called panhandle (Fig 1). However, there is not enough knowledge to

accurately predict the scale, significance and resilience of ecosystem responses within the Delta to the anticipated decreased flows (Ashton and Neal, 2003).

Currently, the Delta is still relatively pristine (Milzow et al 2009; Black et al., 2011), which however, does not discount threats to its ecological integrity. Threats to the Delta do not only come from within the country driven by local population development pressures (Porter and Muzila, 1989), but there are also transboundary threats which have increased with the advent of peace in Angola (Andersson et al., 2003; Milzow, et al 2009; 2010). After a prolonged civil war, a repopulation of the headwaters of the Okavango has begun (Mendelsohn et al., 2010), where approximately one million people are expected to settle within the river basin (Andersson et al., 2003). Concomitant human activities like agriculture (including irrigation), water abstraction and hydropower development in both Angola and Namibia are expected to place an increased demand on the water resources of the basin (Andersson et al., 2003; Junk et al., 2006; Milzow et al., 2009). Being the endpoint of a large river in a desert, the Okavango Delta may undergo the same environmental threats from dams and irrigation schemes that are now observed in Lake Turkana of Northern Kenya (Gownaris et al. 2016).

### *1.3.1 Flooding dynamics in the Delta*

The Okavango Delta is a mosaic of various habitats consisting of swamps, islands and river channels whose aquatic, semi-aquatic and terrestrial phases change constantly at different temporal scales, driven by the flood regime (McCarthy et al., 2003; Ramberg and Wolski, 2008). It is located in a dry sub-tropical area with a mean annual rainfall of 475 mm and experiences large annual variations in temperature where October is the hottest month while July is the coldest (Milzow et al., 2009). Rain normally falls in the period November – March while annual flooding from the Angolan highlands occurs in the period April - September (Ramberg and Wolski, 2008). Annual precipitation, which is out of phase with seasonal flooding (Porter and Muzila, 1989; Ramberg et al 2006a), contributes approximately between 5% (Andersson et al., 2003) and 42% ( Ramberg and Wolski, 2008) of the total water input into the Delta, while the rest comes as discharge from the Angolan highlands

(Ramberg and Wolski, 2008). Total water storage in the Delta is about 10 000 million m<sup>3</sup> (about a year's inflow of water) which supports diverse vegetation (Porter and Muzila, 1989) aquatic and wildlife species (Ramberg, et al., 2006b). The Delta's hydrology is constantly shifting (i.e. changes in flow patterns from one part of the Delta to the other), and is driven by various factors such as seismic activity, vegetation dynamics, animal activity and human intervention ( Wilson, 1973; Porter and Muzila, 1989; Wolski and Murray-Hudson, 2006; Milzow et al 2009). This suggests that flow in the anastomosis of channels can change at any given time due to variations in these factors.

Peak discharge in the Delta's panhandle occurs in March/ April (Wolski, et al 2005) and the flood pulse continues progressively down the Delta, taking a maximum of 6 months (Andersson et al., 2003) to reach the distal ends of the system. This sinusoidal flooding cycle in the Delta results in a period of minimum inundation (November - March) to a period of maximum inundation (May - September) (Andersson et al 2003; McCarthy et al 2003; Wolski et al 2005). There is a time lag between inflow and flood extent in the Delta. According to Ramberg et al (2006b), water depth variations in the permanently flooded areas are usually very small, while these are normally in the order of 1-2 m in the seasonally inundated parts of the Delta.

Annual average, minimum and maximum flow years in the Delta have a cyclical behaviour with a 17.5 year periodicity in the annual average and maximum flows (Mazvimavi and Wolski, 2006). However, there is high inter-annual variability in flooding patterns where good flood years may be followed by poor flood years (Milzow et al 2009; Mendelsohn et al 2010). The extent of flooding in the previous year and local rainfall also determine the extent of flooding in any one year (Mendelsohn et al., 2010; Milzow et al., 2009). While inter-annual variations in rainfall cause variability (lows and highs) in its flooding regime (Wolski and Murray-Hudson, 2006), earth movements with shifts in the flows also cause different parts of the Delta to periodically undergo drying episodes (Milzow et al., 2009). Flooding dynamics in the Delta are critical towards a comprehensive understanding of ecological processes in the Delta.

#### **1.4 Floodplain ecology: Primary and secondary production dynamics**

Seasonal flooding liberates nutrients from the inundated soils as new floodwaters enter the floodplains (Welcomme, 1988; Paper III). The Delta has a heterogeneous mosaic of micro-habitats (Siziba et al., 2011a) characterized by low nutrient (Krah et al 2006) and oligotrophic waters (Cronberg et al 1995; McKay et al 2011). Despite the oligotrophic nutrient status, the Delta is a productive system (Hoberg et al 2002) as evidenced by relatively high fish production/biomass in some lower Delta lagoons (Fox, 1976; Mosepele et al, 2011) and fast vegetation growth (Ramberg et al., 2006a). Several key processes contribute to nutrient dynamics in the Delta; (i) surface waters (Cronberg et al 1995; Garstang et al 1998; McKay et al 2011) (ii) soil nutrients (Krah et al 2006), (iii) dung from mammals in the seasonal floodplains (Paper VII), (iv) mineralization (from senescent plant material and peat) (Ramberg et al., 2006a), and (v) windblown dust/ atmospheric deposition (Krah et al 2006), the latter which is a major nutrient source at receding water levels in the seasonal floodplains.

When the new floods arrive, they carry with them allotropic nutrients from upstream runoff, which facilitate the primary production processes in the Delta. The new floods also dissolve embedded soil nutrients from the terrestrial dry phase, which increase nutrient concentration and availability. This is also coupled with an increase in Dissolved Organic Carbon (DOC) in the seasonal floodplains (Mladenov, et al 2005), due to high organic matter loading (Mladenov, et al 2007). Additionally, dung from the herds of large herbivores (elephants, buffaloes, antelopes) also contributes to the organic matter loading in the seasonal floodplains (Paper IV). Hippos also play a major role in nutrient cycling of aquatic ecosystems by converting terrestrial biomass (ingested grass) into aquatic nutrients into the Delta's waters where they defecate (Garstang et al., 1998). Ultimately nutrient loading switches to atmospheric deposition when the floods have reached their maximum extent in the seasonal floodplains (Krah et al 2006). The alternating wetting and drying processes in the Delta facilitate optimum conditions for enhanced primary production in the system (Ramberg et al., 2006b). This is consistent with studies from elsewhere (Junk et al, 1989; Ward and Stanford, 1995) which observed that regular flooding and drying in floodplains is an essential nutrient pump for biological production.

Biomass of large mammals in the Delta is approximately  $12 \text{ t km}^{-2}$ , and is among the highest in wetlands around the world (Junk et al., 2006). The density of mammals in the Okavango Delta is 4-8x higher than expected from its standing nutrient status, primarily because of its high efficiency in primary productivity from recycling nutrients (Ramberg et al 2006b). This positive feedback loop in fertilization makes the Delta highly efficient in transforming plant carbon into higher food-web levels through terrestrial mammals (Junk et al., 2006).

Regular flooding and drying episodes in the Delta increase plant diversity (Tsheboeng et al 2014), in accordance with Huston's (1979) "intermediate disturbance hypothesis". Other factors in this habitat "disturbance" include erosion and sediment deposition, and actions by biological engineers like elephants, hippopotamus and termites (Paper VII). Frequent disturbances in the Delta create small-scale habitat patches, which facilitate the co-existence of different successional stages of plant communities. Flood pulsed systems provide diverse food items to food webs, and also act as dry season refuges for migrating mammals. Flooding dynamics in the Delta, coupled with the "out-of-phase" rainfall season, ensure that fresh primary vegetation is available much longer in the Delta for herbivore mammals, which increases the land's carrying capacity (Junk et al 2006). All these interrelated dynamics enhance ecosystem productivity, and contribute to the high productivity in the Delta, despite its oligotrophic water.

In addition to a high average biological basis production, the aquatic processes in subtropical and tropical floodplains systems undergo "boom and bust" conditions driven by seasonal flooding (Junk et al 1989; Lowe-McConnel, 1987; Bunn et al 2006; Schongart and Junk, 2007). The seasonal flooding in the Okavango Delta initiates a "boom" in the aquatic primary production when the new annual floods inundate the peripheral floodplains (Hoberg et al 2002). As the floodwaters submerge the floodplains, microbial decomposition begins to degrade the accumulated detritus, dung and other organic matter. There is an initial build-up in nitrogen and phosphorous concentrations at the start of the flooding season, but these are gradually depleted over time through photolytic degradation and burning in the dry floodplains. There are spatio-temporal variations in dissolved oxygen (DO) (Hoberg et al 2002),



conductivity and phosphorous concentrations (Paper I). DO levels are initially low at the onset of the floods and increase gradually, before reducing again at decreasing flood levels (Hoberg et al 2002). There is also diurnal variability in DO levels where anoxic conditions are observed at sunrise while peak DO saturation levels occur at sunset (Hoberg et al 2002).

The initial flooding in the delta results in a “boom” in chlorophyll *a* and primary production processes, followed by a “bust” towards the end of the flooding cycle. During the first week of flooding, chlorophyll *a* concentration increases from 2.6 to 23.5  $\mu\text{g L}^{-1}$  before receding to 10  $\mu\text{g L}^{-1}$  by the end of the flooding season (Hoberg et al 2002). Similarly, primary production increases from 63  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  at the onset to 264  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  within a week of flooding, before settling to 82  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  by the end of the first month of flooding. However, there is spatial variability in chlorophyll *a* concentration across the Delta’s microhabitats (Siziba et al., 2011a). The seasonally inundated floodplains in the Delta have higher concentrations of DOC, K, SiO<sub>2</sub>, Mg, HCO<sub>3</sub>, Na and NO<sub>3</sub> than permanently flooded areas (Mackay et al., 2011). Like the mosaic pattern of the delta itself, there are spatial and temporal variations in water chemistry. This complex system is further exacerbated by a surging time lag where new floods arrive at Mohembo (northern Delta), while the previous year’s flood are still receding at Maun (southern Delta) (Mackay et al., 2011).

The sharp increase in zooplankton biomass “boom” at the onset of the floods is inoculated from egg banks in the seasonal floodplains (Hoberg et al 2002; Siziba et al 2012). Regular flooding is important in maintaining micro-crustacean propagules and the diversity of these micro-fauna in the Delta’s floodplains (Siziba et al., 2012). Cladocerans, copepods and ostracods are the three major groups whose emergence from floodplain sediments is driven by inundation. These micro-crustacea, which are key fish food (Paper II), then inoculate new flood waters in the seasonal floodplains (Siziba et al., 2012). Riding on the wave of seasonal flooding are strong fluctuations in zooplankton biomass over the flooding season in the seasonal floodplains (Hoberg et al 2002). Zooplankton biomass peaks at about 10 mg DW L<sup>-1</sup> during the first month of flooding, which gradually declines to 1 mg DW L<sup>-1</sup> towards the end of the flooding

season. Hoberg et al (2002) also observed a species succession in zooplankton species during the flooding season. *Moina micrura* is the dominant species during the onset of the flood, whose populations then decrease to the end of the first month of flooding. Zooplankton populations are then dominated by *Daphnia laevis* during the second month of flooding, while *Chydorus* spp. dominates the zooplankton community at the end of the flooding season.

## **1.5 The flood pulse and fish community dynamics**

### *1.5.1 Juvenile and small fish species dynamics*

Newly inundated floodplains are an important nursery habitats for fish recruitment (King et al 2003). In the Okavango delta the inundated areas are dominated by juvenile cichlids (e.g. *Oreochromis andersonii*, *Tilapia sparrmanii* and *Coptodon rendalli*), catfish (*Clarias gariepinus*), and cyprinids (e.g. *Barbus bifrenatus* and *B. barnardi*) during the first month of flooding. Fish fry and juveniles were observed at increasing frequency starting from the second month of flooding (Hoberg et al 2002). The boom of primary producers and zooplankton initiated by the seasonal flooding (Siziba et al., 2012), serves as abundant food sources for the juvenile fish and small fishes (Paper II) and also some adult fish (Paper IV). The subsequent decrease in zooplankton biomass corresponding with an increased frequency of juvenile fish over the flooding season is due to predation ( Hoberg et al 2002, Paper II). This suggests that failed or poor floods cause a bottle neck in fish production due to failed zooplankton production (Siziba et al., 2012).

Juvenile fish growth on the inundated floodplains is rapid within the first year of life (Dudley, 1974). Rapid growth ensures that juvenile fish are large enough to (i) avoid being stranded in the floodplains at receding floods, and (ii) avoid heavy predation when migrating into the permanent channels at draw-down (Booth and Merron, 1996). Foraging by juvenile fish in the inundated areas is an adaptation for taking advantage of high zooplankton biomass that is triggered by the flood pulse (Paper III). Less frequently flooded areas (those only flooded occasionally at very high flows) show exceptional “booms” in zooplankton biomass and juvenile fish (Paper I), especially after a low flood year (Paper II). During poor flood years, the zooplankton

biomass are less exposed to fish grazing, while predation appears to be a strong regulator of zooplankton biomass during good flood years (Paper III). Large flood years result in extensive flooded areas which appear to particularly facilitate fish breeding, growth and survival and ultimately increased fish production (Lowe-McConnell, 1987; de Graaf, 2003). The flood volume in the Okavango Delta is a major driver of fish production, where relative fish biomass during a high flood year can be double that of a low flood year (Paper III).

Alternating wetting and drying processes are necessary in floodplains to increase nutrient turnover, maintain primary production dynamics (Junk et al., 1989) and hence fish production. However, the pattern of rise and fall of the hydrograph is influencing floodplain fish production. According to King et al (2003), a “relatively slow rate of rise and fall” of the seasonal hydrograph creates optimum conditions for fish species to utilize the floodplain for recruitment. Conversely, a rapid rise and fall in the hydrograph may offset the balanced time lag between primary production and fish production (Tockner et al 2000), which may result in less successful fish production. However, short lived hardy species in floodplain systems can adjust quickly to extreme hydrological events (Junk et al 1989; Junk, 2002).

### *1.5.2 Adult fish*

***Community structure and distribution:*** Floodplain fish communities are structured along a hydrology-water chemistry gradient (Zeug and Winemiller, 2007; Zeug et al 2005; Paper V). However, due to inter-annual differences in flooding regimes, fish communities among years are stochastically different driven by the seasonal dilution and expansion dynamics (Paper V; Paper VII) of the hydrological cycle.

Studies from other areas have shown that poor flood years are dominated by opportunistic fish species (Lae, 1995; Petry et al 2003), which have fast growth rates and high fecundities. Other studies show that good flood years are dominated by iliophagous (mud-eaters) species, which are preceded by piscivores in poor flood years (Agostinho et al 2001). Similar kinds of species dynamics driven by flooding at an annual scale have also been observed in the Okavango Delta. The Delta’s fish community, as judged by experimental catch rates, is dominated by *C. gariepinus* at

maximum flooded area, while tiger fish (*H. vittatus*) dominates the fish community at minimum flooded area (Paper V). Furthermore, poor flood years are dominated by hardy, multiple spawning species (i.e. *C. gariepinus*) while good/ high flood years are dominated by opportunistic, highly fecund, total spawning species (i.e. *Schilbe intermedius*) (Paper V). Mosepele et al (2011) observed spatial differences in fish community structure among several lagoons in the Delta. Generally, upper Delta lagoons have higher fish species richness than lower Delta lagoons. It is possible that one factor contributing to these community differences is relative hydrological stability in the upper Delta vs. increased hydrological variability in the lower Delta.

**Reproduction:** While spawning for some floodplain fish species is cued by rising water levels (Dudley, 1974; van der Waal, 1985; Welcomme, 1985; Godinho et al 2010; Montcho et al 2011), others spawn at low water levels (Humphries et al 1999; Vasquez et al 2009). In the Okavango Delta, peak spawning for some fish species occurs at low flood levels in the main channel at high water temperatures, while other species spawn during high water levels in the floodplains at low water temperatures (Merron et al 1990; Paper V). Van der Waal (1985) observed that spawning for some cichlids was apparently not associated with hydrology, while other studies (Dudley, 1974; Paper V), found that spawning for the majority of cichlids is associated with a hydrological gradient. However, for some cichlids (e.g. *Serranochromis macrocephalus* and *C. rendalli*) spawning was mostly associated with water temperature, which agrees with van der Waal's (1985) observations.

**Growth and Feeding:** Floodplain fish growth is fastest during increasing water levels (Power, 1984; Bayley, 1988; Paper VI) and peaks at maximum flooded area to take advantage of the available abundant food in the floodplains (Booth and Merron, 1996; Paper VI). During the low flood season, intra-specific competition for food (Paper IV) decreases growth rates (Dudley, 1974; Martin et al 2011). At inter-annual scale, growth of floodplain fish in Kafue, Zambia, differed significantly among years according to flooding and temperature (Dudley, 1974). In the Okavango, studies have shown that there are significant differences in maximum size between upper and lower delta *Clarias gariepinus* populations (Mosepele et al, 2011). Other research suggests that upper Delta populations follow *K* life histories while lower Delta

populations are more  $r$  selected (Merron and Bruton, 1988; Paper VI). Similarly, some cichlid species also appear to follow  $K$  selected life history strategies in the upper delta and are more  $r$  selected in the lower Delta (Mosepele and Mosepele, 2005).

Like most other features, the diet and feeding ecology of floodplain fish species is flood-pulse driven (Lowe-McConnell, 1987; Paper IV). After the feeding and growth of the juveniles on the floodplains during high water, a dominant feature is increased piscivory at receding water levels by fish predators when all the young fish are forced back into the main channels (Bayley, 1988; Paper IV). This “concentration effect” at receding water levels facilitates predation by piscivorous fish, as well as fishers. Thus, while prolonged inundation or years of good flooding might enhance fish growth and production (Bayley, 1988; de Graaf, 2003), this may have an adverse impact on large, resident channel living piscivorous fish (Hoeinghaus et al 2003). These dynamic processes illustrate the variability of floodplain fish dynamics and the need for adaptive approaches in both exploitation and regulations.

### *1.5.3 Floodplain fisheries management*

***Nature of the fisheries:*** The preceding overview has highlighted the dynamic interactions and processes between floodplain fish communities and the highly dynamic environment. Floodplains are unstable, seasonally fluctuating ecosystems characterized by strong intra and inter annual variability, where the flood pulse is a key driver of practically all processes (Junk et al 1989; Schongart and Junk, 2007). Inland fisheries in Africa are generally small scale and labor intensive (Welcomme, 2011). They are characterized by multi-species assemblages, of different sizes exploited by diverse fishing gears and methods (van Zwieten et al 2003; Welcomme, 2011; Kolding and van Zwieten 2014; Paper IX). In the Okavango Delta, the hydrological regime is a major driver of change in the biology and ecology of the fish community (Paper III, IV, V, VI, VII, and VIII). Like other floodplains, the fisheries are dynamic, and constantly changing due to the environmental driver, and are never in constant equilibrium. This makes conventional management approaches based on

steady state equilibrium assumptions inconsistent and difficult ( Staples et al 2004; Mosepele, 2008, 2014; Welcomme et al 2010).

Except for a few highly commercialized fisheries in freshwater systems like the Amazon and Mekong (Welcomme et al 2014), most floodplain fisheries are a major source of localized food and nutrition and mostly serving as subsistence for riparian households (Junk, 2002; Mosepele et al 2006; Welcomme, 2011). Their primary value to local communities is their contribution towards household income and food security (Mosepele et al., 2006), though some African inland fisheries are slowly morphing towards commercial or recreational fishing as well (Kolding and van Zwieten, 2014). Fishers in floodplain fisheries systems use various traditional techniques ( Cerdeira et al 2000; Kolding et al 2003; van Zwieten et al 2003) to adapt and optimize utilization of the ever changing fish assemblages, and the same is observed in the Okavango Delta (Mosepele et al 2007; Mmopelwa et al 2009; Paper IX). Floodplain fisheries are thus also a major source of traditional ecological knowledge (Mosepele, 2008) and cultural heritage (Junk, 2002) and any floodplain fisheries management regime should incorporate these characteristics into its management objectives.

***Effort regulation:*** Gear restrictions and mesh regulations are fixed attributes and remain some of the easiest and cheapest regulations to implement in fisheries management regimes (Misund et al, 2002), and these have been widely implemented in floodplain fisheries. The fundamental questions in fisheries management is how to regulate the fishing mortality, which is a combination of how to catch the fish (this is based on gear and mesh restrictions) and how much fish to catch (which is based on effort regulation). The key approach to regulate the ‘how’ question is to control gear selectivity, while effort on the other hand is sometimes regulated to maintain the aggregate fishing effort in order to obtain a “maximum economic yield” (MEY). An efficient economic exploitation of the fishery is assumed to save fish stocks from over-exploitation/ collapse ( Bene et al 2010; Kolding and van Zwieten, 2014). Arguments such as these are attractive to policy makers and introduce policies aimed at effort reduction. The classical argument is that fishers are the main factor influencing fish stock dynamics, which is otherwise assumed in ‘steady state’. Since

catch is a function of effort, it needs to be managed. The alternative assumption would be that effort is controlled by the current production (Kolding and van Zwieten 2011, 2014), and therefore largely self-regulated,

The Okavango delta, like other floodplains, is environmentally driven and primarily forced by the seasonal flood pulse. Poor floods result in reduced fish production while good floods facilitate high productivity. Accordingly, fishing effort is also relatively driven by the seasonal flood pulse, where fishers regulate their effort and fishing methods based on seasonal flooding (Paper IX). In addition, the structural heterogeneity of the Delta also has a major regulating impact on fishing pressure in the Delta (Paper IX). According to Mendelsohn et al (2010), there are places in the Delta which are inaccessible to fishers, and most fishing activities is conducted in areas close to human settlements, such as the panhandle (Figure 1).

***Mesh or gear regulation:*** A key theoretical argument for regulating the gear selectivity is to protect the young fish and target the big fish in order to prevent so-called growth overfishing (Kolding and van Zwieten, 2011). Most fishing gears are selective regarding species, sizes and habitats fished (Kolding and van Zwieten, 2014) but regulating selectivity on certain sizes will invariably unbalance the fishing mortality on the various components in the ecosystem (Garcia et al. 2012). For example, males of *O. andersonii*, *O. macrochir* and *C. rendalli* (which are important commercial species in the Okavango Delta), grow larger than females (Dudley, 1974). Hence, selective harvesting with large mesh sizes would tend to select the males from the populations of these three species resulting in unbalanced sex ratios. Such scenario can alter the breeding sex ratio of an exploited population and ultimately reduce its reproductive potential (Fenberg and Roy 2008). Focusing exploitation exclusively on the mature part of the population will also alter the demographic composition. It therefore makes ecological sense to also target younger age classes than only old big fish, which are the engines of population growth. Big Old Fat Fecund Females (BOFFFs) are more fecund than smaller/ younger fish (Trippel, 1995; Walsh et al 2006; Kolding et al 2015). Smaller/ younger fish are also more productive than bigger/ older fish (Law et al. 2012). In order to maintain the natural structure and composition of fish communities it has been suggested to exploit

populations in proportion to their natural productivity, of the so-called ‘Balanced harvest’ concept (Garcia et al., 2012; Law et al., 2012).

Similar species from different habitats in the Delta have different life history strategies (Merron and Bruton, 1988; Mosepele, 2000; Mosepele and Mosepele 2005; Paper VI) where lower Delta species are generally smaller and *r* selected while upper Delta species are generally larger and more *K* selected (Merron and Bruton, 1988, Mosepele et al, 2011). While *O. andersonii* from the lower Delta has slower growth than those from upper Delta, *O. macrochir* and *C. rendalli* from the lower Delta grow faster than their upper Delta conspecifics (Mosepele, 2000). Moreover, lower Delta populations of these three cichlids were found to mature earlier than those from the upper Delta (Mosepele and Mosepele 2005). A similar observation was made for *C. gariepinus* (Paper VI).

From a multispecies point of view, the smallest fish species (Total Length) in the Delta is approximately 32 mm while the largest species is over 1 m with a graduation of sizes in between them (Paper IX). Implementing mesh (or gear) regulations will certainly skew fishing mortality towards one side of the community size spectrum, causing a structural and demographic change of the fish community, and possibly also effecting functional changes. According to the Convention on Biological Diversity (CBD), a major component of the Ecosystem Approach to Fisheries (EAF) is to maintain the structure and function of the natural communities as close as possible to the natural stages.

Selective fishing, on the contrary, can cause evolutionary change in exploited populations (Rochet, 1998; Law, 2000) which occurs through a three stage process; (a) fishery managers set the parameters of selection, (b) fishers apply the mortality and, (c) the exploited fish stocks are then exposed to the selective mortality (Law, 2000). As a consequence, exploited stocks undergo changes in growth and maturation (Rochet, 1998; Law, 2000), and selective fishing essentially causes ecosystem imbalances (Schindler et al, 1998; Law, 2000; Kolding and van Zwieten, 2011).

***A new paradigm:*** Classical single-species assessment models are incompatible with multi-species, multi-gear fisheries (Mosepele, 2008; Welcomme, et al 2010;



Welcomme, 2011). A more balanced exploitation pattern harvesting species of all sizes and all trophic levels is likely the best management approach for floodplain fisheries in terms of both yield and maintaining the fish community structure (Kolding et al 2003, Mosepele 2014; Paper IX). There are nine different fishing gears/ methods observed in the Okavango delta, which collectively harvest the fish community across different age classes and trophic levels (Fig 2) and species (Mosepele et al 2003; Mmopelwa et al 2009), thus an approximate “balanced harvesting” (BH) regime by the diversified gear assemblage; Fig 2) is actually applied by fisher communities in the Okavango Delta and is a common attribute of floodplain fisheries (Kolding and van Zwieten, 2014). The so far only fish stock assessment of the Delta (Paper IX), showed that i) the fish stocks were generally under-exploited and ii) that the fish community was being rationally exploited by using several different fishing gears and methods to harvest the Delta’s diverse species assemblage (Paper IX, Fig 2).

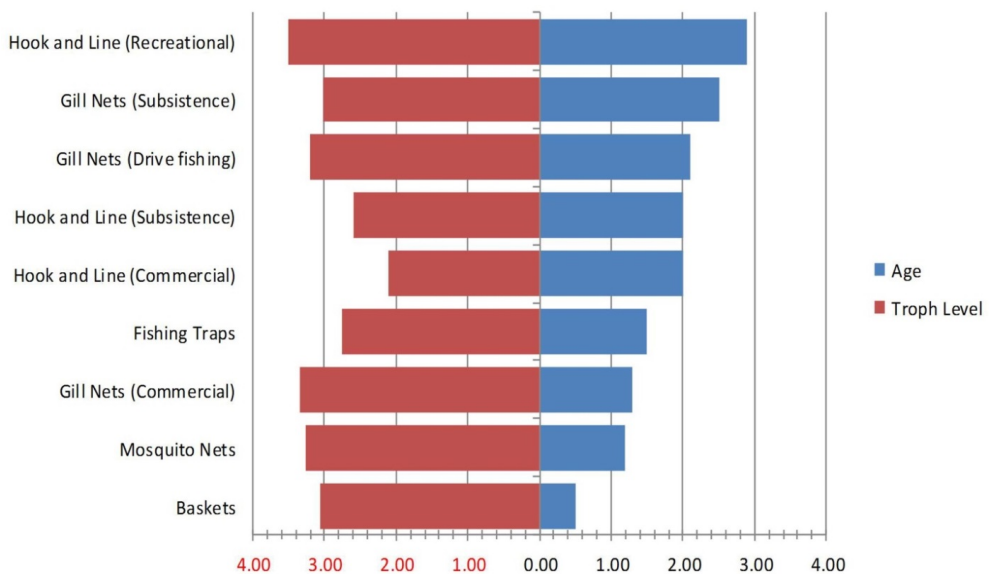


Fig 2 Effect of various fishing gears and methods on the Okavango Delta’s fish community where the red scale on the x-axis represents the mean trophic level of each species calculated from Paper IV, while the black scale represents the mean age of each fish species calculated from Froese and Binohlan (2000) (Source: Paper IX)

Currently, some of these gears (e.g. mosquito nets) and fishing methods (e.g. drive fishing) are prohibited in the Delta (Botswana Government, 2008; Mosepele, 2008, 2014). However, there is no empirical evidence to justify these regulations. About 70% of the species exploited by mosquito nets are generally very small species (e.g. *Barbus radiatus*, *Aplocheilichthys johnstoni*, etc.), which are not caught by other methods (Mosepele et al 2003; Paper IX). Restricting this gear will result in decreased catches of these small sized underutilized species, which are primarily harvested by women for household consumption. Drive fishing is a traditional and efficient method for exploiting cichlids ( Mosepele et al 2007). Thus, prohibiting drive fishing will skew gill net fishing mortality towards *O. andersonii*, while *Coptodon rendalli*, well known for escaping stationary gillnets (Kolding et al., 2003), will remain relatively unexploited.. In addition, prohibiting drive fishing will result in reduced revenue for the Delta's commercial fishers which are primarily targeting cichlids. Blankly prohibiting some fishing methods and gears, without informed justification may not only cause ecosystem imbalances, but may also reduce the food security aspect and socio-economic value of the fishery to riparian communities. The principle of Balanced Harvest (BH) has been strongly criticized by Froese et al (2015), because they argue it does not conform to 'basic population dynamics' as developed by Beverton and Holt. However, BH is a concrete proposal for implementing the Ecosystem Approach to Fisheries (EAF) (Kolding et al 2016), which does not only make ecological and biological sense in floodplain fisheries (Mosepele, 2014), but it is also sensitive to the cultural value of floodplain fisheries (Mosepele, 2008).

Diversified fishing techniques, as it is traditionally practiced in the Okavango Delta and many other African inland fisheries, ensure that most species across various sizes and habitats- in the fish community are exploited. It also allows impoverished households (especially those headed by women), to have access to high quality protein, which again ensures that young children from these fishing households have a relatively good nutritional status (Nnyepi et al 2007). BH was intended to reduce adverse ecological impacts of fishing while also supporting sustainable fisheries (Garcia et al., 2012). Fisheries management should also preserve cultural and heritage

practices of fishing communities when these are not proven destructive, because, “culture is a fundamental human right” (Junk, 2002).

## **1.6 Conclusion**

The seasonal flood pulse in the Delta, driving the dry and wet floodplain phases, is the main contributor towards enhanced ecosystem production in an otherwise oligotrophic environment. Seasonal flooding not only changes the physical landscape of the Delta, by re-connecting isolated lagoons and creating a multitude of diverse micro-habitats, it also enhances nutrient dynamics in both the terrestrial and aquatic system. These alternating micro-habitats ensure continuous succession in plant communities and enhanced plant biomass production (much of which is grazed by large herbivores), thereby contributing to nutrient recycling in the system. This shifting terrestrial and aquatic based food webs is eventually transformed into fish biomass.

Management interventions in floodplain fisheries should be adaptive, practical, realistic and implementable, which in particular means acceptable to the stakeholders. Most developing countries have limited resources, and these should be spent on achievable and practical activities. Informed management also necessitates continuous long-term monitoring of exploited fisheries to follow changes and to gradually improve our understanding fishing patterns and their impact on the fish communities. This involves the collection of fisheries related data across a broad spectrum of activities (e.g. fish consumption, employment creation, various kinds of biological data on species exploited, gear use and efficiencies, etc.) and associated factors/ variables (e.g. environmental factors, various land-use activities, etc.). Once these have been documented and understood, they can be integrated into a flexible management system, which will allow for more adaptive management of these resources. Such integration is currently lacking in floodplain fisheries.

## Source of data

- Agostinho, A. A., Gomes, L. C and Zalewski, M. (2001). The importance of floodplains for the dynamics of fish communities of the upper river Parana. *Ecology and Hydrobiology*, 1(1-2): 209 – 217
- Allan, J. D., Abell, R., Hogan, Z., Revenga, C., Taylor, B. W., Welcomme, R. L., and Winemiller, K. (2005). Overfishing of Inland Waters. *Bioscience*, 55(12): 1041–1051.
- Allanson, B. R., Hart, R. C., O’Keeffe, J. H. and Robarts, R. D. (1990). Inland Waters of Southern Africa; An Ecological Perspective. Kluwer Academic Publishers, Netherlands
- Andersson, L. G., Thomas, H., Denis, K. D., Ringrose, S., Savenije, H. T., Martin, W. J., Wolski, P. (2003). Water flow dynamics in the Okavango River Basin and Delta—a prerequisite for the ecosystems of the Delta. *Physics and Chemistry of the Earth*, 28: 1165–1172
- Ashton, P and Neal, M. (2003). An overview of key strategic issues in the Okavango basin. In Turton, A.R., Ashton, P.J and Cloete, T.E (Editors), *Transboundary Rivers, Sovereignty and Development: Hydropolitical Drivers in the Okavango River Basin*. Green Cross International, Geneva. Pages 31–63
- Bayley, P. B. (1991). The flood pulse advantage and the restoration of river-floodplain systems. *Regulated Rivers, Research and Management*, 6: 75–86.
- Bayley, P. B. (1988). Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. *Environmental Biology of Fishes*, 21(2): 127–142.
- Bene, C., Hersoug, B., and Allison, E. H. (2010). Not by rent alone: analyzing the pro-poor functions of small-scale fisheries in developing countries. *Development Policy Review*, 28(3): 325–358.
- Béné, C., Barange, M., Subasinghe, R., Pinstup-Andersen, P., Merino, G., Hemre, G and Williams, M. (2015). Feeding 9 billion by 2050 – Putting fish back on the menu. *Food Security*, 7:261–274
- Booth, A. J and Merron, G. S. (1996). The age and growth of the greenhead tilapia *Oreochromis macrochir* (Pisces: Cichlidae) from the Okavango Delta, Botswana. *Hydrobiologia*, 321(2): 9-34
- Black, F. J., Bokhutlo, T., Somoxa, A., Maethamako, M., Modisaemang, O., Kemosedile, T., Mosepele, K. and Chimbari, M. (2011). The tropical African mercury anomaly: Lower than expected mercury concentrations in fish and human hair. *Science of the Total Environment*, 409(10): 1967–1975.

- Boko, M., I. Niang, A. Nyong, C. Vogel, A. Githeko, M. Medany, B. Osman-Elasha, R. Tabo and P. Yanda, (2007). Africa Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, (Eds.), Cambridge University Press, Cambridge UK, 433-467.
- Botswana Government. (2008). Fish protection regulations. Botswana Government Printing and Publishing Services Gaborone, Botswana.
- Bunn, S.E., Thoms, M.C., Hamilton, S. K and Capon, S. J. (2006). Flow variability in Dry Land Rivers: boom, bust and the bits in between. *River Research Applications* 22: 179–186
- Cronberg, G., Gieske, A., Martins, E., Nengu, J., and Stenstrom, I-M. (1995). Hydrobiological studies of the Okavango Delta and the Kwando/Linyanti/Chobe River, Botswana. I. Surface water quality analysis. *Botswana Notes and Records*, 27: 151 – 226.
- Clark, B. M. (2006). Climate change: A looming challenge for fisheries management in southern Africa. *Marine Policy*, 30: 84–95.
- de Graff, G. (2003). The flood pulse and growth of floodplain fish in Bangladesh. *Fisheries Management and Ecology*, 10: 241–247
- Dudley, R.G. (1974). Growth of Tilapia of the Kafue Floodplain, Zambia: Predicted Effects, of the Kafue Gorge Dam. *Transactions of the American Fisheries Society*, 2: 281 – 291.
- Fenberg, P. B. and Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology*, 17: 209–220
- Froese R., Binohlan C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity, and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology* 56: 758–773.
- Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O.L.F., Demirel, N., Tsikliras, A.C. and J. Holt, S.J. (2015). A critique of the balanced harvesting approach to fishing. *ICES Journal of Marine Science*, doi: 10.1093/icesjms/fsv122.
- Garcia, S. M., Kolding, J., Rice, J., Rochet, M.-J., Zhou, S., Arimoto, T., Beyer, J. E., Borges, L., Bundy, Dunn, A., Fulton, D. E. A., Hall, M., Heino, M., Law, R., Makino, M., Rijnsdorp, A. D., Simard, F and Smith A. D. M. (2012). Reconsidering the Consequences of Selective Fisheries. *Science*, 335(6072): 1045–1047.

- Garstang, M., Ellery, W.N., McCarthy, T.S., Scholes, M.C., Swap, R.J and Tyson, P.O. (1998). The contribution of aerosol and water borne nutrients to the functioning of the Okavango Delta ecosystem, Botswana. *South Africa Journal of science*, 94(5): 223 - 229
- Godinho, A.L., Lamas, I.R and Godinho, H.P. (2010). Reproductive ecology of Brazilian freshwater fishes. *Environmental Biology of Fishes*, 87: 143–162
- Gownaris, N.J., E. Pikitch, J.Y. Aller, L. Kaufman, J. Kolding, K.M.M Lwiza, K.O. Obiero, W.O. Ojwang, J.O. Malala and K.J. Rountos (2016). Fisheries and Water Level Fluctuations in the World’s Largest Desert Lake. *Ecohydrology* DOI: 10.1002/eco.1769
- Høberg, P., Lindholm, M., Ramberg L. and Hessen D.O. (2002) .Aquatic food web dynamics on a floodplain in the Okavango Delta, Botswana. *Hydrobiologia*, 470: 23–30.
- HLPE, 2014. Food losses and waste in the context of sustainable food systems. A report by the High Level Panel of Experts on Food Security and Nutrition of the Committee on World Food Security, Rome
- Hoeninghaus, D. J., Layman, C. A., Arrington, D. A., and Winemiller, K. O. (2003). Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes*, 67(4): 379–387.
- Humphries, P.K., Alison J. and Koehn, J. D. (1999).Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia- *Environmental Biology of Fishes*, 56: 129–151.
- Huston, M. (1979). A General Hypothesis of Species Diversity. *The American Naturalist*, 113(1): 81-101
- Junk, W.J., Brown, M., Campbell, I.C., Finlayson, M., Gopal, B., Ramberg, L and Warner, B.G. (2006). The comparative biodiversity of seven globally important wetlands: a synthesis. *Aquatic Sciences*, DOI 10.1007/s00027-006-0856-z
- Junk W.J., Bayley P.B and Sparks, R.E. (1989). The flood pulse concept in river-floodplain systems, p 110-127. In Dodge, D.P (ed.) Proceedings of the International Large River Symposium. *Canadian Special Publications in Fisheries and Aquatic Sciences* 106.
- Junk, W. (2002). Long-term environmental trends and the future of tropical wetlands. *Environmental Conservation*, 29 (4): 414–435
- King, A.J., Humphries, P and Lake, P.S. (2003). Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Can. J. Fish. Aquat. Sci.* 60: 773–786

- Kolding, J., Musando, B., and Songore, N. (2003). Inshore fisheries and fish population changes in Lake Kariba. Pp 67 – 99 In: Jul-Larsen E., Kolding J., Overa R., Nielsen J.R., Zwieten P.A.M. (eds.) Management, Co-management or No Management? Major Dilemmas in Southern African Freshwater Fisheries, 2: Case Studies. Rome: Food and Agriculture Organization. FAO Fisheries Technical Paper 426/2. FAO, Rome.
- Kolding, J and P. A. M. van Zwieten. (2006). Improving productivity in tropical lakes and reservoirs. Challenge Program on Water and Food - Aquatic Ecosystems and Fisheries Review Series 1. Theme 3 of CPWF. Cairo: WorldFish Center.
- Kolding, J and van Zwieten, P. A.M. (2011). The Tragedy of Our Legacy: How do Global Management Discourses Affect Small Scale Fisheries in the South? *Forum for Development Studies*, 38(3): 267-297.
- Kolding, J., Bundy, A., van Zwieten, P. A.M., and Plank, M. J. (2015). Fisheries, the inverted food pyramid. – *ICES Journal of Marine Science*, doi: 10.1093/icesjms/fsv225.
- Kolding, J., Jacobsen, N. S., Andersen, K. H., and P.A.M., van Zwieten. (2016). Maximizing fisheries yields while maintaining community structure. *Canadian Journal of Fisheries and Aquatic Sciences*, 73: 644–6551.
- Kolding, J., and Van Zwieten, P. A. M. (2014). Sustainable fishing of inland waters. *Journal of Limnology*, 73(1): 132–148.
- Krah, M., McCarthy, T. S., Mapila, P.H., Wolski, P., Annegarn, H. and Sethebe K. (2006). Nutrient budget in the seasonal wetland of the Okavango Delta, Botswana. *Wetlands Ecology and Management*, 14: 253–267
- Laë, R. (1995). Climatic and anthropogenic effects on fish diversity and fish yields in the Central Delta of the Niger River. *Aquatic Living Resources*, 8(1): 43–58
- Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57: 659–668.
- Law, R., Plank, M. J., and Kolding, J. (2012). On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science*, doi:10.1093/icesjms/fss031.
- Lowe-McConnell, R.H., 1987. *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, Cambridge, p. 400.

- Mackay, A. W., Davidson, T., Wolski, P., Mazebedi, R., Masamba, W. R. L., Huntsman-Mapila, P., and Todd, M. (2011). Spatial and Seasonal Variability in Surface Water Chemistry in the Okavango Delta, Botswana: A Multivariate Approach. *Wetlands*, 31(5): 815–829.
- Martin, S. M., Lorenzen, K., Arthur, R. I., Kaisone, P., and Souvannalangsy, K. (2011). Impacts of fishing by dewatering on fish assemblages of tropical floodplain wetlands: A matter of frequency and context. *Biological Conservation*, 144(1): 633–640
- Mazvimavi, D. and Wolski, P. (2006). Long-term variations of annual flows of the Okavango and Zambezi Rivers. *Physics and Chemistry of the Earth* 31 944-951.
- McCarthy, J.M., Gumbrecht, T., McCarthy, T., Frost, P., Wessels, K and Seidel, F. (2003). Flooding Patterns of the Okavango Wetland in Botswana between 1972 and 2000. *AMBIO*, 32(7):453-457
- Mendelsohn, J.M., van der Post, C., Ramberg, L., Murray-Hudson, M., Wolski, P and Mosepele, K. (2010). Okavango Delta: Floods of Life. RAISON (Windhoek, Namibia).
- Merron, G.S., Holden, K.K and Bruton, M.N. (1990). The reproductive biology and early development of the African pike, *Hepsetus odoe*, in the Okavango Delta, Botswana. *Environmental Biology of Fishes*, 28: 215-235
- Merron, G.S. and Bruton, M.N. (1988). The ecology and management of the fishes of the Okavango delta, Botswana, with special reference to the role of the seasonal floods. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. Investigational Report No. 29. 291p
- Milzow, C., Kgotlhang, L., Gottwein, P. B., Meier, P and Kinzelbach, W. (2009)- Regional review: the hydrology of the Okavango Delta, Botswana—processes, data and modelling. *Hydrogeology Journal*, 17: 1297–1328.
- Misund, O.A., Kolding, J. and Fréon, P. 2002. Fish capture devices in industrial and artisanal fisheries and their influence on management. pp. 13-36 In P.J.B. Hart and J.D. Reynolds (eds.). *Handbook of Fish Biology and Fisheries, vol. II*, Blackwell Science, London
- Mladenov, N., McKnight, D.M., Wolski, P and Ramberg, L. (2005). Effects of annual flooding on dissolved organic carbon dynamics within a pristine wetland, the Okavango Delta, Botswana. *Wetlands*, 25(3): 622 – 638
- Mladenov, N., Mcknight, D. M., Wolski, P and Murray-Hudson, M. (2007). Simulation of DOM fluxes in a seasonal floodplain of the Okavango Delta, Botswana. *Ecological Modelling*, 205: 181 - 195



- Mmopelwa, G., Mosepele, K., Mosepele, B., Moleele, N., and Ngwenya, B. (2009). Environmental variability and the fishery dynamics of the Okavango delta, Botswana: The case of subsistence fishing. *African Journal of Ecology*, 47(1): 119–127.
- Molden, D and de Fraiture, C. (2004). Investing in Water for Food, Ecosystems and Livelihoods. Blue Paper Stockholm Comprehensive Assessment of Water Management in Agriculture
- Montcho, S. A., Chikou, A., Lalèyè, P. A and Linsenmair, K. E. (2011). Population structure and reproductive biology of *Schilbe intermedius* (Teleostei: Schilbeidae) in the Pendjari River, Benin. *African Journal of Aquatic Science*, 36(2): 139-145.
- Mosepele, K. (2000). Length based fish stock assessment of the main exploited fish stocks of the Okavango delta, Botswana. MPhil Thesis with the University of Bergen, Bergen, Norway.
- Mosepele, K, Mmopelwa, T.G, and Mosepele, B., 2003. Characterization and monitoring of the Okavango delta artisanal fishery, pp 391 – 413. In Bernard, T, Mosepele, K and Ramberg, L (Editors). Environmental Monitoring of Tropical and Subtropical Wetlands. University of Botswana, Maun and University of Florida, Gainesville, FLA.
- Mosepele, K., Mmopelwa, G., Mosepele, B and Kgathi, D. L (2007). Indigenous knowledge and fish utilization in the Okavango Delta, Botswana: Implications for food security, pages 292 - 302. In Ahmed, A (Editor). Managing knowledge, technology and development in the era of information revolution. Griffith University: Australia.
- Mosepele, K., 2008. Flood pulse in a subtropical floodplain fishery and the consequences for steady state management, pages 56 – 62. In Totolo, O (Editor). “Water Resource Management; Science and technology innovation for sustainable development.” (Acta Press: Canada).
- Mosepele, K., 2014. Classical fisheries theory and inland (floodplain) fisheries management; is there need for a paradigm shift? Lessons from the Okavango Delta, Botswana. *Fisheries and Aquaculture Journal* 5: 101. doi:10.4172/2150-3508.1000101
- Mosepele, K., Mosepele, B., Bokhutlo, T and Amutenya, K (2011). Spatial variability in fish species assemblage and community structure in four subtropical lagoons of the Okavango Delta, Botswana. *Physics and Chemistry of the Earth*, 36(14-15): 910-917
- Mosepele, K and Mosepele, B. 2005. Spatial and Temporal Variability in Fishery and Fish Community Structure in the Okavango Delta, Botswana: Implications towards fisheries management. *Botswana Notes and Records*, 37: 280 – 291.

- Mosepele, K. (2001). Description of the Okavango delta fishery. Technical Report to the Fisheries Section, Ministry of Agriculture, Gaborone, Botswana
- Mosepele, K., Ngwenya, B.N and Bernard, T. (2006). Artisanal fishing and food security in the Okavango Delta, Botswana, pages 159 – 168. In Ahmed, A (Editor). Global and local resources in achieving sustainable development. Interdescience Publishers: Geneva, Switzerland.
- Nnyepi, M., Ngwenya, B and Mosepele, K. (2007). Food (in) security and child nutrition in Ngamiland, pages 281 - 291. In Ahmed, A (Editor). Managing knowledge, technology and development in the era of information revolution. Griffith University: Australia.
- Paper I: Siziba, N., Chimbari, M.J., Mosepele, K and Masundire, H. (2011). Spatial and temporal variations in densities of small fishes across different temporary floodplain types of the lower Okavango Delta, Botswana. *African Journal of Aquatic Science*, 36(3): 309-320.
- Paper II: Siziba, N., Chimbari, M.J., Masundire, H., Mosepele, K and Ramberg, L. (2013). Variation in Assemblages of Small Fishes and Micro-crustaceans After Inundation of Rarely Flooded Wetlands of the Lower Okavango Delta, Botswana. *Environmental Management*. DOI 10.1007/s00267-013-0183-9
- Paper III: Lindholm, M., Hessen, D.O., Mosepele, K and Wolski, P. (2007). Flooding size and energy pathways on a floodplain of the Okavango Delta. *Wetlands*, 27 (4): 775–784
- Paper IV: Mosepele K., Mosepele B., Wolski P., Kolding J. (2012). Dynamics of the feeding ecology of selected fish species from the Okavango River delta, Botswana. *Acta Ichthyologica et Piscatoria*, 42 (4): 271 – 289.
- Paper V: Mosepele, K., Kolding, J and Bokhutlo, T., 2017. Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. *Ecohydrology and Hydrobiology*. DOI: 10.1016/j.ecohyd.2017.01.005
- Paper VI: Thethela, B., Weyl, O., Mosepele, K and Wilson, G. (2015). Age and growth of sharp-tooth catfish, *Clarias gariepinus* (Burchell 1822) (Clariidae), in the Lower Okavango Delta, Botswana. *Marine and Freshwater Research*, 66: 1-9
- Paper VII: Mosepele, K., Moyle, P.B., Merron, G.S., Purkey, D and Mosepele, B. (2009). Fish, floods and ecosystem engineers; interactions and conservation in the Okavango Delta, Botswana. *Bioscience*, 59 (1): 53 – 64
- Paper VIII: Linhoss, A.C., R. Muñoz-Carpena, M. Allen, G. Kiker, K. Mosepele. (2012). A flood pulse driven fish population model for the Okavango Delta, Botswana. *Ecological Modelling*, 228: 27 – 38

- Paper IX: Mosepele, K., Kolding, J and Bokhutlo, T. Fish stock assessment in inland floodplain fisheries; the case of the Okavango Delta. *Internal Journal of Limnology* (Submitted)
- Petry, A.C., Agostinho, A.A and Gomes, L.C. (2003). Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year. *Neotropical Ichthyology*, 1(2): 111-119.
- Porter, J.W and Muzila, I.L. (1989). Aspects of swamp hydrology in the Okavango. *Botswana Notes and Records*, 21: 73 – 91.
- Power, M. (1984). Depth distributions of armoured catfish Predator-induced resource avoidance? *Ecology*, 65(2): 523 – 528
- Ramberg, L., Wolski, P. and Krahn, M. (2006a). Water balance and infiltration in a seasonal floodplain in the Okavango Delta, Botswana. *Wetlands*, 26 (3): 677–690
- Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., van As, J and Vander, C. P. (2006b). Species diversity of the Okavango Delta, Botswana. *Aquatic Science*, 68: 310–337.
- Ramberg, L., and Wolski, P. (2008). Growing islands and sinking solutes: processes maintaining the endorheic Okavango Delta as a freshwater system. *Plant Ecology*, 196(2): 215-231
- Rochet, M.-J. (1998). Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science*, 55(3): 371–391.
- Schindler, D.E., Kitchell, J.F., Ogutu-Ohwayo, R. (1998). Ecological Consequences of Alternative Gill Net Fisheries for Nile Perch in Lake Victoria. *Conservation Biology*, 12(1): 56-64.
- Schongart, J and Junk, W.J. (2007). Forecasting the flood-pulse in Central Amazonia by ENSO-indices. *Journal of Hydrology*, 335: 124– 132.
- Siziba, N., Chimbari, M.J., Masundire, H and Mosepele, K., 2011. Spatial and temporal variations of microinvertebrates across temporary floodplains of the lower Okavango Delta, Botswana- *Physics and Chemistry of the Earth*, 36 (14-15): 939-948
- Siziba, N., Chimbari, M. J., Masundire, H., and Mosepele, K. (2012). Spatial variations of microinvertebrates across different microhabitats of temporary floodplains of lower Okavango Delta, Botswana. *African Journal of Ecology*, 50(1): 43–52.
- Staples, D., Satia, B., Gardiner, P.R. (2004). A research agenda for small-scale fisheries. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand. RAP PUBLICATION No. 2004/21 and FIPL/C 10009 (En)

- Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *BioScience*, 45(11): 759-771.
- Tsheboeng, G., Bonyongo, M., and Murray-Hudson, M. (2014). Flood variation and soil nutrient content in floodplain vegetation communities in the Okavango Delta. *South African Journal of Science*, 110(3/4): 1–5.
- Tockner, K., Malard, F and Ward, J.V. (2000). An extension of the flood pulse concept. *Hydrological Processes*, 14: 2861 – 2883
- van der Waal, B.C.W (1985). Aspects of the biology of larger fish species of Lake Liambezi, Caprivi, South West Africa. *Madouqua*, 14(2): 101-1441.
- van Zwieten, P.A.M., Goudswaard, P.C., Kapasa, C.K. (2003). Mweru-Luapula is an open exit fishery where a highly dynamic population of fishermen makes use of a resilient resource base. In: Jul-Larsen E, Kolding J, Overa R, Nielsen JR, Zwieten PAM (eds) Management, Co-management or No Management? Major Dilemmas in Southern African Freshwater Fisheries, 2: Case Studies. FAO Fisheries Technical Paper 426/2, Rome, pp 1 - 33
- Vasquez, A.G., Alonso, J.-C., Carvajal, F., Moreau, J., Nunez, J., Renno, J.-F., Tello, S. (2009). Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. *Journal of Fish Biology* 75: 2527–2551
- Walsh, M.R., Munch, S.B., Chiba, S and Conover, D.O. (2006). Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letters*, 9: 142–148
- Ward, J.V and Stanford, J.A. (1995). The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers Research and Management*, 10: 159-168.
- Welcomme, R.L. (1985). River fisheries. FAO, Fisheries Technical Paper 262, Rome
- Welcomme, R.L. (1988). Concluding Remarks I: On the Nature of Large Tropical Rivers, Floodplains, and Future Research Directions. *Journal of the North American Benthological Society*, Vol. 7, No. 4, Community Structure and Function in Temperate and Tropical Streams: Proceedings of a Symposium. pp. 525-526.
- Welcomme, R. L. (2009). World prospects for floodplain fisheries. *Ecohydrology and Hydrobiology*, 8(2-4): 169–182.
- Welcomme, R. L. (2011). An overview of global catch statistics for inland fish. *ICES Journal of Marine Science*, 68: 1751–1756.

- Welcomme, R. L., Cowx, I. G., Coates, D., Béné, C., Funge-Smith, S., Halls, A., and Lorenzen, K. (2010). Inland capture fisheries. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1554): 2881–96.
- Welcomme, R. L., Valbo-Jorgenson, J., and Halls, A. (2014). Inland fisheries evolution and management: Case studies from four continents. FAO, Rome
- Wilson, B. H. (1973). Some Natural and Man-Made Changes in the Channels of the Okavango Delta. *Botswana Notes and Records*, 5: 132-153
- Wolski, P and Murray-Hudson, M. (2006). Flooding dynamics in a large low-gradient alluvial fan, the Okavango Delta, Botswana, from analysis and interpretation of a 30-year hydrometric record. *Hydrology and Earth System Sciences*, 10: 127–137.
- Wolski, P., Masaka, T., Raditsebe, L and Murray-Hudson, M. (2005). Aspects of Seasonal Dynamics of Flooding in the Okavango Delta. *Botswana Notes and Records*, 37: 179-195
- Zeug, S. C., and Winemiller, K. O. (2007). Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(10):1291–1301.
- Zeug, S. C., Winemiller, K. O., and Tarim, S. (2005). Response of Brazos River oxbow fish assemblages to patterns of hydrologic connectivity and environmental variability. *Transactions of the American Fisheries Society*, 134(5):1389–1399.

## 5. Chapter 5

**Paper IV:** Mosepele K., Mosepele B., Wolski P., Kolding J. (2012). Dynamics of the feeding ecology of selected fish species from the Okavango River delta, Botswana. *Acta Ichthyologica et Piscatoria*, 42 (4): 271 – 289.

ACTA ICHTHYOLOGICA ET PISCATORIA (2012) 42 (4): 271–289

DOI: 10.3750/AIP2012.42.4.01

### DYNAMICS OF THE FEEDING ECOLOGY OF SELECTED FISH SPECIES FROM THE OKAVANGO RIVER DELTA, BOTSWANA

Ketlhatlogile MOSEPELE <sup>1\*</sup>, Belda MOSEPELE <sup>1</sup>, Piotr WOLSKI <sup>1</sup>, and Jeppe KOLDING <sup>2</sup>

<sup>1</sup> Okavango Research Institute (University of Botswana), Maun, Botswana

<sup>2</sup> Department of Biology, University of Bergen, Bergen, Norway

Mosepele K., Mosepele B., Wolski P., Kolding J. 2012. Dynamics of the feeding ecology of selected fish species from the Okavango River delta, Botswana. *Acta Ichthyol. Piscat.* 42 (4): 271–289.

**Background.** This study contributes to the understanding of the potential impact of changes in flooding patterns and (potential) fish production as a consequence of upstream developments in floodplain systems. Therefore, stomachs of eight fish species from the Okavango Delta were analysed to evaluate the feeding ecology of floodplain fish (and the effect of seasonal flooding), using the delta as a case study.

**Materials and methods.** In total, 2101 fish stomachs of eight species, representing six families, were collected (in all seasons) from the delta using experimental fishing nets, from 2004 to 2009. Frequency of occurrence, Levin's diet breadth index, Pianka's overlap index, trophic levels, and Bray–Curtis similarities were used to evaluate feeding preferences. Detrended correspondence analysis was used to study temporal variations in diet. Multiple linear regressions were used to determine the influence of flooding on diet. ANOVA and MANOVA were used to determine the level of significance among variables, while LSD post hoc analysis revealed the source of significance.

**Results.** Cluster analysis and Pianka's index highlighted inter- and intra-specific competition for food among different species and age classes. ANOVA highlighted dynamic changes in inter- and intra-specific trophic level partitioning, while detrended analysis showed that the terrestrial environment is subsidizing the aquatic environment. Regression analysis showed that *Schilbe intermedius* diet was driven by discharge ( $F = 7.03$ ;  $P = 0.045$ ;  $R^2 = 0.58$ ) while that of *Marcusenius macrolepidotus* was driven by water depth ( $F = 25.88$ ;  $P = 0.04$ ;  $R^2 = 0.93$ ).

**Conclusion.** The terrestrial–aquatic ecotone is important in fish growth of seasonal floodplains. Energy uptake is optimised through cannibalism to ensure species survival. Furthermore, species inter-relations are dynamic due to variations in food availability driven by seasonal flooding, which shortens and lengthens the food chain periodically. This dynamic relation is pronounced at low floods when predation and competition increases within the fish community. The evidence from this study has shown that predation, cannibalism, inter- and intra-specific competition are regulating factors in floodplain fish communities, driven by seasonal flooding.

**Keywords:** trophic level, resource partitioning, flood pulse, seasons, cannibalism

#### INTRODUCTION

Floodplain fisheries are considered to be some of the most productive ecosystems in the tropics (Welcomme 1979, Junk et al. 1989) and appear to take advantage of most of the biological principles for high productivity. They are fluvial, shallow and unstable, continuously oscillating, generally but not always with a high predictability between a terrestrial and an aquatic phase, and with a high external nutrient loading. Combined with high insolation and temperatures, the basis for primary- and higher order productivity in these areas is optimal (Kolding and van Zwieten 2005). Tropho-dynamic relations such as energy flow, predation, intra- and inter-specific competition determine community structure (Begon and Mortimer 1986, Ricklefs 1990) in conjunction with abiotic factors

(Claessen et al. 2004). Dynamic species interactions also result in cannibalism which Claessen et al. (2004) describe as a "short-circuited predator-prey system" where individuals ensure their survival by opportunistically preying on juveniles. Therefore, studying these factors is essential towards assessing the stability of fish food web structure (Ney 1993) in (fluctuating) floodplain systems.

Most floodplain fish species undergo horizontal and vertical migrations due to seasonal flooding (Lowe-McConnell 1987). These migrations are an integral stage in the life history of floodplain fish and facilitate the transport of nutrients from nutrient rich floodplains into the more oligotrophic riverine system (Hoeninghaus et al. 2006). This dynamic nutrient flow, characterised by a pulsing system (Odum 1994) is based on the flood-pulse concept (Junk et

\* Correspondence: Dr. Ketlhatlogile Mosepele, University of Botswana, Okavango Research Institute (ORI), Private Bag 285, Maun, Botswana, phone (direct): +(267) 681 7228, phone (switchboard): +(267) 686 1833, fax: +(267) 686 1835, e-mail: amosepele@ori.ub.bw.



al. 1989), which suggests that periodic flooding in floodplain systems is a natural event to which biological populations are adapted (Odum and Barret 2005). This periodic flooding produces "boom and bust" (Bunn et al. 2006) conditions which provide key ingredients for floodplain fish production (de Graaf 2003). Therefore, many floodplain fish species migrate as a response to seasonal flooding and resource availability (Lowe-McConnell 1987, Roach et al. 2009). Ultimately, the resultant terrestrial-aquatic ecotone in pulsing floodplain systems facilitates high fish biomass production (Eberle and Stanford 2010).

This study used several techniques to establish dynamics in the feeding ecology of several Delta species in relation to the flood pulse and to also highlight trophic inter-relations among different species. Merron and Bruton (1988) conducted the most comprehensive diet studies in the Delta using the volumetric method. However, Hyslop (1980) argues that this univariate approach can underestimate the relative importance of small food items. Also, Merron and Bruton (1988) give a detailed qualitative analysis of the feeding ecology of selected species in relation to the flood pulse but without quantitative analyses to establish the "flood-pulse vs. feeding" relation that has been done in other floodplain systems. Quantification of diet is important, because it helps to identify the roles of predators in ecosystems (Baremore et al. 2010). Therefore, using several techniques (to study fish diet) agrees with Marshall and Elliot (1997) who argued that a variety of techniques should be used to assess fish feeding behaviour due to various weaknesses inherent in all the different methods. Additionally, each approach provides different insights into feeding habits (Baldoa and Drake 2002). Testing this approach in the Okavango Delta will contribute to the knowledge on floodplain fish feeding ecology and factors structuring these populations in dynamic systems. Furthermore, this study also investigates the intrinsic importance of the aquatic-terrestrial system interface (the so called ecotone) dynamics for fish productivity in flood-pulsed floodplains. It subsequently increases the understanding of why shallow fluctuating tropical wetlands are among the most productive ecosystems (Junk 1996, Zalewski et al. 2001).

The main aim of this study was to establish the effect of the flood pulse on floodplain fish feeding ecology, such as spatio-temporal variations, (potential) inter- and intra-specific competition. Establishing this relation would then highlight the role of Junk's et al. (1989) flood pulse concept on floodplain fish ecology.

## MATERIALS AND METHODS

**Study area.** Fish samples for diet analysis were collected from the Upper Delta, Lower Delta, sump lakes (Lake Ngami), and outlet rivers (Boteti; see Fig. 1). The habitats sampled within each area were riverine habitats; seasonally inundated floodplains and lagoon habitats, except for Lake Ngami which is a shallow sump lake on the edge of the Delta (see Table 1). The Okavango Delta is a flood-driven, pulsing system fed with water annually

from the Angolan highlands (Ramberg et al. 2006) whose surface area changes annually depending on the magnitude of hydrological inputs (Wolski et al. 2006). The flood waters arrive in the Panhandle portion of the Delta, peaking in this region between April and May (Wolski and Murray-Hudson 2005, Wolski et al. 2006) and may take several months to traverse the Delta's breadth peaking as late as August in Maun, i.e., may result in a time lag between the floods' arrival at the panhandle and their arrival at different parts of the Delta (Wolski and Murray-Hudson 2005).

**Sampling.** Two kinds of experimental fishing nets were used to collect fish specimens for diet studies in several areas around the Delta, three days per month from 2005 until 2008. Nets were set every evening at approximately 1800 h and removed in the morning at approximately 0600 h (12 h soaking time). The net mesh size used ranged from 8 mm to 150 mm stretched mesh. After removal from the nets, each fish specimen was identified to species level and total length (TL) measured of each fish specimen selected for diet analysis. Fish were then divided into 5-cm length classes. Fish lengths were then transformed into age using the von Bertalanffy growth function (VBGF) similar to Froese and Binohlan (2000). The VBGF parameters used in this study were derived by Mosepele and Nengu (2004) in their analysis of selected species from the Okavango Delta.

Similar to Watanabe et al. (2003), after removal, fish guts were preserved in 70% alcohol before laboratory analyses. Prey items were separated into major groups where aquatic macro-invertebrate taxa were identified to order only due to high degree of digestion. Where possible, fish were identified to species level or otherwise classified as "fish" (when they were too digested to identify them), plant material was identified to general groups like "seeds, tree bark, grass, etc.", while terrestrial insects were generally classified as one group (apart from ants, Arachnidae and arthropods). The vacuity index (percentage of empty stomachs) was also calculated. Trophic levels were estimated using TrophLab (Pauly et al. 2000) based on the percentage contribution (by weight) of each prey item to the diet. Similar to Stergiou and Karpouzi (2002), we used the "Diet composition" routine in the model to estimate the trophic levels. Fish were then classified according to Stergiou and Karpouzi's (2002) fractional trophic levels as:

- Pure herbivores (TROPH = 2.0–2.1);
- Omnivores with preference for plants (2.1 < TROPH < 2.9);
- Omnivores with preference for animals (2.9 < TROPH < 3.7);
- and
- Carnivores with preference for fish (3.7 < TROPH < 4.5).

**Univariate analyses.** Frequency of occurrence (FO), which is the simplest approach to conducting diet analysis (Hyslop 1980) and has consequently been used extensively (Vaz et al. 1999, Agostinho et al. 2003, Watanabe et al. 2003, Navia et al. 2007) was the main index used in this study. Feeding strategy was determined through Levin's diet breadth index ( $B_i$ ) in a manner similar to

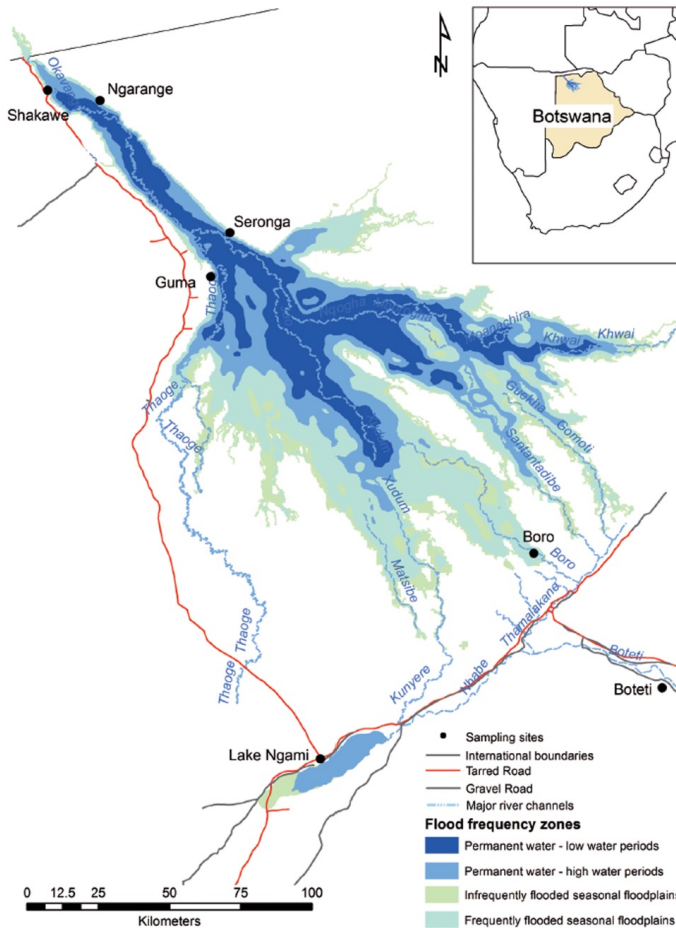


Fig. 1. Sampling areas in the Okavango River delta where fish specimens were sampled for fish diet analysis

Rosas-Alayala et al. (2002), where low values ( $1 < B_i < 2$ ) indicated predators with specialised diet, medium values ( $2.1 < B_i < 3$ ) indicated predators with less specialised diet, while high values ( $B_i > 3$ ) indicated generalist predators. This index has been widely used to study shifts in diet of many fish species (Feinsinger et al. 1981, Vázquez et al. 2008, Baremore et al. 2010).

**Multivariate analyses.** Pianka's Overlap Index (POI), implemented in Ecosim 7 routine (Gotelli and Entsminger 2007) was used to determine the level of spatial and temporal variations in diet for selected species (Rosas-Alayola et al. 2002, Agostinho et al. 2003, Navia

et al. 2007) where values exceeding 0.6 were considered to be biologically significant (Navia et al. 2007). Ecosim 7 was then used to test the significance of the overlap using randomisation procedures. Multivariate analyses were performed using Primer (Clarke and Gorley 2001). Prey items were grouped by order (or class, depending on the ease at which the digested items could be identified) and then root transformed similar to Baldoia and Drake (2002). Subsequently, Bray-Curtis coefficients were calculated providing a measure of dietary overlap as observed by Marshall and Elliot (1997). Thereafter, cluster analysis was employed using the group-average link-



ing approach based on Bray–Curtis similarities to explore potential intra- and inter-specific competition for food among several selected species, across different age classes. The importance of different food items to different feeding groups was assessed using SIMPER analysis (Sá et al. 2006) where data were standardised, then square-root transformed and cut-off for low contributions set at 90% (based on Bray–Curtis mean similarity).

Temporal variations in diet were determined through a detrended correspondence analysis (DCA–DECORANA) in PC-ORD (McCune and Mefford 1999). Only the scores of the axis with eigenvalues higher than 0.2 were retained for analysis, similar to Corrêa et al. (2009), while the rest were discarded. A multiple linear regression was then conducted between the diet scores from axis 1 (which represents frequency of occurrence of food items) and water depth (and discharge) to explore the influence of hydrological conditions on feeding behaviour of *Schilbe intermedius*

Rüppell, 1832 (Schilbeidae) and *Marcusenius macroleptodotus* (Peters, 1852) (Mormyridae). According to Mosepele et al. (2011) these two species are the most dominant in the Delta's fish community. They were also the most abundant in the samples collected during this study which therefore allowed for detailed analysis. Due to data paucity for *Clarias gariepinus* (Burchell, 1822) (Clariidae) and *Tilapia rendalli* (Boulenger, 1897) (Cichlidae), Principal Component Analysis (PCA in PC-ORD) was used instead of the DCA–DECORANA routine.

**Other statistical analyses.** Significance levels for all statistical tests were set at 95% confidence level. Multiple linear regressions were conducted to determine the relation between feeding indices and flooding parameters (e.g., water depth and discharge). Analysis of Variance (ANOVA) and Multivariate Analysis of Variance (MANOVA) (using STATISTICA® software) were used to determine and test the level of significance between

Table 1  
Brief description and location of the various study sites at the Okavango River delta, Botswana

SA	Site	Coordinates		Description
Shakawe	1	18°16'27.8"S	21°48'05.6"E	Backwater channel dominated by papyrus ( <i>Cyperus papyrus</i> ) and common reed ( <i>Phragmites australis</i> )
	2	18°20'29.0"S	21°50'10.2"E	Main river channel dominated by papyrus, hippo grass ( <i>Echinochloa stagnina</i> ) and common reed
	3	18°25'59.7"S	21°58'18.4"E	Side channel from main river. Hippo grass on littoral area
	4	18°26'22.8"S	21°54'41.6"E	Lagoon connected to the main channel. The common reed on littoral area
Guma	1	18°57'42.0"S	22°23'08.7"E	Next to inflow channel into lagoon dominated by common reed and papyrus
	2	18°57'42.0"S	22°23'08.7"E	Centre of lagoon next to a bed of water caltrop ( <i>Trapa natans</i> ) and papyrus
	3	18°57'42.9"S	22°23'13.2"E	Centre of lagoon next to a bed of <i>Pycurus mundii</i> , papyrus and <i>Ceratophyllum</i> sp. beds
	4	18°58'01.1"S	22°22'40.5"E	Next to the outflow channel from the lagoon dominated by papyrus
Xakanaxa	1	19°10'07.0"S	23°23'38.9"E	Centre of the lagoon next to a <i>Trapa natans</i> mat
	2	19°10'07.7"S	23°23'38.9"E	On the littoral region of the lagoon next to common reed
	3	19°09'22.4"S	23°16'12.2"E	River channel flowing into the lagoon next to common reed
Boro River	1	19°32'57.0"S	23°10'38.8"E	On the fringe of the river channel next to papyrus
	2	19°32'57.0"S	23°10'38.8"E	Floodplain habitat, dominated mostly by hippo grass
	3	19°31'44.2"S	23°10'57.1"E	Floodplain river channel dominated mostly by hippo grass and sedges (plants from family Cyperaceae)
	4	20°12'99.89"S	23°15'15.93"E	Various sites in the lagoon. Open water and littoral habitats
LN	1	20°27'43.25"S	22°47'55.08"E	Various sites in the lake. Open water and littoral habitats
Boteti R.	1	20°09'10.16"S	23°39'26.76"E	Open water and littoral habitats dominated by common reed and papyrus
	2	20°78'0.54"S	23°27'40.14"E	Open water and littoral habitats dominated by common reed and papyrus
	3	20°13'19.70"S	24°08'16.76"E	Open water and littoral habitats dominated by common reed and papyrus

SA = study area, LN = Lake Ngami.

variables, while Fischer's Least Significance Difference (LSD) post hoc analysis was conducted to determine the source of the significance among the variables.

## RESULTS

**General diet description.** In total, 2101 fish stomachs of eight species, representing six fish families, sampled from 2004 to 2009, were collected and analysed for diet. The largest fish specimen collected was *Clarias gariepinus* (464 mm) while the smallest was *Brycinus lateralis* (Boulenger, 1900) (Alestidae) (111 mm; see Table 2). *B. lateralis* had the highest vacuity index (40%) while none was observed for *Oreochromis andersonii* (Castelnau, 1861) (Cichlidae) (Table 2). The highest richness of prey groups was observed for *Schilbe intermedius* while the lowest was observed for cichlids (*Oreochromis andersonii* and *Tilapia rendalli*) and *Hepsetus odoe* (Bloch, 1794) (Hepsetidae). *Clarias ngamensis* Castelnau, 1861 (Clariidae) had the highest diet breadth index, suggesting a more general feeding strategy than the other species, while *H. odoe* had the most specialised feeding strategy (see Table 2). Algae is a key diet food (based on weight) for three fish species (*C. gariepinus*, *M. macrolepidotus*, and *T. rendalli*), while detritus is key diet item for two fish species (*C. ngamensis* and *O. andersonii*). Fish is a key food item for *S. intermedius* and *H. odoe* while seeds dominate *B. lateralis* diet (see Table 3). Fish and algae are the most frequently eaten food items (by three fish species each as shown in Table 3), while detritus and Odonata are the most frequently eaten food item by one fish species each. Cannibalism was observed in *S. intermedius*, *C. gariepinus*, and *C. ngamensis*.

**Competition (intra- and inter-specific).** Classification based on dietary overlap using Bray-Curtis similarities

revealed two major feeding guilds (Fig. 2) at the 34% similarity level. Guild 1 (piscivores) is composed of two age classes of *H. odoe* (1+ and 2+), 1+ *C. ngamensis* and *T. rendalli*, and 3+ *S. intermedius*. All the other species across their different age groups are grouped together into Guild 2 (algavores). Dietary separation between these two guilds was highly significant (ANOSIM:  $r = 0.616$ ,  $P = 0.001$ ). Furthermore, three sub-guilds are discernable within Guild 2 at between the 50%–60% similarity levels. Sub-guild 2A (omnivorous on fish, detritus and vegetation) is composed of 1+ and 2+ *S. intermedius* (at approximately 65% similarity) and 2+ and 3+ *C. ngamensis* (at approximately 70% similarity) and 2+ and 3+ *C. gariepinus* (at approximately 80% similarity). Sub-guild 2B (omnivorous on algae, Diptera, and vegetation) is composed of all the age classes of *M. macrolepidotus* (e.g., 1+–3+) and *B. lateralis*. Finally, sub-guild 2C (omnivorous on algae, vegetation and fish) is composed of 0+ and 1+ *O. andersonii*, and 0+, 1+ *T. rendalli*.

The most "potentially" intense intra-specific competition for food was found between the *H. odoe* age groups (POI = 0.99) while the least intense intra-specific competition was observed between 1+ and 3+ *S. intermedius* (POI = 0.61). Similarly, the most intense inter-specific competition for food was observed between 1+ *T. rendalli* and *C. ngamensis* (POI = 0.96), while the least inter-specific competition (but still biologically significant) was observed between 2+ *C. ngamensis* and 3+ *C. gariepinus* (POI = 0.62). There was virtually no competition for food between 1+ *H. odoe* and 2+ *M. macrolepidotus* (POI  $\approx$  0.02), and in fact *H. odoe* preys on *M. macrolepidotus* (Table 3).

Despite the dietary classification of the different species into two major feeding guilds, there was a signif-

**Table 2**  
Summary statistics illustrating the mean size, diet breadth and key food items for fish species sampled from the Okavango River delta, Botswana

Species	TL [mm]	V	n	B	TrL	PGN	KPG	FP	Key diet taxon	Key fish species
<i>Schilbe intermedius</i>	192 ± 58	27	792	5.78	3.69 ± 0.59	30	Fish	OPA	<i>Barbus</i> spp.	<i>B. thamalakanensis</i>
<i>Marcusenius macrolepidotus</i>	182 ± 56	24	460	5.62	2.91 ± 0.34	21	Diptera	OPA	Chironomidae	<i>Aplocheilichthys</i> spp.
<i>Brycinus lateralis</i>	111 ± 25	40	195	7.44	2.92 ± 0.45	18	Odonata	OPA	Libellulidae	–
<i>Clarias gariepinus</i>	464 ± 142	24	148	5.29	3.5 ± 0.61	23	Detritus	OPA	Detritus	<i>Tilapia sparrmanni</i>
<i>C. ngamensis</i>	396 ± 106	14	185	10.95	2.40 ± 0.29	22	Vegetation	OPP	Grass	<i>Clarias</i> spp.
<i>Oreochromis andersonii</i>	205 ± 61	0	104	3.18	2.10 ± 0.15	7	Algae	OPP	Algae	<i>Barbus</i> spp.
<i>Tilapia rendalli</i>	163 ± 63	24	65	2.62	2.18 ± 0.21	7	Algae	OPP	Algae	–
<i>Hepsetus odoe</i>	275 ± 64	37	152	1.27	4.44 ± 0.79	16	Fish	CPF	<i>Barbus</i> spp.	<i>B. thamalakanensis</i>

Values of total length (TL) and trophic level are mean ± standard deviation; V = vacuity index; n = total number of stomach sampled; B = Levin's diet breadth index; TrL = fractional trophic level; PGN = number of prey groups; KPG = key prey groups based on frequency of occurrence; FP = food preference; OPA = omnivores with preference for animals; OPP = omnivores with preference for plants; CPF = carnivores with preference for fish.

**Table 3**  
Diet composition and frequency of occurrence of individual prey items of eight fish species from the Okavango River delta, Botswana

Prey Group/ item	Fish species							
	<i>C. gariepinus</i>	<i>C. ngamensis</i>	<i>S. intermedius</i>	<i>H. odoe</i>	<i>B. lateralis</i>	<i>M. macrolepidotus</i>	<i>O. anderssonii</i>	<i>T. rendalli</i>
Algae	14.21 (29.61)	4.73 (3.5)	7.19 (6.24)	1.04 (<0.01)	19.00 (3.09)	29.80* (26.48)	53.07* (37.38)	56.26* (73.60)
Ants	0.6 (<0.01)	2.98 (0.16)	0.31 (<0.01)	3.13 (0.03)	13.00 (8.78)	2.69 (0.24)	1.02 (0.17)	
Aquatic invertebrates U	4.11 (<0.01)	0.6 (<0.01)	11.31 (3.79)					
Arachnidae			0.46 (0.54)					
Arthropoda			0.15 (<0.01)			0.3 (<0.01)		
Bird remains	0.68 (<0.01)	2.39 (0.1)	3.06 (5.56)		1.00 (<0.01)	5.98 (7.63)		
Coleoptera		1.76 (<0.01)	1.22 (<0.01)		5.00 (0.12)	0.30 (0.02)		
Decapoda	25.50* (0.76)	10.12 (60.87)	7.34 (0.82)		2.00 (0.09)	2.09 (3.31)	15.31 (58.11)	6.25 (0.09)
Detritus	0.68 (<0.01)	6.55 (2.62)	3.52 (0.70)		2.00 (<0.01)	31.34 (22.42)		
Diptera		2.38 (<0.01)	2.29 (2.45)		3.00 (0.01)	0.60 (<0.01)		
Ephemeroptera		11.31* (3.54)	28.77* (49.10)		3.00 (0.77)	0.60 (<0.01)		8.33 (7.36)
Fish U	18.25 (16.48)							
<i>Hepsetus odoe</i>	0.68 (<0.01)							
<i>Petrocephalus catostoma</i>	0.68 (0.02)							
<i>Tilapia sparrmanii</i>	2.03 (11.04)			4.17 (9.23)				
<i>Brycinus lateralis</i>	0.68 (0.03)							
<i>Barbus paludinosus</i>	1.35 (18.05)			1.04 (0.08)	1.00 (2.74)			
<i>B. thomalakanensis</i>			0.31 (<0.01)	8.33 (4.05)				
<i>Mareusenius macrolepidotus</i>			0.15 (<0.01)	1.04 (8.52)	1.00 (24.17)			
<i>Schilbe intermedius</i>			0.76 (<0.01)					
<i>Barbus haasiensis</i>				4.17 (0.12)				
<i>Aplocheilichthys johnstonii</i>						0.90 (0.59)		
<i>Clarias</i> sp.	2.71 (11.68)	1.79 (<0.01)	1.22 (<0.01)	6.25 (18.5)				
<i>Barbus</i> sp.	2.7 (3.13)	1.19 (2.91)	0.92 (<0.01)	6.25 (1.55)		0.30 (7.04)	12.24 (3.07)	
<i>Synodontis</i> sp.	0.68 (<0.01)							
Cichlidae	2.03 (<0.01)	0.6 (3.01)	0.15 (<0.01)	1.04 (<0.01)				
Anabantidae				1.04 (0.01)				
Frogs	0.68 (<0.01)							
Gastropoda	2.03 (<0.01)	10.72 (3.96)	1.07 (0.01)		2.00 (0.34)			3.89 (0.75)
Grass	4.09 (2.36)	7.14 (5.06)	0.46 (0.01)	1.04 (0.01)				7.16 (7.90)
Hemiptera		6.55 (<0.01)	5.34 (4.06)					1.20 (0.37)
Lepidoptera			0.15 (<0.01)					

Table 3 (cont.)

Mice	0.68 (<0.01) 2.7 (0.01)	0.6 (<0.01)	0.31 (<0.01)				
Millipedes							
Mollusca							
Odonata	7.43 (0.65)	9.53 (3.62)	12.07 (6.02)	31.00* (0.02)	5.97 (1.37)		
Oligochaeta		3.57 (<0.01)	0.92 (0.01)	1.00 (0.33)	0.90 (<0.01)	1.02 (0.24)	
Orthoptera			0.76 (2.06)				
Seeds		2.98 (7.74)	0.15 (<0.01)	10.00 ( <b>54.01</b> )	2.09 (1.38)	7.14 (0.25)	2.08 (<0.01)
Terrestrial insects	0.68 (<0.01)	2.38 (<0.01)	1.38 (0.03)	1.00 (<0.01)			
Tree bark, leaves, roots		9.53 (2.91)			0.61 (2.41)		2.08 (0.12)
Trichoptera					0.30 (0.87)		
Vegetation U	4.74 (6.18)		7.8 (8.45)	1.00 (0.81)	0.60 (<0.01)		6.25 (<0.01)
Zooplankton			0.31 (0.13)	3.00 (4.72)	2.39 (17.22)		

Values with an \* indicate the top most frequently eaten food item by each species; Values in parentheses indicate the % proportion of prey items (based on weight); Values in bold indicate the prey/food item with the largest contribution to the food; U = unidentified.



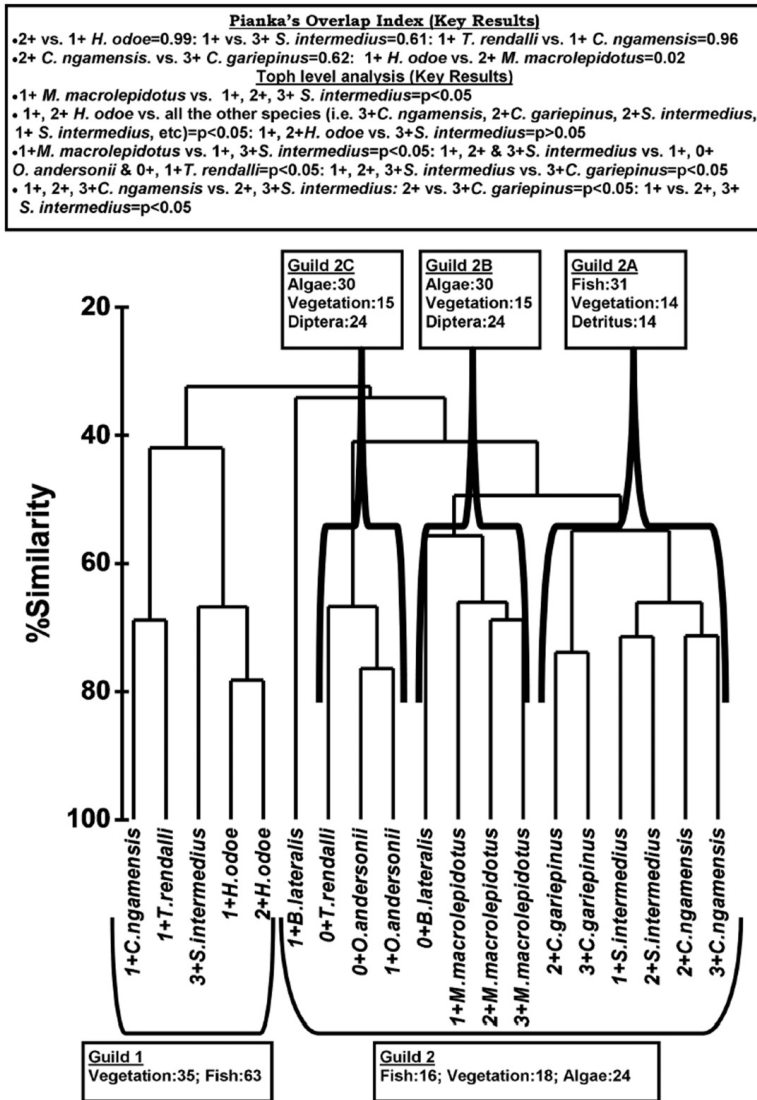


Fig. 2. Dendrogram using group-average linking on Bray–Curtis similarities of fish species sampled at the Okavango River delta across several size classes based on diet occurrence data; Information in text boxes refers to results from SIMPER analysis highlighting the % contribution of the respective food item to the diet of the particular feeding guild

icant trophic partitioning among the different species and size classes (see Fig. 3), i.e., between *H. odoe* and all the other species in this study (ANOVA:  $P < 0.05$ ), with the exception of 3+ *S. intermedius*. Various permutations between the different size classes showed (inter-specific) trophic partitioning among the different species (e.g., 1+ *M. macrolepidotus* vs. 1+, 2+, and 3+ *S. intermedius*; all age classes of *S. intermedius* vs. all age classes of *O. andersonii* and *T. rendalli*; all age classes of *S. intermedius* vs. 3+ *C. gariepinus*; all age classes of *C. ngamensis* vs. 2+ and 3+ *S. intermedius*, etc.). Furthermore, the only (intra-specific) trophic separation observed in this study occurred between 2+ vs. 3+ *C. gariepinus*, and between 1+ *S. intermedius* vs. 2+ and 3+ *S. intermedius* (Fig. 2). These suggest ontogenetic feeding behaviour.

#### Spatial variations in food resource partitioning

*Schilbe intermedius*. Pseudo-habitat partitioning based on diet differences was observed in 1+ *S. intermedius* which were clustered into two feeding guilds at the 40% similarity level (Fig. 3), i.e., generalist predators from Boteti, Boro River and Xakanaxa, and specialist

predators from Shakawe (Table 4). No significant trophic differences were found between 1+ (ANOVA:  $P = 0.22$ ,  $DF = 4$ ) and 2+ (ANOVA:  $P = 0.16$ ,  $DF = 4$ ) *S. intermedius* among the sites.

2+ *S. intermedius* were clustered into two major feeding guilds around the 45% similarity level. Guild 1 is composed of fish from Boteti, Shakawe, and Xakanaxa while Guild 2 includes fish from Boro River and Guma (Fig. 3) even though the diet differences were not significant (ANOSIM:  $r = 0.75$ ,  $P = 0.1$ ; see Table 4). Odonata, Hemiptera, and Diptera, respectively, contributed (cumulatively) 39% of the two guilds' dissimilarity with 2+ *S. intermedius* from Boro River being specialist predators while those from the other areas were relatively generalist in their diet.

*Marcusenius macrolepidotus*. 1+ *M. macrolepidotus* were clustered into two feeding guilds around the 50% similarity level using Bray-Curtis similarities (Fig. 4). Guild 1 was composed of fish from Boro (generalist predators: Table 4), Guma (specialist predators: Table 4), and Xakanaxa while Guild 2 consisted of fish from Boteti

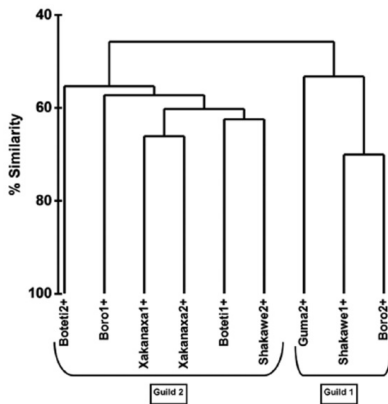


Fig. 3. Dendrogram illustrating pseudo-habitat partitioning (based on diet differences) of 1+ and 2+ *Schilbe intermedius* from five different areas of the Okavango River delta, based on diet analysis. 1+ refers to one-year-old fish while 2+ refers to two-year-old

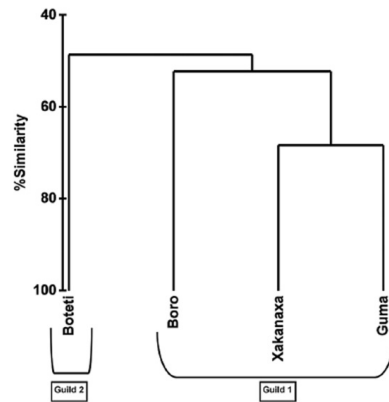


Fig. 4. Bray-Curtis similarity dendrogram, illustrating habitat partitioning on feeding behaviour of one-year-old *Marcusenius macrolepidotus* among several habitats in the Okavango River delta

Table 4  
Diet breadth index illustrating feeding behaviour of two age classes of *Schilbe intermedius* and *Marcusenius macrolepidotus* among different areas

Species and age class	Study area				
	Boteti	Shakawe	Boro River	Guma	Xakanaxa
<i>M. macrolepidotus</i> 1+	2.99	—	7.00	2.41	4.35
<i>M. macrolepidotus</i> 2+	3.55	—	4.18	—	—
<i>S. intermedius</i> 1+	5.41	2.27	6.54	—	6.69
<i>S. intermedius</i> 2+	3.47	3.75	2.62	3.84	6.38

River (specialist predators: Table 4) only. No significant trophic partitioning (ANOVA:  $P = 0.61$ ,  $DF = 3$ ) of 1+ *M. macrolepidotus* was found among the four different areas.

2+ *M. macrolepidotus* from Boro were generalist predators while those from Boteti were specialist predators (Table 4). No significant trophic partitioning between the two areas was found (ANOVA:  $P = 0.999$ ,  $DF = 3$ ).

#### Diet variations with flood stage

DCA-DECORANA (and PCA for *Tilapia rendalli* and *Clarias gariepinus*) was used to evaluate changes in feeding behaviour of several floodplain fish species over various age groups in Boro River (Fig. 5). At floods' onset in the area, 1+ *Schilbe intermedius* fed on detritus and ants but switched to a diet consisting of algae, bees,

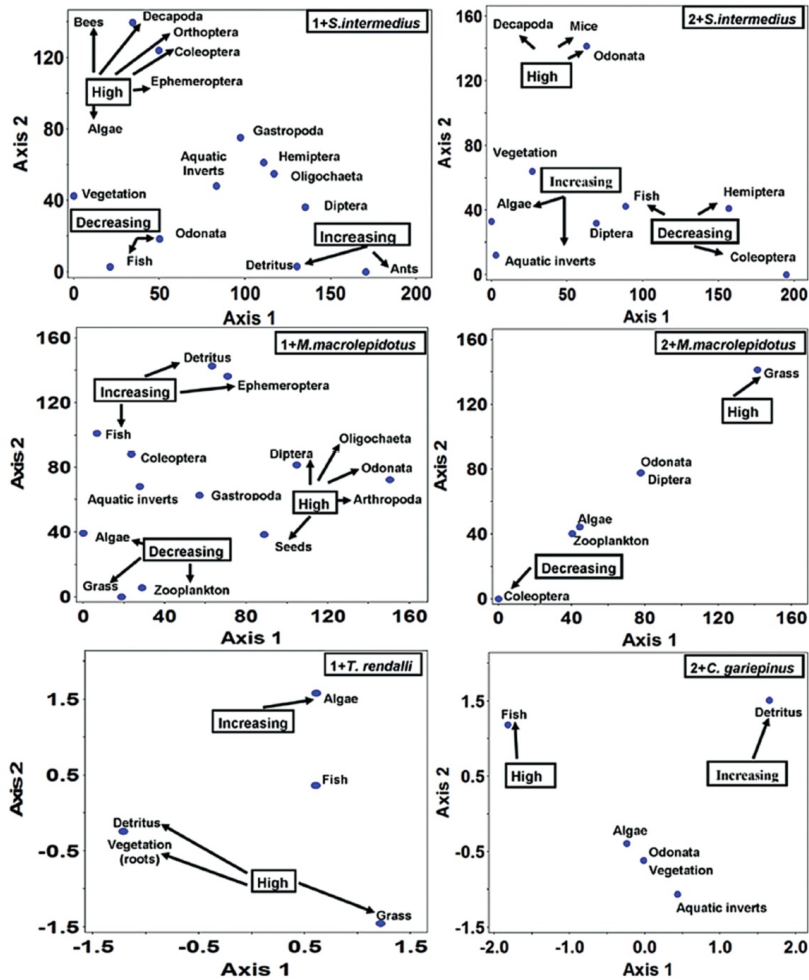


Fig. 5. DCA-DECORANA analysis (and PCA analysis for *Tilapia rendalli* and *Clarias gariepinus*) illustrating flood pulse induced diet shifts of selected fish species (different ages) in the Boro River seasonal floodplain (Note: the length of the arrows does not indicate the strength of the influence)

Ephemeroptera, Coleoptera, Decapoda, and Orthoptera as the flood progressed. This diet then changed to fish and Odonata at decreasing water levels. Other diet items such as Diptera and Oligochaeta did not show any major seasonality. Similar diet shifts were observed for 2+ *S. intermedius* where algae and (unidentified) aquatic invertebrates were key food items at increasing water levels. This diet then switched to mice, Decapoda, and Odonata at peak floods and then changed to Hemiptera, fish, and Coleoptera at decreasing water levels.

Several diet shifts were also observed for 1+ and 2+ *Marcusenius macrolepidotus* in Boro (Fig. 5). The key items preyed by 1+ fish at increasing water levels were detritus, Ephemeroptera, and fish, which then changed to Diptera, Odonata, Arthropoda, Oligochaeta and seeds at high water levels. Their diet then shifted to algae, zooplankton, and grass at decreasing water levels. Similarly, grass was the key food item at peak floods for 2+ fish and they subsequently switched to Coleoptera at decreasing water levels. 1+ *Tilapia rendalli* fed more on algae at increasing water levels and switched to a diet dominated by detritus and vegetation (grass and tree roots) at peak floods. 2+ *Clarias gariepinus* fed more on detritus at increasing water levels and switched to a diet dominated by fish at peak floods.

Bray-Curtis similarities were used to determine the resultant species interactions during different flood stages and feeding behaviour (Fig. 6) while SIMPER analysis was used to determine the key prey items in each guild. Two major feeding guilds (Bray-Curtis similarity) composed of piscivores and detritivores (SIMPER analysis) were identified in all the flood stages, except for the decreasing water level period where "piscivores" and "algivores" were the major feeding guilds. Based on SIM-

PER analysis, the relative contribution of fish to the "piscivorous" guild was lowest at peak floods (43%), and highest at decreasing water levels (84%). Similarly, while detritus contributed 100% to the diet of the "detritivorous" guild at peak floods, it only contributed 47% to this guild at increasing water levels. These changes were caused by variations in species interactions within these flooding seasons. While both 1+ and 2+ *Hepsetus odoe* belonged to the "piscivorous" guild throughout the different flooding stages, species such as 0+ *Oreochromis andersonii* moved in and out of this guild. Both age classes of *O. andersonii* were the only members of the "detritivorous" guild at peak floods. Moreover, fish were eaten by most species (and age classes) at peak floods than in the other two flood stages.

Trophic level and diet overlap dynamics were observed among and within the different species (Tables 5–6). Essentially, these observations suggest that generally, intra-specific competition for food was highest at decreasing water levels, while inter-specific competition was highest at increasing water levels.

Ecosim 7 analysis (using Pianka's niche overlap) revealed some significant (e.g.,  $POI > 0.6$ ) diet overlaps between and within feeding guilds on account of diet similarities at different flooding stages (Tables 5–6). While juvenile (0-year-old) *O. andersonii*, 1+ *T. rendalli* and *H. odoe* were piscivores at increasing water levels and peak floods for *T. rendalli* (Fig. 6), the cichlids occupied significantly different (ANOVA:  $P < 0.05$ ) trophic levels compared to *H. odoe*. There was no overlap in their diet with *H. odoe* (Pianka's index  $< 0.6$ ) (Table 5).

Similarly, while significant diet overlaps ( $POI > 0.6$ ) were observed between *Clarias ngamensis* and *C. gariepinus*,

ANOVA indicating food partitioning among different species (and different ages) at increasing water levels in the Boro River

Table 5

	N-1	N-2	N-3	M-1	G-2	G-3	A-0	O-1	O-2	R-1	I-2
N-1											
N-2	<b>0.1</b>										
N-3	<b>0.1</b>	0.8									
M-1	0	0.6	0.5								
G-2	0.2	<b>0.6</b>	0.5	0.8							
G-3	0	<b>0.6</b>	<b>0.6</b>	0.7	1						
A-0	0	0.1	0	0.5	0.2	0					
O-1	<b>0</b>	<b>0.3</b>	<b>0</b>	<b>0.2</b>	<b>0.2</b>	<b>0.1</b>	<b>0</b>				
O-2	<b>0</b>	<b>0.3</b>	<b>0</b>	<b>0.2</b>	<b>0.2</b>	<b>0.1</b>	<b>0</b>	1			
R-1	0	0.2	0	0.5	0.2	0	0.8	<b>0.5</b>	<b>0.5</b>		
I-2	<b>0.3</b>	0.3	0.1	0.4	<b>0.3</b>	<b>0.1</b>	<b>0.3</b>	0.9	0.9	0.7	
I-1	<b>0</b>	0.8	0.6	0.7	<b>0.8</b>	<b>0.8</b>	0	<b>0.4</b>	<b>0.4</b>	0.3	0.5

Interactions showing significant differences in mean trophic level are marked in bold. The values are Pianka's overlap values derived from the Ecosim7 routine. NOTE: N-1 = 1+ *Clarias ngamensis*, N-2 = 2+ *C. ngamensis*, N-3 = 3+ *C. ngamensis*; M-1 = 1+ *Marcusenius macrolepidotus*; G-2 = 2+ *Clarias gariepinus*, G-3 = 3+ *C. gariepinus*; A-0 = 0+ *Oreochromis andersonii*; O-1 = 1+ *Hepsetus odoe*, O-2 = 2+ *H. odoe*; R-1 = 1+ *Tilapia rendalli*; I-2 = 2+ *Schilbe intermedius*, I-1 = 1+ *S. intermedius*.



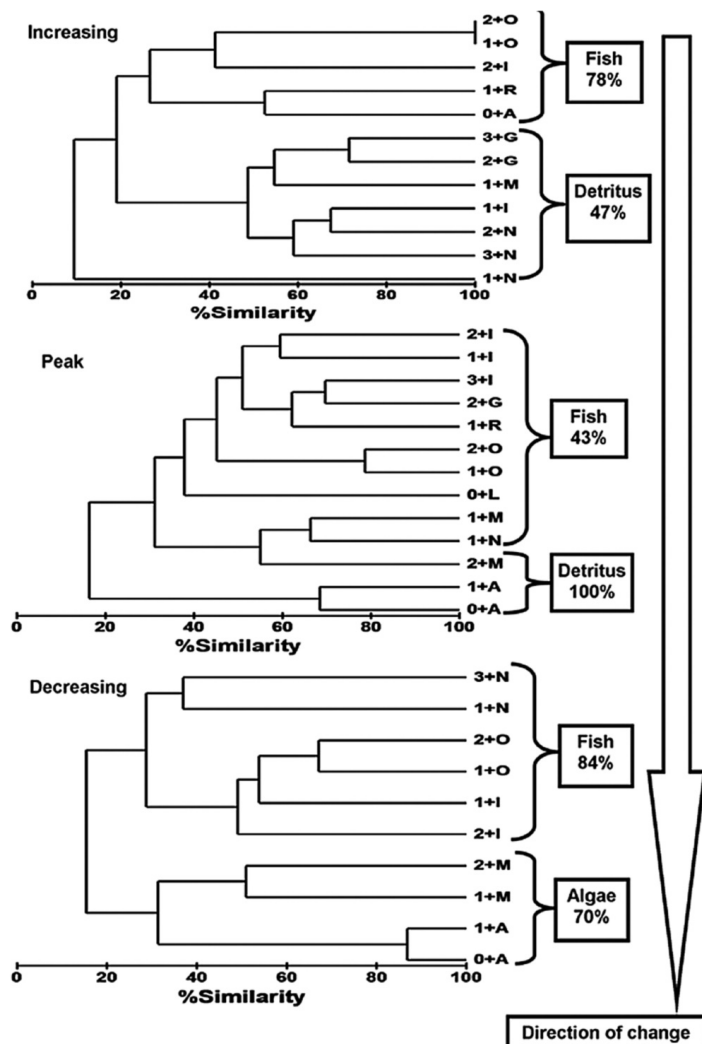


Fig. 6. Dendrogram using group-average linking on Bray-Curtis similarities illustrating species interactions (changes in diet guilds) over three flooding stages (increasing, peak floods and decreasing water levels) in the Boro River floodplains based on occurrence data; Note: 0+ A = 0+ *Oreochromis andersonii*; 1+ A = 1+ *O. andersonii*; 2+ G = 2+ *Clarias gariepinus*; 3+ G = 3+ *C. gariepinus*; 1+ I = 1+ *Schilbe intermedium*; 2+ I = 2+ *S. intermedium*; 3+ I = 3+ *S. intermedium*; 0+ L = 0+ *Brycinus lateralis*; 1+ M = 1+ *Marcusenius macrolepidotus*; 2+ M = 2+ *M. macrolepidotus*; 1+ N = 1+ *Clarias ngamensis*; 2+ N = 2+ *C. ngamensis*; 3+ N = 3+ *C. ngamensis*; 1+ O = 1+ *Hepsetus odoe*; 2+ O = 2+ *H. odoe*; 1+ R = 1+ *Tilapia rendalli*

these species occupied significantly different trophic levels. Some significant diet overlaps were observed between *Marcusenius macrolepidotus* and *C. gariepinus*, and they occupied similar trophic levels (ANOVA:  $P > 0.05$ ).

At peak floods, not only was there a significant diet overlap (POI > 0.6) between 0 and 1+ *O. andersonii*, they also occupied the same trophic level (Table 6) in the "detritivorous" guild. However, there was perfect resource partitioning between *H. odoe* and other species in the "piscivorous" guild, where Pianka's diet overlap was 0 and there were significant differences (ANOVA:  $P < 0.05$ ) in mean trophic level.

**Water levels vs. feeding.** There was no significant relation between Levin's index and mean trophic level ( $P > 0.05$ ) with either mean water depth or discharge at Boro (Table 7) for *Marcusenius macrolepidotus*. However, there was a significant relation ( $F = 25.88$ ;  $P \leq 0.05$ ) between feeding rate and mean water depth, where 93% of the variations in feeding rates can be explained by changes in mean water depth. While the relations were not significant, diet scores from axis 1 of the DCA analysis responded more to discharge ( $F = 12.91$ ;  $P = 0.07$ ) than to mean water depth ( $F = 0.01$ ;  $P = 0.93$ ).

There were no significant relations ( $P > 0.05$ ) between either discharge or mean water depth with either feeding rate (g per fish) or mean trophic level for *Schilbe intermedius*. However, there was a significant relation ( $F = 7.03$ ;  $P \leq 0.05$ ) between the feeding strategy of 1+ *S. intermedius*

and water discharge, where 58% of the variations in the Levin's index was explained by discharge. There was a significant relation between diet scores of 1+ *S. intermedius* from axis 1 of DCA analysis and mean discharge ( $F = 7.12$ ;  $P \leq 0.05$ ) while none was observed between diet scores and mean water depth ( $F = 5.75$ ;  $P = 0.06$ ).

#### DISCUSSION

Plasticity in diet is common in floodplain fish where most species feed on aquatic invertebrates and fish (Lowe-McConnell 1987). Our study agrees with this observation where fish species feed on a wide range of food items, with fish, algae and aquatic invertebrates as key prey, agreeing with previous studies from the Delta (Merron and Bruton 1988, Merron unpublished). Earlier studies (Merron and Bruton 1988, Winemiller and Kelso-Winemiller 2003) indicate that *Tilapia rendalli* is a herbivore grazing mostly on aquatic macrophytes (and algae), however, this study showed that it occasionally feeds on fish (apart from grass, seeds, algae and detritus) corroborating Skelton (2001). *O. andersonii*, which was previously described as a detritivore (Merron and Bruton 1988, Skelton 2001, Winemiller and Kelso-Winemiller 2003), preyed actively on *Barbus* spp. in a newly inundated Lake Ngami, which had been dry for 20 years. This feeding strategy suggests that most floodplain fish species (e.g., *O. andersonii*) are opportunistic and take advantage of available food resources for their survival.

Table 6

ANOVA indicating food partitioning among different species (and different ages) at peak floods and decreasing floods in the Boro River

	N-1	N-2	N-3	M-1	M-2	G-2	L-0	A-0	A-1	O-1	O-2	R-1	I-2	I-3
N-1														
N-2														
N-3	0.5 <sup>d</sup>													
M-1	0.4 <sup>d</sup>	0.8 <sup>p</sup>	0.3 <sup>d</sup>											
M-2	0 <sup>d</sup>	0.6 <sup>p</sup>	0.3 <sup>d</sup>	0.8 <sup>p</sup> , 0.7 <sup>d</sup>										
G-2		0.3 <sup>p</sup>		0.2 <sup>p</sup>	0.2 <sup>p</sup>									
L-0		0.1 <sup>p</sup>		0.2 <sup>p</sup>	0.1 <sup>p</sup>	0.2 <sup>p</sup>								
A-0	0 <sup>d</sup>	0.4 <sup>p</sup>	0.3 <sup>d</sup>	0.4 <sup>p</sup> , 0.8 <sup>d</sup>	0.1 <sup>p</sup> , 0.7 <sup>d</sup>	0.4 <sup>p</sup>	0.1 <sup>p</sup>							
A-1	0 <sup>d</sup>	0.3 <sup>p</sup>	0.3 <sup>d</sup>	0.3 <sup>p</sup> , 0.6 <sup>d</sup>	0 <sup>p</sup> , 0.4 <sup>d</sup>	0.3 <sup>p</sup>	0 <sup>p</sup>	0.9 <sup>p</sup> , 0.8 <sup>d</sup>						
O-1	0.1 <sup>d</sup>	0 <sup>p</sup>	0 <sup>d</sup>	0 <sup>p</sup> , 0.1 <sup>d</sup>	0 <sup>p</sup> , 0 <sup>d</sup>	0.9 <sup>p</sup>	0.2 <sup>p</sup>	0 <sup>p</sup> , 0 <sup>d</sup>	0 <sup>p</sup> , 0 <sup>d</sup>					
O-2	0.3 <sup>d</sup>	0 <sup>p</sup>	0 <sup>d</sup>	0 <sup>p</sup> , 0.1 <sup>d</sup>	0 <sup>p</sup> , 0 <sup>d</sup>	0.9 <sup>p</sup>	0.2 <sup>p</sup>	0 <sup>p</sup> , 0 <sup>d</sup>	0 <sup>p</sup> , 0 <sup>d</sup>	1 <sup>p</sup> , 1 <sup>d</sup>				
R-1		0.2 <sup>p</sup>		0.2 <sup>p</sup>	0.2 <sup>p</sup>	0.5 <sup>p</sup>	0.3 <sup>p</sup>	0.3 <sup>p</sup>	0.2 <sup>p</sup>	0.4 <sup>p</sup>	0.4 <sup>p</sup>			
I-2	0.3 <sup>d</sup>	0.4 <sup>p</sup>	0.2 <sup>d</sup>	0.4 <sup>p</sup> , 0.2 <sup>d</sup>	0.4 <sup>p</sup> , 0.2 <sup>d</sup>	0.8 <sup>p</sup>	0.6 <sup>p</sup>	0.2 <sup>p</sup> , 0.1 <sup>d</sup>	0.1 <sup>p</sup> , 0 <sup>d</sup>	0.7 <sup>p</sup> , 0.9 <sup>d</sup>	0.7 <sup>p</sup> , 0.9 <sup>d</sup>	0.4 <sup>p</sup>		
I-3		0.2 <sup>p</sup>		0.3 <sup>p</sup>	0.2 <sup>p</sup>	0.9 <sup>p</sup>	0.3 <sup>p</sup>	0.3 <sup>p</sup>	0.3 <sup>p</sup>	0.9 <sup>p</sup>	0.9 <sup>p</sup>	0.5 <sup>p</sup>	0.9 <sup>p</sup>	
I-1	0.1 <sup>d</sup>	0.4 <sup>p</sup>	0.1 <sup>d</sup>	0.4 <sup>p</sup> , 0.1 <sup>d</sup>	0.4 <sup>p</sup> , 0 <sup>d</sup>	0.8 <sup>p</sup>	0.6 <sup>p</sup>	0.2 <sup>p</sup> , 0 <sup>d</sup>	0.1 <sup>p</sup> , 0.1 <sup>d</sup>	0.7 <sup>p</sup> , 0.9 <sup>d</sup>	0.7 <sup>p</sup> , 0.9 <sup>d</sup>	0.4 <sup>p</sup> , 0.9 <sup>d</sup>	0.8 <sup>p</sup>	0.8 <sup>p</sup>

Interactions showing significant differences in mean trophic level are marked in bold. Superscripts p and d denote peak- and decreasing flood, respectively. The values are Pianka's overlap values derived from the Ecosim7 routine. NOTE: N-1 = 1+ *Clarias ngamensis*, N-2 = 2+ *C. ngamensis*, N-3 = 3+ *C. ngamensis*; M-1 = 1+ *Marcusenius macrolepidotus*, M-2 = 2+ *M. macrolepidotus*; G-2 = 2+ *Clarias gariepinus*; L-0 = 0+ *Brycinus lateralis*; A-0 = 0+ *Oreochromis andersonii*, A-1 = 1+ *O. andersonii*; O-1 = 1+ *Hepseus odoe*, O-2 = 2+ *H. odoe*; R-1 = 1+ *Tilapia rendalli*; I-2 = 2+ *Schilbe intermedius*, I-3 = 3+ *S. intermedius*, I-1 = 1+ *S. intermedius*.

Table 7

Summary of linear regression analyses to establish the relation between various feeding indices of *Schilbe intermedius* and *Marcusenius macrolepidotus* against water depth and discharge

Test	<i>S. intermedius</i>	<i>M. macrolepidotus</i>
Discharge vs. Levin's index	0.045 ( $R^2 = 0.58$ )*	0.17 ( $R^2 = 68$ )
Depth vs. Levin's index	0.11 ( $R^2 = 0.43$ )	0.17 ( $R^2 = 68$ )
Depth vs. feeding rate [g per fish]	0.89 ( $R^2 = 0.00$ )	0.04 ( $R^2 = 0.93$ )*
Discharge vs. feeding rate [g per fish]	0.93 ( $R^2 = 0.00$ )	0.75 ( $R^2 = 0.06$ )
Depth vs. trophic level	0.53 ( $R^2 = 0.10$ )	0.35 ( $R^2 = 0.42$ )
Discharge vs. trophic level	0.88 ( $R^2 = 0.01$ )	0.26 ( $R^2 = 0.55$ )
Discharge vs. Eigenvalues	0.04 ( $R^2 = 0.59$ )*	0.07 ( $R^2 = 0.87$ )
Depth vs. Eigenvalues	0.06 ( $R^2 = 0.53$ )	0.93 ( $R^2 = 0.00$ )

Values with an \* indicate a significant relation; g per fish = grams of food eaten per fish.

**Inter- and intra-specific interactions.** Fish partition food between and within species (Labropoulou et al. 1999, de Merona and Rankin-de-Merona 2004), like floodplain fish in the Amazon where partitioning was more evident among specialized than generalized predators (de Merona and Rankin-de-Merona 2004). This study revealed that there was higher (significant:  $P < 0.05$ ) trophic segregation among species than within species, suggesting that inter-specific interactions might be the main driver structuring floodplain fish communities.

Significant inter-specific diet overlaps were observed in this study (e.g., *Tilapia rendalli* vs. *Clarias ngamensis*, *Hepsetus odoe* vs. *Schilbe intermedius*, etc.) which may suggest competition for food. However, *H. odoe* prefers quiet, deep (Skelton 2001), and slow flowing waters (Merron and Bruton 1988) in well vegetated backwaters (Winemiller and Kelso-Winemiller 1994, Merron unpublished\*) while *S. intermedius* is a pelagic species (Merron and Bruton 1988) usually found among emergent or submerged vegetation (Skelton 2001). Furthermore, *S. intermedius* feeds nocturnally (Skelton 2001) relying on its sensory barbels and large eyes to actively seek its prey (Merron unpublished\*) while *H. odoe* is a visual predator relying on light to find its prey (Skelton 2001). *S. intermedius* is also an aggressive predator with high habitat flexibility (Merron unpublished\*) while *H. odoe* is an ambush predator that hides among vegetation waiting for its prey (Skelton 2001). Therefore, this observation suggests the possible existence of food partitioning based on feeding time. A similar observation was made in the Amazon (de Almeida et al. 1997) where niche differentiation among competitive species occurred through differences in feeding times, in habitat utilization, and by the ability of species like *Rhaphiodon vulpinus* Spix et Agassiz, 1829 (Characiformes) to have a greater "feeding flexibility". Diet similarity does not necessarily suggest direct competition for food, but rather that similar food resources are being used (Mathews et al. 1992) which might of course result in direct competition when food becomes limited.

That notwithstanding, except for *Schilbe intermedius* which is ubiquitous in the Delta (Merron unpublished\*)

and has a wide habitat preference (Skelton 2001), there is also trophic differentiation among these species which minimises contact and hence direct competition. That aside, piscivorous species prey on different fish species, of different ages, which is a clear case of resource partitioning that is otherwise not revealed through standard ecological indices. Lindholm and Hesses (2007) made a similar observation in the Delta's seasonal floodplain when they observed a potential diet overlap between larval *Tilapia rendalli* and *Anisops sardea* (aquatic insect in the order Hemiptera).

The trophic flexibility of some species and ontogenetic feeding of *Clarias gariepinus* minimises intra specific competition (for food) and optimise energy intake resulting in an efficient utilization of available food resources. While *C. gariepinus* was classified as an omnivore (Merron unpublished\*), this study has revealed that two-year-old fish were omnivores with a preference for animals (TROPH =  $3.3 \pm 0.47$ ) while three-year-old fish were omnivores with a preference for plants (TROPH =  $2.7 \pm 0.43$ ). The trophic partitioning between these age classes ensures co-existence through low (minimal) intra-specific competition. Merron's (Merron unpublished\*) observation that larger (older) *C. gariepinus* (SL > 300 mm) were piscivores compared to younger fish could have been biased by sampling "pack-hunting" catfish, which prey disproportionately on *Marcusenius macrolepidotus* during draw-down (Bell-Cross 1974, Merron 1993, Hanika and Kramer 2000) due to their electro-receptivity to electric discharges emitted by *M. macrolepidotus* (Hanika and Kramer 2000). While "pack-hunting" *C. gariepinus* were not sampled in this study, this seasonal feeding behaviour highlights the trophic flexibility of this species, driven by the flood pulse. This flood driven high trophic flexibility was also observed by Sá et al. (2006) in the Guadiana River estuary (in Portugal). While Merron (unpublished\*) classified *Schilbe intermedius* as an insectivore and piscivorous predator, this study revealed that older fish (especially 3+<sup>+</sup>s) are piscivores while younger fish are omnivores. This suggests an ontogenetic feeding strategy by *S. intermedius*.

\* Merron G.S. 1991. The ecology and management of the fishes of the Okavango Delta, Botswana, with particular reference to the role of the seasonal flood. PhD Thesis. Rhodes University, Grahamstown, Republic of South Africa.



The majority of fish species from other (floodplain) systems have an ontogenetic feeding strategy (García-Berthou 1999, García-Berthou and Moreno-Amich 2000, Rossi 2001) which facilitates food resource partitioning (Garrison and Link 2000). However, overlap indices and trophic level analysis revealed minimal evidence of ontogenetic feeding among the species studied in the Delta. Apart from *S. intermedius* and *C. gariepinus*, no resource partitioning was observed within the other species, and there were significant overlaps in diet between older and younger fish in most of them. Winemiller and Kelso-Winemiller (2003) also observed significant dietary overlaps between both juvenile and adult *Oreochromis andersonii* and *Tilapia rendalli* in the Zambezi River. That notwithstanding, Stergiou and Karpouzi's (2002) fractional trophic levels revealed the existence of ontogenetic diet shifts within several species in this study. What is particularly important to note is that the system (i.e., the Okavango Delta) is not static, but is dynamically driven by seasonal (and inter-annual) flooding patterns. Therefore, while potential for inter- and intra-specific competition might exist in floodplain fish communities, this is mediated by the flood pulse, which disperses fish into new habitats opened by new floods. According to Amarasekare (2003), fish dispersal (caused by floods' arrival) into new habitats reduces competition in the fish community. This strong seasonality suggests that competition within floodplain fish communities is in constant flux in tandem with the seasonal rhythms of the flooding patterns. Generally, inter- and intra-specific competition for food increase at low water levels when fish become more concentrated in the water body and food resources become more limited (Lowe-McConnell 1987). Conversely, high water levels improve habitat connectivity, which improves habitat partitioning by species and age class, and subsequently food partitioning (and availability), which would then decrease competition for food.

Generally, while mean TROPH values per species increased with increasing size, similar to other studies (Stergiou and Karpouzi 2002, Simon et al. 2009), some species such as *C. gariepinus* and *O. andersonii* showed an opposite trend where younger fish occupied higher trophic levels than older fish. Furthermore, *Brycinus lateralis*, (the smallest species studied) occupied higher trophic levels than some large sized species. Layman et al. (2005) explains that some predators are able to exploit prey at energetically optimal sizes by occupying low trophic positions due to variations in prey body size, morphology and habitat affinity. This feeding strategy then results in non-linearity between body size and trophic level position. *Barbus* spp. (especially *Barbus paludinosus* Peters, 1852) are pioneer species and would have therefore been the most available prey (food) item for younger (smaller-sized) *O. andersonii* (these are able to colonise recently inundated habitats better) than older (larger-sized) fish in Lake Ngami (which was newly inundated). In this scenario, which epitomises a classical opportunistic feeding strategy, younger fish occupy high-

er trophic levels than older fish within the same species. This observation accentuates the highly dynamic opportunistic feeding behaviour of floodplain fish species, where dynamism is the main constant for survival in a highly fluctuating system.

Cannibalism has been reported for *Hydrocynus vittatus* Castelnau, 1861 (Alestidae) and *Hepsetus odoe* (see Merron and Bruton 1988, Winemiller and Kelso-Winemiller 1994, Skelton 2001), and this was also observed for *S. intermedius* in this study. Winemiller and Kelso-Winemiller (1994) observed that *H. odoe* cannibalism in the Zambezi River occurs at decreased water levels while this study showed that older *S. intermedius* exhibited cannibalism (around July) at relatively high water levels (in Boro). Possibly, most hetero-specific species (e.g., cyprinids, mormyrids, etc.) migrate to shallow floodplains, hence reducing their availability to larger (older) *S. intermedius*. In this scenario, where there is low abundance of hetero-specific prey, Rudolf (2008) argues that cannibalism increases, which would explain cannibalism within the *S. intermedius* community during this time. However, this cannibalism might also be caused by what Claessen et al. (2004) define as size dependent interactions. In Winemiller and Kelso-Winemiller's (1994) case, the *H. odoe* cannibalism might be caused by intra-specific competition (Claessen et al. 2004), which is normally high at low water levels due to decreased food supply. Cannibalism in *S. intermedius* and *Clarias ngamensis* (observed in the Delta), suggests that this behaviour might be more widespread than observed before in floodplain fish communities. Dynamic changes in the fish community structure, caused by seasonal flooding may facilitate this behaviour. Cannibalism in predators might cause non-linearity in predator-prey interactions in fish communities (Rudolf 2008) and therefore its impact across trophic levels needs to be understood before it can be integrated into food web theory. Generally, if cannibalism, is stronger than predation, this may alter trophic cascades in the fish community where prey survival increase because predation effects are dampened by cannibalism. It is particularly striking that cannibalism appears to be higher in ubiquitous and abundant species in the Okavango Delta (e.g., *S. intermedius*, *C. gariepinus*, and *C. ngamensis*). This suggests that this "short-circuited predator-system" may be the main strategy used by catfishes to enhance their survival in seasonal floodplains and increase their comparative advantage over other species.

**Spatio-temporal variations in feeding behaviour.** Spatio-temporal variations in food items (observed in this study) highlight fluxes in food availability at spatial and temporal scales (Sá et al. 2006) caused by seasonal flooding. Generally, terrestrial food sources (e.g., ants, grasshoppers, mice, etc.) were eaten more either at increasing or peak water levels, while aquatic food sources (e.g., fish, algae, etc.) were consumed more at decreasing water levels by *Schilbe intermedius*. This feeding strategy, which is strongly regulated by the seasonal flood pulse, affirms the impact of the flood pulse on the

feeding ecology of fish species in flood-pulsed environments. These seasonal variations in feeding ecology are caused by migrations (horizontal and vertical) observed by Merron (unpublished\*) due to the seasonal flood regime. That notwithstanding, this diet flexibility ensures that optimum net energy intake is maintained throughout the year. Subsequently, this opportunistic feeding strategy ensures less spatio-temporal variations in mean trophic levels, which was observed for *Marcusenius macrolepidotus* and *S. intermedius*. These species are effectively utilizing available food resources in different habitats to maintain their energy requirements.

The dynamic aquatic-terrestrial ecotone allows for seasonal changes in the feeding strategy of *S. intermedius* in relation to variations in water depth. At high water levels, *S. intermedius* is a generalist predator eating a wide variety of food items but switches to specialised predation, preying predominantly on fish at receding water levels. This increased piscivory at reduced water levels was also observed for 1+ and 3+ *Clarias ngamensis* and 1+ and 2+ *Hepsetus odoe*. The increased preference for fish at this time suggests that piscivory is enhanced by "concentration" effects in fish availability observed by Welcomme (1985) in floodplain fisheries. This dynamic change in feeding strategy by floodplain fish is observed by de Merona and Rankin-de-Merona (2004) in the Amazon, where *Triplotheus* spp. (Characiformes) narrowed their diet in the low water season. Vaz et al. (1999) also observed similar changes in the feeding strategy of some detritivorous fish species in the Parana River system (Brazil) which had broad feeding niches at high floods that narrowed considerably at low floods. Temporal changes in feeding strategy were also discussed by Merron (unpublished\*) who observed a higher presence of terrestrial food sources (e.g., mice, termites, Orthoptera, etc.) at increasing flood levels, than at receding floods. Being an active predator, it is anticipated that *S. intermedius*' diet responds more to changes in water discharge than depth. The basic assumption being that its prey items are flushed out into the water column by rapidly advancing water (e.g., drowning mice, ants) in the inundated floodplains. Similarly, fish prey (especially some cyprinids) might respond more to changes in water flow rates (e.g., Hladik and Kubečka 2003) at decreasing water levels which would make them more vulnerable to predation. This increased piscivory at reduced water levels results in a lengthening of the food chain, which in turn results to a less efficient energy transfer. It follows then, that (some) fish may generally lose body condition during this time, until the next flooding season.

Similarly, *Marcusenius macrolepidotus* feeding strategy changes from a generalist predator at high water levels to a more specialist feeder grazing (almost exclusively) on algae at low water levels. Merron and Bruton (1988) observe that *M. macrolepidotus* back-migrate to the main channel from drying up floodplains, and this might explain the switch in feeding strategy. This dependence on algae is similar to Finlay et al. (2002) observa-

tions who observed that trout growth was highly dependent on algal production during low water levels in summer. The presence of seeds in the diet of *M. macrolepidotus* agrees with the observation of Chick et al. (2003) that floodplain fish take advantage of resources in the aquatic-terrestrial ecotone, and may indeed be agents of seeds dispersal. While it has never been known to prey on fish (even algae) in the Delta (Merron and Bruton 1988, Skelton 2001), the presence of fish in *M. macrolepidotus* diet at decreased water levels suggested that it also takes advantage of the "concentration" effect of fish at low water levels. The observation that *M. macrolepidotus* feeding rate responded more to water depth suggests that it takes advantage of the inundated floodplains to feed heavily (on abundant food items) before back migrating to the channel and lagoon habitats at receding (low) water levels, where food is less abundant. This observation is consistent with Lowe-McConnell (1987) who observed that high water is the main feeding (and growing) time for most floodplain fish.

There is evidence that the terrestrial environment is actively subsidizing the aquatic system (i.e., fish species feed on terrestrial food sources) as a consequence of the flood pulse. Possibly because of habitat switching between the different life history stages, and perhaps due to flooding variability, the Delta's fish species are opportunistic feeders actively channelling terrestrial carbon into fish biomass. This is illustrated by *Clarias gariepinus* feeding on Diplopoda (millipedes) and mice; *Schilbe intermedius* feeding on mice, ants, and grasshoppers; and *C. ngamensis* feeding on ants, grasshoppers, and other terrestrial insects. Moreover, the presence of bird remains in the diet of one-year-old *S. intermedius* and *Brycinus lateralis* also attests to this opportunistic feeding strategy. These broad (and opportunistic) feeding strategies are possibly an adoptive strategy against an unpredictable system. Specialised feeding strategies would undoubtedly make the different fish species more vulnerable to changes in the environment, which might affect their survivability. This adoptive strategy agrees with Moss (1980) who observes that several Lake Chilwa fish species have "very" broad diets and unspecialized habitat requirements which allow them to cope with the lake's irregular drying out phases. This study has validated Lowe-McConnell's (1987) observations that riverine fish species have an opportunistic feeding behaviour because of the ephemeral nature of habitats and food resources. Furthermore, opportunistic feeding ensures less cost in searching for food, and optimisation of energy intake during periods of scarcity (Corrêa et al. 2009). Ultimately, floodplain fish species are major conduits of energy flow from the terrestrial to the aquatic environment. This study has validated the effect of the flood pulse on the feeding ecology of floodplain fish. Subject to further investigations, this study has shown that inter- and intra-specific competition for food is a dynamic process driven by the flood pulse.

\* See footnote on page 284.



## CONCLUSIONS

This study has shown that the terrestrial-aquatic ecotone, driven by the seasonal flood pulse, is important towards fish growth in seasonal floodplains where food of terrestrial origin is channelled into fish diet. This affirms Lowe-McConnell's (1987) observations that a large proportion of floodplain fish species rely on floodplain ecotone resources. Therefore, any future upstream management plans need to ensure that this ecotone is maintained for the sustainable production of fish biomass. Another key observation made from this study is that energy uptake is optimised through cannibalism to ensure species survival into successive generations. Furthermore, the feeding behaviour of different fish species is constantly morphing to take advantage of environmental variations which affect food availability. Generally, food chains are short at the start of the flood cycle and lengthen at reduced water levels. This dynamic relation occurs more at decreased water levels when predation and competition (inter- and intra-) increase in the fish community. While the competition theory based on Lotka-Volterra's model predicts species extinction in uniform, stable environments (Begon et al. 1986), Tilman's mechanistic model suggests that a species' competitive ability is regulated by its ability to utilise a limiting resource (Lampert and Sommer 2007). However, these key ecological models are negated by the flood pulse driven feeding behaviour of floodplain fish species, where the system is in constant flux.

This study highlights Lowe-McConnell's (1987) discussions on the maintenance and evolution of tropical fish assemblages. Are floodplain assemblages driven by deterministic processes where food partitioning facilitated by competition (including predation and cannibalism) is the major force structuring tropical fish communities? Evidence from this study has shown that predation, cannibalism and (inter-specific) competition are major attributes of floodplain fish communities. This study has contributed to floodplain fish feeding ecology theory, and also highlights the dynamic processes involved in floodplain fish feeding ecology, and the need for intensive and long term studies which will ultimately aid in management of this key resource. In conclusion, this study has also affirmed Marshall and Eliot's (1997) argument that several techniques should be used to evaluate fish feeding ecology.

## ACKNOWLEDGEMENTS

This study was funded from Project R524 from the Office of Research and Development (ORD) at the University of Botswana. Gratitude is also expressed to Drs. Mike-Murray Hudson and Richard Fynn who reviewed earlier drafts of this paper. Great appreciation is also given to Mr M. Dhlwayo and Mrs A. Makati from the ORI GIS lab who assisted in production of map and figures in this manuscript.

## REFERENCES

- Agostinho C.S., Hahn N.S., Marques E.E. 2003. Patterns of food resource use by two congeneric species of piranhas (*Serrasalmus*) on the upper Paraná River floodplain. *Brazilian Journal of Biology* 63 (2): 177–182.  
DOI: 10.1590/S1519-69842003000200002
- Amarasekare P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6 (12): 1109–1122. DOI: 10.1046/j.1461-0248.2003.00530.x
- Baldoa F., Drake P. 2002. A multivariate approach to the feeding habits of small fishes in the Guadalquivir Estuary. *Journal of Fish Biology* 61 (Suppl. sA): 21–32.  
DOI: 10.1111/j.1095-8649.2002.tb01758.x
- Baremore I.E., Murie D.J., Carlson J.K. 2010. Seasonal and size-related differences in diet of the Atlantic angel shark *Squatina dumeril* in the northeastern Gulf of Mexico. *Aquatic Biology* 8 (2): 125–136.  
DOI: 10.3354/ab00214
- Begon M., Harper J.L., Townsend C.R. 1986. *Ecology: individuals, populations and communities*. Blackwell, Oxford, UK.
- Begon M., Mortimer M. 1986. *Population ecology; a unified study of animals and plants*. Blackwell, London, UK.
- Bell-Cross G. 1974. A fisheries survey of the upper Zambezi River system. *Occasional Papers of the National Museums and Monuments of Rhodesia* 5 (5): 279–338.
- Bunn S.E., Thoms M.C., Hamilton S.K., Capon S.J. 2006. Flow variability in dryland rivers: boom, bust and the bits in between. *River Research and Applications* 22 (2): 179–186.  
DOI: 10.1002/rra.904
- Chick J.H., Cosgriff R.J., Gittinger L.S. 2003. Fish as potential dispersal agents for floodplain plants: first evidence in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 60 (12): 1437–1439.  
DOI: 10.1139/f03-155
- Claessen D., Roos A.M., Persson L. 2004. Population dynamic theory of size-dependent cannibalism. *Proceedings of the Royal Society of London, Part B: Biological Sciences* 271 (1537): 333–340.  
DOI: 10.1098/rspb.2003.2555
- Clarke K.R., Gorley R.N. 2001. *PRIMER v5 (& v6): User manual/tutorial*, PRIMER-E. Plymouth, UK.
- Corrêa C.E., Hahn N.S., Delariva R.L. 2009. Extreme trophic segregation between sympatric fish species: the case of small sized body *Aphyocharax* in the Brazilian Pantanal. *Hydrobiologia* 635 (1): 57–65.  
DOI: 10.1007/s10750-009-9861-2
- de Almeida V.L.L., Hahn N.S., de Vazzoler A.E.A. 1997. Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). *Ecology of Freshwater Fish* 6 (3): 123–133.  
DOI: 10.1111/j.1600-0633.1997.tb00154.x
- de Graaf G. 2003. The flood pulse and growth of floodplain fish in Bangladesh. *Fisheries Management and Ecology* 10 (4): 241–247.  
DOI: 10.1046/j.1365-2400.2003.00341.x
- de Merona B., Rankin-de-Merona J.R. 2004. Food resource partitioning in a fish community of the central Amazon floodplain. *Neotropical Ichthyology* 2 (2): 75–84.  
DOI: 10.1590/S1679-62252004000200004
- Eberle L.C., Stanford J.A. 2010. Importance and seasonal availability of terrestrial invertebrates as prey for juvenile

- salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russian Federation). *River Research and Applications* 26 (6): 682–694.  
DOI: 10.1002/rra.1270
- Feinsinger P., Spears E.E., Poole R.W. 1981. A simple measure of niche breadth. *Ecology* 62 (1): 27–32.  
DOI: 10.2307/1936664
- Finlay J.C., Khandwala S., Power M.E. 2002. Spatial scales of carbon flow in a river food web. *Ecology* 83 (7): 1845–1859.  
DOI: 10.1890/0012-9658(2002)083[1845:SSOCFI]2.0.CO;2
- Froese R., Binohlan C. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology* 56 (4): 758–773.  
DOI: 10.1111/j.1095-8649.2000.tb00870.x
- Garcia-Berthou E. 1999. Food of introduced mosquitofish: ontogenetic diet shift and prey selection. *Journal of Fish Biology* 55 (1): 135–147.  
DOI: 10.1111/j.1095-8649.1999.tb00663.x
- Garcia-Berthou E., Moreno-Amich R. 2000. Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. *Journal of Fish Biology* 57 (1): 29–40.  
DOI: 10.1111/j.1095-8649.2000.tb00773.x
- Garrison L.P., Link J.S. 2000. Diets of five hake species in the northeast United States continental shelf ecosystem. *Marine Ecology Progress Series* 204: 243–255.  
DOI: 10.3354/meps204243
- Gotelli N.J., Entsminger G.L. 2007. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. and Kelsey-Bear, Jericho, VT, USA. Available at <http://garyentsminger.com/ecosim/index.htm>
- Hanika S., Kramer B. 2000. Electrosonary prey detection in the African sharptooth catfish, *Clarias gariepinus* (Clariidae), of a weakly electric mormyrid fish, the bulldog (*Marcusenius macrolepidotus*). *Behavioral Ecology and Sociobiology* 48 (3): 218–228.  
DOI: 10.1007/s002650000232
- Hladik M., Kubečka J. 2003. Fish migration between a temperate reservoir and its main tributary. *Hydrobiologia* 504 (1–3): 251–266.  
DOI: 10.1023/B:HYDR.0000008525.46939.42
- Hoeinghaus D.J., Winemiller K.O., Layman C.A., Arrington D.A., Jepsen D.B. 2006. Effects of seasonality and migratory prey on body condition of *Cichlia* species in a tropical floodplain river. *Ecology of Freshwater Fish* 15 (4): 398–407.  
DOI: 10.1111/j.1600-0633.2006.00152.x
- Hyslop E.J. 1980. Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology* 17 (4): 411–429.  
DOI: 10.1111/j.1095-8649.1980.tb02775.x
- Junk W.J. 1996. Ecology of floodplains—a challenge for tropical limnology. Pp. 255–265. In: Schiemer F., Boland K.T. (eds.) *Perspectives in tropical limnology*. SPB Academic Publishers, Amsterdam, the Netherlands.
- Junk W.J., Bayley P.B., Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. Pp. 110–127. In: Dodge D.P. (ed.) *Proceedings of the International Large River Symposium*. Canadian Special Publication in Fisheries Aquatic Science No. 106.
- Kolding J., van Zwieten P.A.M. 2005. Improving productivity in tropical lakes and reservoirs. Challenge Program on Water and Food - Aquatic Ecosystems and Fisheries Review Series 1. World-Fish Centre, Cairo.
- Labropoulou M., Machias A., Tsimenides N. 1999. Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus, 1758). *Fisheries Bulletin* 97 (3): 495–507.
- Lampert W., Sommer U. 2007. *Limnology: the ecology of lakes and streams*. Oxford University Press, Oxford, UK.
- Layman C.A., Winemiller K.O., Arrington D.A., Jepsen D.B. 2005. Body size and trophic position in a diverse tropical food web. *Ecology* 86 (9): 2530–2535.  
DOI: 10.1890/04-1098
- Lindholm M., Hessen D.O. 2007. Competition and niche partitioning in a floodplain ecosystem: a cladoceran community squeezed between fish and invertebrate predation. *American Zoology* 42 (2): 158–164.  
DOI: 10.3377/1562-7020(2007)42[158:CANPIA]2.0.CO;2
- Lowe-McConnell R.H. 1987. *Ecological studies in tropical fish communities*. Cambridge University Press, Cambridge, UK.
- Marshall S., Elliot E. 1997. A comparison of univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish. *Journal of Fish Biology* 51 (3): 526–545.  
DOI: 10.1111/j.1095-8649.1997.tb01510.x
- Mathews W.J., Gelwick F.P., Hoover J.J. 1992. Food and habitat use by juveniles of species of *Micropterus* and *Morone* in a Southwestern Reservoir. *Transactions of the American Fisheries Society* 121 (1): 54–66.  
DOI: 10.1577/1548-8659(1992)121<0054:FOAHUB>2.3.CO;2
- McCune B., Mefford M.J. 1999. *Multivariate analysis of ecological data*, Version 4.24. Glendon Beach, OR, USA.
- Merron G.S. 1993. Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis* in the Okavango Delta, Botswana. *Journal of Fish Biology* 43 (4): 575–584.  
DOI: 10.1111/j.1095-8649.1993.tb00440.x
- Merron G.S., Bruton M.N. 1988. The ecology and management of the fishes of the Okavango delta, Botswana, with special reference to the role of the seasonal floods. I.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. Investigational Report No. 29.
- Mosepele K., Nengu S. 2004. Growth, mortality, maturity and length-weight parameters of selected fishes from the Okavango Delta, Botswana. Pp. 67–74. In Pauly D., Diouf B., Samb B., Vakily M.J., Palamores M.L.D. (eds.) *Fish biodiversity: Local studies as basis for global inferences*. ACP-EU Fisheries Research Initiative. Brussels, Belgium.
- Mosepele K., Mosepele B., Bokhutlo T., Amutenya K. 2011. Spatial variability in fish species assemblage and community structure in four subtropical lagoons of the Okavango delta, Botswana. *Physics and Chemistry of the Earth*, 36 (14–15): 910–917.  
DOI: 10.1016/j.pce.2011.07.060
- Moss B. 1980. *Ecology of freshwaters: man and medium*. Blackwell, London, UK.



- Navia A.F., Mejia-Falla P.A., Giraldo A. 2007. Feeding ecology of elasmobranch fishes in coastal waters of the Colombian Eastern Tropical Pacific. *BMC Ecology* 7 (8): [10 pages without official numbering.]  
DOI: 10.1186/1472-6785-7-8
- Ney J.J. 1993. Practical use of biological statistics. Pp 137–177. In: Kohler C.C., Hubert, W.A. (eds.) *Inland fisheries management in North America*. American Fisheries Society, Bethesda, MD, USA.
- Odum H.T. 1994. *Ecological and general systems: an introduction to systems ecology*. University Press of Colorado, Niwot CD, USA.
- Odum E.P., Barret G.W. 2005. *Fundamentals of ecology*. 5th edn. Thompson Brooks/ Cole, Pacific Grove, CA, USA.
- Pauly D., Froese R., Sa-a P.S., Palomares M.L., Christensen V., Rius J. 2000. *TrophLab Manual*. ICLARM, Manila, Philippines.
- Ramberg L., Wolski P., Krah M. 2006. Water balance and infiltration in a seasonal floodplain in the Okavango Delta, Botswana. *Wetlands* 26 (3): 677–690.  
DOI: 10.1672/0277-5212(2006)26[677:WBAIIA]2.0.CO;2
- Ricklefs R.E. 1990. *Ecology*. 3rd edn. Freeman and Company, New York, NY, USA.
- Roach K.A., Winemiller K.O., Layman C.A., Zeug S.C. 2009. Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: Evidence from stable isotopes. *Acta Oecologica* 35 (4): 513–522.  
DOI: 10.1016/j.actao.2009.03.007
- Rosas-Alayala J., Hernández-Herrera A., Galvan-Magaña F., Abitia-Cárdenas L.A., Muhlia-Melo A.F. 2002. Diet composition of sailfish (*Istiophorus platypterus*) from the southern Gulf of California, Mexico. *Fisheries Research* 57 (2): 185–195.  
DOI: 10.1016/S0165-7836(01)00344-7
- Rossi L.M. 2001. Ontogenetic diet shifts in a neotropical catfish, *Sorubim lima* (Schneider) from the River Paraná System. *Fisheries Management and Ecology* 8 (2): 141–152.  
DOI: 10.1046/j.1365-2400.2001.00237.x
- Rudolf V.H.W. 2008. The impact of cannibalism in the prey on predator-prey systems. *Ecology* 89 (11): 3116–3127.  
DOI: 10.1890/08-0104.1
- Sá R., Bexiga C., Veiga P., Vieira L., Erzini K. 2006. Feeding ecology and trophic relationships of fish species in the lower Guadiana River Estuary and Castro Marim e Vila Real de Santo António Salt Marsh. *Estuarine Coastal and Shelf Science* 70 (1–2): 19–26.  
DOI: 10.1016/j.eess.2006.05.038
- Simon K.D., Bakar Y., Samat A., Zaidi C.C., Aziz A., Mazlan A.G. 2009. Population growth, trophic level, and reproductive biology of two congeneric archer fishes (*Toxotes chatareus*, Hamilton 1822 and *Toxotes jaculatrix*, Pallas 1767) inhabiting Malaysian coastal waters. *Journal of Zhejiang University SCIENCE B* 10 (12): 902–911.  
DOI: 10.1631/jzus.B0920173
- Skelton P.H. 2001. *A complete guide to freshwater fishes of southern Africa*. Struik Publishers, Cape Town, Republic of South Africa.
- Stergiou K.L., Karpouzi V.S. 2002. Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries* 11 (3): 217–254.  
DOI: 10.1023/A:1020556722822
- Vaz M.M., Petrere M., Martinelli L.A., Mozeto A.A. 1999. The dietary regime of detritivorous fish from the River Jacaré Pepira, Brazil. *Fisheries Management and Ecology* 6 (2): 121–132.  
DOI: 10.1046/j.1365-2400.1999.00123.x
- Vázquez R.I., Rodríguez J., Abitia L.A., Galván F. 2008. Food habits of the yellow snapper *Lutjanus argentiventris* (Peters, 1869) (Percoidae: Lutjanidae) in La Paz Bay, Mexico. *Revista de Biología Marina y Oceanografía* 43 (2): 295–302.
- Watanabe H., Kubodera T., Kawahara S. 2003. Feeding habits of Pacific pomfret *Brama japonica* in the transition zone of the central North Pacific. *Fisheries Science* 69 (2): 269–276.  
DOI: 10.1046/j.1444-2906.2003.00617.x
- Welcomme R.L. 1979. *Fisheries ecology of floodplain rivers*. Longman Publishers, New York, NY, USA.
- Welcomme R.L. 1985. *River Fisheries*. FAO Fisheries Technical Paper No. 262. FAO, Rome.
- Winemiller K.O., Kelso-Winemiller L.C. 1994. Comparative ecology of the African pike, *Hepsetus odoe*, and tiger-fish, *Hydrocynus forskahlii*, in the Zambezi River floodplain. *Journal of Fish Biology* 45 (2): 211–225.  
DOI: 10.1111/j.1095-8649.1994.tb01301.x
- Winemiller K.O., Kelso-Winemiller L.C. 2003. Food habits of tilapia cichlids of the upper Zambezi River and floodplain during the descending phase of the hydrologic cycle. *Journal of Fish Biology* 63 (1): 120–128.  
DOI: 10.1046/j.1095-8649.2003.00134.x
- Wolski P., Murray-Hudson M. 2005. Flooding dynamics in a large low-gradient alluvial fan, the Okavango Delta, Botswana, from analysis and interpretation of a 30 year hydrometric record. *Hydrology and Earth System Sciences* J1 – HESS 10: 127–137.
- Wolski P., Savenije H.H.G., Murray-Hudson M., Gumbricht T. 2006. Modelling of the flooding in the Okavango Delta, Botswana, using hybrid reservoir-GIS model. *Journal of Hydrology* 331 (1–2): 58–72.  
DOI: 10.1016/j.jhydrol.2006.04.040
- Zalewski M., Thorpe J.E., Naiman R.J. 2001. Fish and riparian ecotones—a hypothesis. *Ecology and Hydrobiology* 1 (1–2): 11–24.

Received: 25 January 2012

Accepted: 9 October 2012

Published electronically: 31 December 2012



## 6. Chapter 6

**Paper V:** Mosepele, K., Kolding, J and Bokhutlo, T. (2017). Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. *Ecohydrology and Hydrobiology*. DOI: 10.1016/j.ecohyd.2017.01.005

G Model  
ECOHYD-132; No. of Pages 14

ARTICLE IN PRESS

*Ecohydrology & Hydrobiology xxx (2016) xxx–xxx*



Contents lists available at ScienceDirect

**Ecohydrology & Hydrobiology**

journal homepage: [www.elsevier.com/locate/ecohyd](http://www.elsevier.com/locate/ecohyd)



Original Research Article

### Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana

Kethlatlogile Mosepele<sup>a,\*</sup>, Jeppe Kolding<sup>b</sup>, Thethela Bokhutlo<sup>c</sup>

<sup>a</sup> University of Botswana, Okavango Research Institute, Private Bag 285, Maun, Botswana

<sup>b</sup> University of Bergen, Department of Biology, High Technology Centre, N-5020 Bergen, Norway

<sup>c</sup> Botswana International University of Science and Technology, College of Science, Private Bag 16, Palapye, Botswana

#### ARTICLE INFO

**Article history:**  
Received 6 November 2016  
Accepted 31 January 2017  
Available online xxx

**Keywords:**  
Inter-annual variability  
Seasonal variability  
Flood pulse  
Floodplain fish ecology  
Okavango Delta

#### ABSTRACT

Tropical floodplain fish populations fluctuate at temporal scales and understanding the variability in these systems will contribute to comprehensive management of these resources. Therefore, the aim of this study was to assess the dynamics of a floodplain fish assemblage. Data were collected using standard methods between 1999 and 2009 from the delta's panhandle. Various analytical tools (e.g. CCA, SIMPER, ANOVA, etc.) were used to assess fish assemblage dynamics at seasonal and annual scales. ANOVA and cluster analyses showed that the fish assemblage underwent significant changes along the seasonal hydrograph, while index of relative abundance (IRI) revealed that the fish assemblage was dominated by *Clarias gariepinus*, *Schilbe intermedius* and *Hydrocynus vittatus* respectively. These species, including *Clarias ngamensis* and *Marcusenius altisambesi*, contributed more than 50% to variations in fish assemblage structure along the seasonal hydrograph (based on SIMPER analysis). Furthermore, canonical correspondence analysis (CCA) revealed a significant ( $p = 0.004$ ) association between environmental factors and fish assemblage structure. CCA analysis also showed that spawning for different species is associated with various environmental factors. Annually, results showed that *C. gariepinus* dominated the fish assemblage during low flood years, while *S. intermedius* dominated during high flood years. Detrended correspondence analysis (DCA) showed that the hydrological gradient had a significant effect on fish assemblage structure at an annual scale, while SIMPER analysis established significant variations in fish assemblage structure among years characterized by different hydrological features. One major conclusion we made was that fish assemblages are stochastically different at an annual scale. This study contributes knowledge to floodplain fish ecology and thus enhances fisheries management.

© 2017 European Regional Centre for Ecohydrology of the Polish Academy of Sciences. Published by Elsevier Sp. z o.o. All rights reserved.

#### 1. Introduction

In tropical floodplains fish biomass is directly related to seasonal flooding (Lowe-McConnell, 1987; Welcomme

et al., 2006). The underlying dynamic relationships are encapsulated in the flood pulse concept (Junk et al., 1989) which integrates the interactions between hydrological and ecological processes (Tockner et al., 2000). The flood pulse enhances biological productivity and maintains species diversity (Bayley, 1995) and seasonal fish migrations caused by the flood pulse facilitate the transmission of energy from the terrestrial environment to the aquatic system (Junk et al., 1989). Fish growth, mortality and

\* Corresponding author. Fax: +267 686 1835.  
E-mail addresses: [kmosepele@ori.ub.bw](mailto:kmosepele@ori.ub.bw), [mosepelek@gmail.com](mailto:mosepelek@gmail.com) (K. Mosepele).

<http://dx.doi.org/10.1016/j.ecohyd.2017.01.005>

1642-3593/© 2017 European Regional Centre for Ecohydrology of the Polish Academy of Sciences. Published by Elsevier Sp. z o.o. All rights reserved.

Please cite this article in press as: Mosepele, K., et al., Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. *Ecohydrology and Hydrobiology* (2017), <http://dx.doi.org/10.1016/j.ecohyd.2017.01.005>

breeding are directly related to the flood strength (Halls et al., 1999; de Graaf, 2003). Despite this highly dynamic relationship between climate driven hydrology and biological productivity, most fisheries management in floodplain systems is based on managing internal drivers (e.g. fishing effort) only (Welcomme, 2007) which is largely based on steady state assumptions. Therefore, there is a strong need to understand the effects of environmental variability on floodplain fish assemblages to inform fisheries management.

A suite of factors is responsible for spatio-temporal fluctuations in the floodplain fish assemblage structure. The seasonally inundated floodplain, lagoons and riparian zones are the most important habitats that regulate fish productivity, community structure, and diversity (Ward and Tockner, 2001). Fish species diversity within floodplain communities is typically highest at high floods and is lowest at low flood levels when there is low connectivity (Ward and Tockner, 2001). The aim of this study was to explore Junk et al.'s (1989) flood pulse concept in the Okavango Delta by exploring the presence of the flood pulse in the delta's fish assemblage.

## 2. Materials and methods

### 2.1. Study area

The Okavango Delta (Fig. 1) is one of the world's largest inland deltas (Ramberg et al., 2006a). While local rainfall has a localized impact (Wolski et al., 2005), the delta's hydrology is driven by annual flooding from Angola (Wolski and Savenije, 2006) with a strong inter-annual variability (Fig. 1). Discharge into the delta's northern panhandle peaks in April (Fig. 1) and is generally out of phase with the rainy season in the delta (Wolski and Savenije, 2006). The peak flood pulses through the entire system and usually takes 1–2 months from Mohembo to Seronga and another 2–3 months to reach the distal end of the delta in Maun (Wolski et al., 2005). There are 71 fish species in the delta (Ramberg et al., 2006b) distributed heterogeneously throughout the system (Mosepele et al., 2009).

### 2.2. Data collection

**Fish data:** Experimental fish data were collected between 1999 and 2009 (there was no sampling in 2003) at Ngarange and Seronga (Fig. 1) sampling stations. Two types of experimental nets were used: (i) multifilament, multi-mesh, nets made up of 9, 10 m long panels of mesh sizes 22–150 mm stretched; (ii) multifilament, multi-mesh nets made up of 5.5 m long panels of mesh sizes 50–125 mm stretched mesh. Sampling was done at each station 2–3 days monthly. Nets were set for approximately 12 h overnight and 10 h during the day (to account for diurnal variations in fish movements). Nets were set along the margins of the main channel and in a lagoon in each sampling station. The main channel has a sandy bed, fringed by papyrus (*Cyperus papyrus*) and reeds (*Phragmites australis*) rooted in mud rich peat, with water flow velocity ranging between 0.4 and 0.8 ms<sup>-1</sup> (McCarthy

et al., 1998; Wolski et al., 2006). Lagoons are seasonally connected to the main channel by narrow channels (Gondwe and Masamba, 2013) and fringed by papyrus, reeds and typha beds (Smith, 1976) with relatively sluggish water velocity (Mendelsohn et al., 2010). Catches from each panel were separated and recorded separately. The sampling regime and data treatment are described in Mosepele (2000). Maturity stages were based on Nikolsky's (1969) six stage key where stage 5 is ripe running (spawning). The data from the two nets were harmonised by using only data from mesh sizes 49–125 mm. This amounted to 57,222 fish records that were used in this study.

### 2.3. Data analysis

**General statistics:** Multiple linear step-wise regression in STATISTICA (Version 6.0, StatSoft) was used to determine the strength and significance of relationships between variables (with a significance level of 0.05, except a few cases of 0.1). The relative strength of independent variables was determined by the magnitude of the *p* value (Zeug and Winemiller, 2007). ANOVA was used to test for the level of differences among variables along temporal scales.

**Univariate analysis:** Fish indices (in either numbers/set or grams/set), spawning, index of relative abundance (%IRI), and mean length were calculated in Paspear (Kolding and Skalevik, 2010). Spawning season was defined as a period when a minimum of 5% of the adult population was spawning. The %IRI is considered a good measure of abundance, as it combines numbers, weight and frequency of occurrence (Hart et al., 2002). Fish abundance data were clustered into four seasonal discharge stages (increasing, peak, decreasing and minimum). The assemblage stability was assessed using the coefficient of variation (CV) (Grossman et al., 1990; Oberdorff and Porcher, 1992). Scaling population variation by the mean permits comparison of populations with different mean abundances which makes it less ambiguous than other metrics (Grossman et al., 1990). CV percentage values were classified into equal quartiles as stable, moderately stable, moderately fluctuating and fluctuating (Freeman et al., 1988).

**Multivariate analysis:** Cluster analysis in PRIMER 6 (Clarke and Gorley, 2001) was used to establish assemblage patterns (Minns, 1989). All data for analysis in Primer were standardized, and then square-root transformed before using Bray–Curtis similarity analysis. Spatio-temporal differences in fish assemblage structure were assessed using SIMPER analysis (Rayner et al., 2015). SIMPER scores were then plotted to explore patterns over temporal scales and hydrological variables. Environmental effects on the delta's fish species assemblage and spawning behavior were assessed by direct gradient analysis using canonical correspondence analysis (CCA) (ter Braak, 1986) implemented in PcoRD v6 (McCune and Mefford, 2006). Data were log transformed (log(*x* + 1)) to minimize the range and skew of distributions (Cantu and Winemiller, 1997). The Euclidean distance was used as the dissimilarity measure while *p* was estimated by a Monte

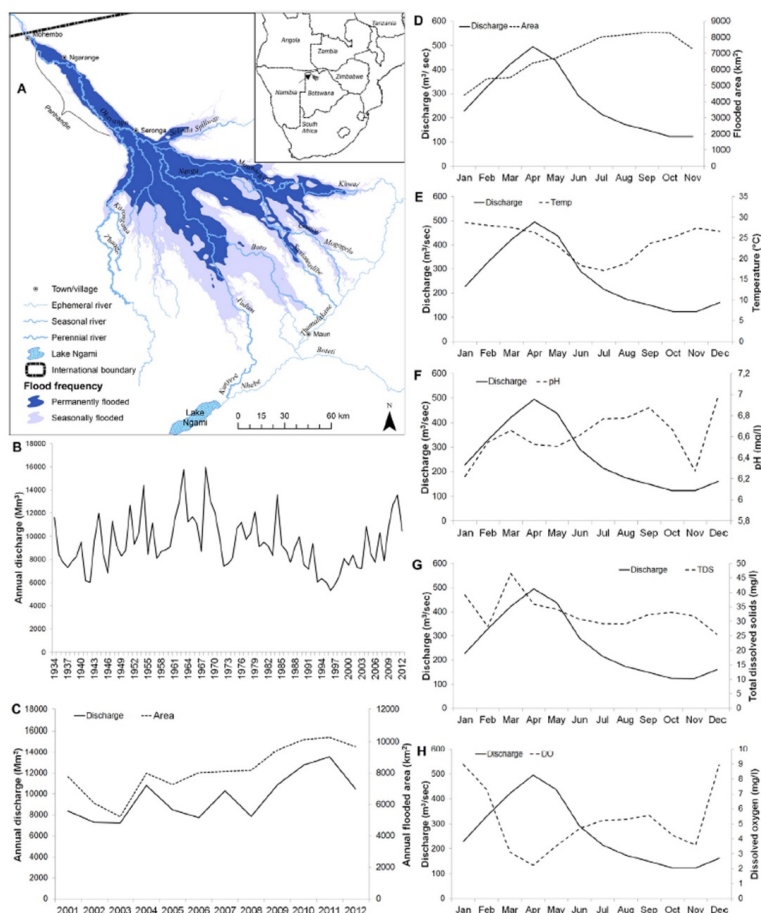


Fig. 1. Map of the Okavango Delta highlighting the panhandle (A). This figure also illustrates environmental variability in the delta through inter-annual variability in discharge (B), inter-annual variability in discharge and flooded area during the study period (C), and seasonal variability in discharge and flooded area (D), temperature, pH, total dissolved solids (G), and dissolved oxygen (H). (Note: Graphs D–H present mean values over the study period).

Carlo test using 999 permutations (McCune and Mefford, 1999). We also used detrended correspondence analysis (DCA/DECORANA) to search for patterns in assemblage shifts (Ibarra and Stewart, 1989) using Shannon's diversity index. Regression analysis was used to explore the strength and nature of relationship between diversity and hydrological variables. Only axis scores from DCA analysis that had significant relationships were included in the analysis.

### 3. Results

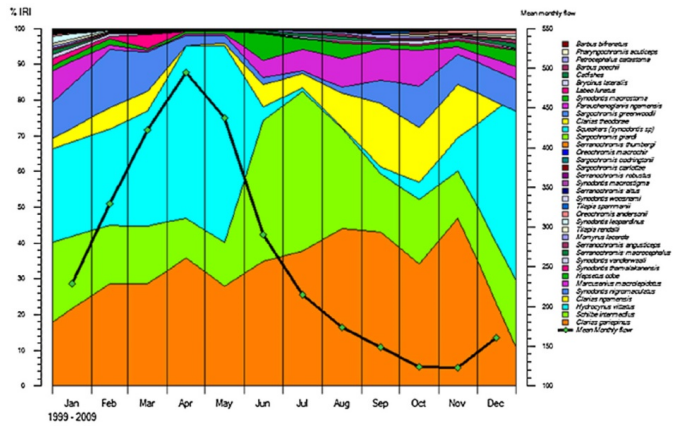
#### 3.1. General observations

*Clarias gariepinus*, *Schilbe intermedius* and *Hydrocynus vittatus* (all predators) dominated the fish assemblage at both seasonal and annual scales (Fig. 2). As summarized in Table 1, *C. gariepinus* was the most abundant species by relative weight (443 g/set) and *S. intermedius* by relative

Please cite this article in press as: Mosepele, K., et al., Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. Ecohydrology. Hydrobiol. (2017), <http://dx.doi.org/10.1016/j.ecohyd.2017.01.005>

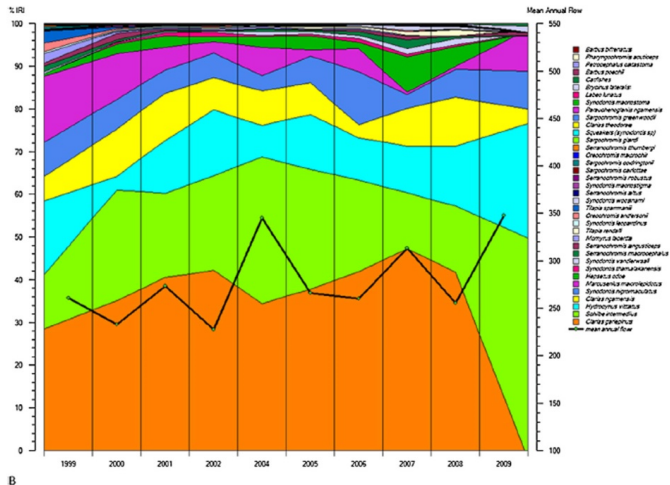


Okavango Delta - Panhandle. Seasonal trends in relative fish importance 1999-2009



A

Okavango Delta - Panhandle. Annual trends in relative fish importance 1999-2008



B

Fig. 2. Intra and inter annual variations in biodiversity in the Okavango Delta within the study period where the black lines show (A) intra-annual and (B) inter-annual variability in mean discharge.

numbers (0.970 fish/set) over the study period. The top three largest species (mean length, ML) in the composition were *C. gariepinus* (52.72 cm), *C. ngamensis* (44.85 cm) and *H. vittatus* (40.14 cm) respectively. Conversely, *Petrocephalus okavangensis* (8.53 cm), *Barbus poechii* (9.09 cm) and *Brycinus lateralis* (10.12 cm) were the smallest sized

species. The feeding guilds with the largest frequencies in the assemblage were insectivores (approximately 28%), omnivores (approximately 23%) and predators/carnivores (approximately 16%) respectively.

As summarized in Table 1, populations of the top three species had different stability dynamics (based on CV

Please cite this article in press as: Mosepele, K., et al. Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. *Ecology and Hydrobiology*. (2017), <http://dx.doi.org/10.1016/j.ecohyd.2017.01.005>

**Table 1**

Species composition and relative abundance from the study area based on data collected between 1999 and 2009. Letters in () indicate the feeding guild of each species where superscript <sup>M</sup> is Mosepele et al. (2012), <sup>MB</sup> is Merron and Bruton (1988). Fecundity estimates are also derived from various sources where superscript <sup>M</sup> is Mosepele et al. (2012), <sup>MB</sup> is Merron and Bruton (1988), <sup>W</sup> is van der Waal (1985), <sup>S</sup> is Skelton (2001) and <sup>MM</sup> is Merron and Mann (1995).

Family	Species	Species code	%IRI	No/set (density)	g/set (relative abundance)	Mean length (cm)	Fecundity	Mean weight (g)	CV (seasonal)	CV (annual)
Bagridae	<i>Pimuchonoglanis ngamensis</i> (O) <sup>MB</sup>	30	0.002	0.004	0.338	19.694	1000 <sup>MB</sup>	78.954	91	177
	<i>Zaireichthys cf. conspicuus</i> (I) <sup>MB</sup>	40	0	0	0.052	36.000	16 <sup>S</sup>	390.000	346	283
Characidae	<i>Hydrocymus vittatus</i> (C) <sup>MB</sup>	3	10.617	0.244	166.891	40.144	150000 <sup>MB</sup>	685.169	87	44
	<i>Brycinus lateralis</i> (OPA) <sup>M</sup>	31	0.002	0.008	0.076	10.120	10000 <sup>MB</sup>	9.454	175	267
Cichlidae	<i>Serranochromis macrocephalus</i> (P)(C) <sup>MB</sup>	9	0.451	0.056	17.713	26.527	225 <sup>MB</sup>	314.381	86	81
	<i>Serranochromis angusticeps</i> (P)(C) <sup>MB</sup>	10	0.432	0.058	17.144	26.653	5000 <sup>MB</sup>	297.207	93	121
	<i>Oreochromis andersonii</i> (OPP) <sup>M</sup>	14	0.187	0.031	15.729	29.177	2000 <sup>MB</sup>	502.267	117	90
	<i>Coptodon rendalli</i> (OPP) <sup>M</sup>	15	0.178	0.037	11.262	23.909	7000 <sup>MB</sup>	300.526	118	55
	<i>Tilapia sparrmannii</i> (O) <sup>MB</sup>	17	0.142	0.052	4.439	14.972	800 <sup>MB</sup>	86.143	144	148
	<i>Serranochromis altus</i> (P)	18	0.074	0.017	10.824	33.398	–	652.242	95	102
	<i>Serranochromis robustus</i> (P)(C) <sup>MB</sup>	19	0.061	0.015	8.904	31.733	1500 <sup>MB</sup>	583.591	105	72
	<i>Sargochromis carlotae</i> (O) <sup>MB</sup>	20	0.057	0.022	3.479	19.489	500 <sup>MB</sup>	157.526	81	120
	<i>Oreochromis macrochir</i> (D) <sup>MB</sup>	22	0.037	0.014	5.061	25.001	572 <sup>W</sup>	356.771	136	101
	<i>Sargochromis codringtonii</i> (M) <sup>MB</sup>	23	0.037	0.018	3.185	20.817	700 <sup>MB</sup>	178.920	75	88
	<i>Serranochromis thumbergi</i> (P)(C) <sup>MB</sup>	24	0.025	0.014	2.193	21.125	300 <sup>MB</sup>	157.578	76	180
	<i>Sargochromis giardi</i> (O) <sup>MB</sup>	25	0.019	0.010	4.227	25.869	1200 <sup>MB</sup>	421.083	96	180
	<i>Sargochromis greenwoodii</i> (M) <sup>MB</sup>	28	0.002	0.004	0.875	23.007	–	218.006	183	165
	<i>Pharyngochromis acuticeps</i> (P)(C) <sup>MB</sup>	35	0	0.001	0.097	18.867	–	120.833	233	278
	<i>Tilapia ruweti</i> (D) <sup>MB</sup>	36	0	0.001	0.114	19.775	400 <sup>MB</sup>	121.750	280	283
	<i>Hemichromis elongatus</i> (O) <sup>MB</sup>	37	0	0	0.022	15.567	500 <sup>MB</sup>	54.667	205	283
	<i>Pseudocrenilabrus philander</i> (P)(C) <sup>MB</sup>	38	0	0	0.012	11.933	–	30.000	195	271
	<i>Serranochromis longimanus</i> (P)(C) <sup>MB</sup>	39	0	0	0.037	20.250	400 <sup>MB</sup>	137.500	287	283
	Clariidae	<i>Clarias gariepinus</i> (OPA) <sup>M</sup>	1	39.111	0.376	443.903	52.717	200000 <sup>MB</sup>	1180.372	44
<i>Clarias ngamensis</i> (OPP) <sup>M</sup>		4	8.568	0.228	163.383	44.850	200000 <sup>MB</sup>	715.592	100	44
<i>Clarias theodorae</i> (O) <sup>MB</sup>		27	0.004	0.005	2.048	37.383	–	425.083	203	159
Catfishes		–	0	0.001	0.719	34.000	–	488.073	346	–
Cyprinidae	<i>Labeo lunatus</i> (D) <sup>MB</sup>	32	0.001	0.003	0.833	31.225	–	311.100	133	106
	<i>Barbus poechii</i> (I) <sup>MB</sup>	34	0	0.005	0.032	9.085	–	7.002	229	276
Hepsetidae	<i>Hepsetus cuvieri</i> (CPF) <sup>M</sup>	7	2.429	0.166	47.59	30.733	8000 <sup>MB</sup>	287.230	84	93
Mochokidae	<i>Synodontis nigromaculatus</i> (O) <sup>MB</sup>	5	5.995	0.427	31.672	20.101	31333 <sup>W</sup>	74.116	67	31
	<i>Synodontis thamalakanensis</i>	8	0.538	0.093	5.835	18.069	–	62.824	124	42
	<i>Synodontis vanderwaali</i>	11	0.420	0.088	6.416	18.953	–	72.742	72	94
	<i>Synodontis leopardinus</i> (O) <sup>MB</sup>	13	0.196	0.054	4.089	19.687	40334 <sup>W</sup>	76.009	82	109
	<i>Synodontis woosnami</i> (O) <sup>MB</sup>	16	0.163	0.052	4.049	18.023	40334 <sup>W</sup>	77.379	135	48
	<i>Synodontis macrostigma</i>	21	0.048	0.027	1.557	16.024	45000 <sup>W</sup>	57.322	123	143
	Squeakers ( <i>Synodontis</i> sp.)	26	0.008	0.016	0.787	15.631	–	50.250	136	110
	<i>Synodontis macrostoma</i>	29	0.002	0.005	0.314	16.222	–	57.293	287	157
	<i>Marcusenius altisambesi</i> (OPA) <sup>M</sup>	6	5.537	0.534	36.672	18.926	5000 <sup>MB</sup>	68.641	90	86
Mormyridae	<i>Mormyrus lacerdai</i> (I) <sup>MB</sup>	12	0.365	0.052	18.420	33.361	7000 <sup>S</sup>	355.636	108	110
	<i>Petrocephalus okavangensis</i> (I) <sup>MB</sup>	33	0.001	0.005	0.026	8.531	–	5.494	224	282
	<i>Schilbe intermedius</i> (OPA) <sup>M</sup>	2	24.293	0.970	106.137	23.303	27000 <sup>MM</sup>	109.432	56	52

Note: 1 net set = 1 net set for 12 h overnight; IRI = index of relative importance; O = Omnivore; I = Insectivore; D = Detritivore; M = Molluscivore; P/C = Predator/Carnivore; OPA = Omnivore with preference for animals; OPP = Omnivore with preference for plants; CPF = Carnivore with preference for fish.

values) at intra and inter annual scales. Intra-annually, *C. gariepinus* population was moderately stable (44); *S. intermedius* moderately fluctuating (56), while *H. vittatus* was highly fluctuating (87). Inter-annually, *C. gariepinus* (35) and *H. vittatus* (44) populations were moderately stable, while *S. intermedius* (52) were moderately fluctuating. Populations of the three smallest species were fluctuating at both seasonal and annual scales. Generally, 90% of the populations were fluctuating at the seasonal scale compared to 78% at the annual scale. In general, more species were moderately stable (15%) at the annual than at the seasonal scale (2%).

### 3.2. Intra-annual variability

The fish assemblage showed strong seasonal variability while regression analysis (Fig. 3) revealed that flooded area had a stronger effect on assemblage dynamics than discharge. Generally, changes in discharge explained 41% of the observed variability in fish assemblage patterns while flooded area explained 54% of the variability (Fig. 3). SIMPER analysis (Fig. 4) showed varying similarity among the fish assemblages at a seasonal scale and also along the two hydrological gradients (i.e. discharge and flooded area). Similarity was highest between September and

Please cite this article in press as: Mosepele, K., et al., Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. *Ecology and Hydrobiology*. (2017), <http://dx.doi.org/10.1016/j.ecohyd.2017.01.005>

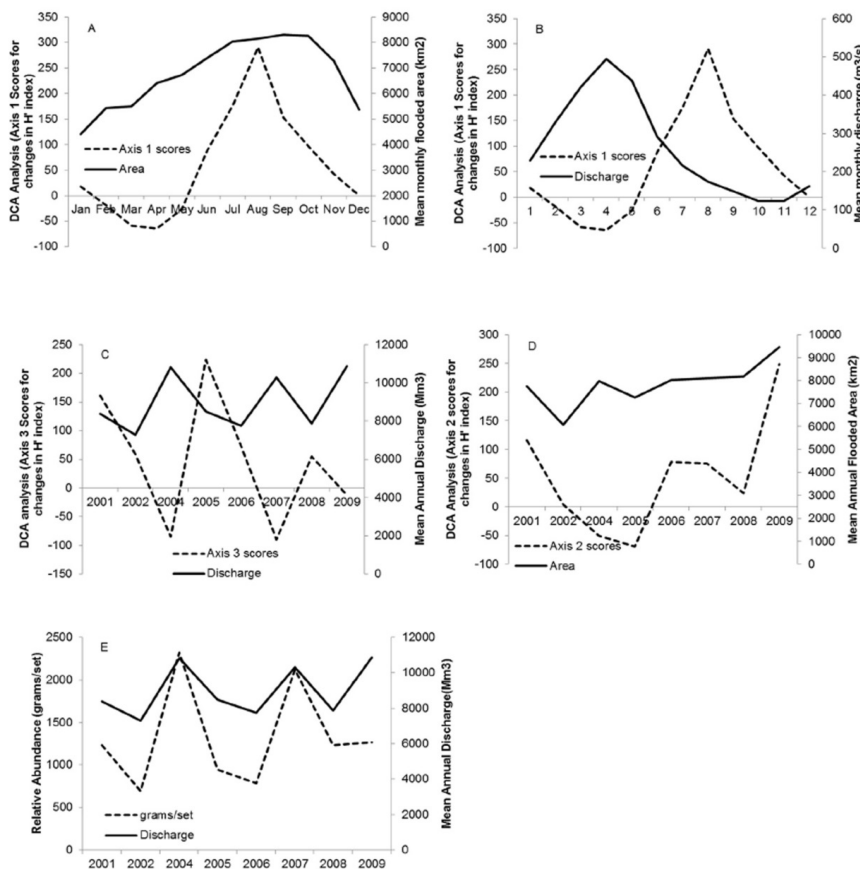


Fig. 3. (i) Results of seasonal DCA analysis (diversity) scores against (A) inundated area (ANOVA: DF = 11;  $F = 11.67$ ;  $p = 0.01$ ;  $R^2 = 0.54$ ;  $\text{Beta} = 0.73$ ), (B) discharge (Regression: DF = 11;  $F = 7.01$ ;  $p = 0.02$ ;  $R^2 = 0.41$ ;  $\text{Beta} = -0.64$ ), and annual DCA analysis (diversity) scores against (C) discharge (Regression: DF = 7;  $F = 4.91$ ;  $p = 0.07$ ;  $R^2 = 0.45$ ;  $\text{Beta} = -0.67$ ) and (D) flooded area (Regression: DF = 7;  $F = 4.98$ ;  $p = 0.07$ ;  $R^2 = 0.45$ ;  $\text{Beta} = 0.67$ ) from the study area. Also illustrated is (E) inter-annual variability in relative abundance and discharge (Regression: DF = 7;  $F = 10.43$ ;  $p = 0.02$ ;  $R^2 = 0.63$ ;  $\text{Beta} = 0.80$ ).

October, which coincides with maximum inundated area (see Fig. 1D), and lowest between April and August (increasing water volume). Conversely, similarity in the fish assemblage was lowest between peak vs decreasing discharge stage and highest at peak discharge stage (Fig. 4E). Moreover, ANOVA analysis (Table 2) revealed that assemblage stability (CV) changed significantly during the season. Cluster analysis (Fig. 5A) confirmed the strong intra annual variability into four hydrological groups (increasing, decreasing, minimum and peak discharge). *H. vittatus*, *S. intermedius*, *C. gariepinus*, *C. ngamensis* and *Marcusenius altisambesi* were the key species which contributed at least 50% to fish assemblage shifts (SIMPER analysis) within each hydrological cluster. ANOVA

(Table 2) showed that these species underwent significant seasonal changes in relative abundance. Regression analysis (Table 3) also revealed a significant relationship between hydrological variables (discharge and inundated area) and selected variables of these key fish species. Furthermore, *C. gariepinus* dominated the fish assemblage at peak inundation, while *H. vittatus* dominated the fish assemblage at peak discharge (Fig. 5A).

CCA analysis (Table 4) revealed a strong (Pearson correlation: Axis 1 = 0.993) and significant (Monte Carlo randomization:  $p = 0.004$ ) correlation between fish species distribution in the study area. Overall, pH had a minimal effect on species distribution while temperature and discharge had a major effect (Fig. 6A). According to

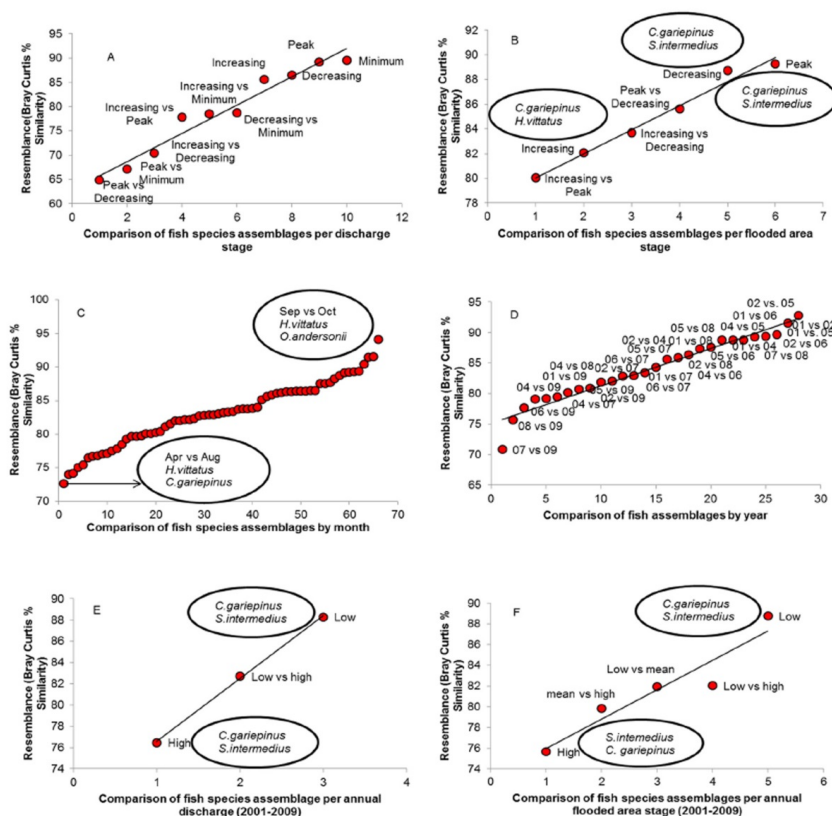


Fig. 4. SIMPER analysis illustrating intra (A–C) and inter (D–F) annual variability in fish species assemblages, where the trend line illustrates the strength of the relationship between the species assemblages.

Table 2

Summary of ANOVA analysis illustrating changes in relative abundance of selected fish species and assemblage stability (CV) along the seasonal (discharge) hydrograph (M = minimum; D = decreasing; I = increasing; P = peak). Significant values (at 95% confidence level) are in **bold**.

Index	Test	<i>H. vittatus</i>	<i>C. gariepinus</i>	<i>S. intermedius</i>	<i>C. ngamensis</i>	<i>M. altisambesi</i>
Relative abundance (g/set)	M vs. D	<b>0.018</b>	0.064	0.665	<b>0.023</b>	0.488
	M vs. I	<b>0.023</b>	0	<b>0.009</b>	<b>0</b>	<b>0.049</b>
	M vs. P	0.085	<b>0.004</b>	<b>0.034</b>	<b>0.004</b>	0.105
	D vs. I	<b>0</b>	<b>0.043</b>	<b>0.004</b>	0.135	0.087
	D vs. P	<b>0.001</b>	0.095	<b>0.022</b>	0.077	0.101
	P vs. I	0.770	<b>0.006</b>	0.135	<b>0.021</b>	0.329
Assemblage stability (CV)	M vs. D	0.078				
	M vs. I	0.186				
	M vs. P	<b>0.018</b>				
	D vs. I	<b>0.014</b>				
	D vs. P	0.253				
	P vs. I	<b>0.006</b>				



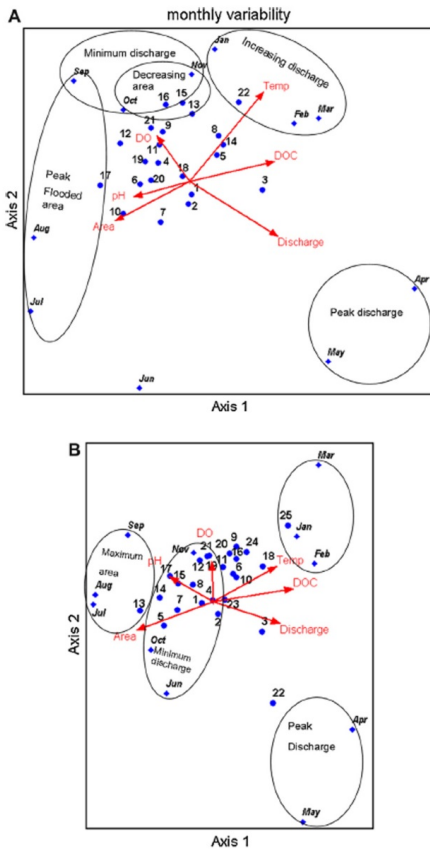


Fig. 5. CCA biplot illustrating the environmental effects on fish assemblage (A) distribution and (B) spawning behavior in the study area.

Table 4, discharge and DOC were associated with Axis 1, temperature with Axis 2, while area and DO were associated with Axis 3. Fig. 6A shows that *H. vittatus* was associated with a Discharge: DOC gradient during the peak discharge season. Several cichlid species and some *Synodontis* species were linked with a Temperature: DO gradient. *Oreochromis macrochir* was associated with an increasing discharge period, while *Synodontis leopardinus*, *Synodontis woosnami* and *C. rendalli* were associated with a decreasing area period. *Serranochromis angusticeps* and *Hepsetus cuvieri* were associated with a pH: Area gradient. All three axes in the ordination cumulatively explained approximately 78% of the total variation in the fish assemblage.

Spawning: CCA (Fig. 6B) revealed a strong (Pearson correlation: Axis 1 = 0.99) and significant (Monte Carlo

randomization;  $p = 0.00$ ) association between spawning of selected fish species and the environment (Table 4). Cumulatively, the three axes explained approximately 69% of the observed variance in spawning behavior. Spawning by different fish species was associated with different environmental gradients (Fig. 6B, Table 4). Spawning for some species like *H. vittatus* and some cichlids (e.g. *Serranochromis altus*, *O. macrochir*, etc.) was associated with Axis 1, Axis 2 for some cichlids (e.g. *Sargochromis giardi*, *Serranochromis macrocephalus*, etc.) while spawning for species like *C. gariepinus* and *S. intermedius* was associated with Axis 3 (Table 4). Regression analysis (Table 5) revealed that discharge and temperature (each) had significant relationship with 24% of the species, mean flooded area with 36% of the species, and DO with 8% of the species. Most of the species had extended, but different, spawning seasons (Table 5). Approximately 38% of the cichlids in the study start spawning between June and August, about 67% of *Synodontis* spp. start in October; approximately 67% of Silurids start in November, while about 67% of Mormyrids start in December. Approximately 52% of the species were spawning by September. Spawning season for 32% of the species ended in January (three months before peak discharge), and season for 36% of the species ended in March (a month before peak discharge). Peak spawning period for *B. poechnii* and *B. lateralis* coincided with maximum flooded area (see Table 5).

### 3.3. Inter-annual variability

The fish assemblage structure underwent inter-annual variability (Fig. 2), while DCA analysis revealed that variability in the fish assemblage structure was driven by the inter-play of discharge and flooded area (Fig. 3C and D). Generally, DCA/DECORANA analysis showed that hydrology accounted for inter-annual variability in fish species distribution (Fig. 7). SIMPER analysis revealed that similarity in fish assemblage shifted along a hydrological gradient (Fig. 4C and D) and along a time scale (Fig. 4F). Similarity was highest during low discharge (Fig. 4C) and inundated area (Fig. 4D) years and least during high discharge and inundated area years. *C. gariepinus* and *S. intermedius* were the two main species that contributed most to these assemblage dynamics. Generally, the highest similarity in fish assemblages was observed between 2001 vs. 2002 while the lowest similarity was observed between 2007 vs. 2009 (Fig. 4F). Regression analysis (Table 6) revealed that hydrology was a driver of change among the key fish species dynamics. Cluster analysis (Fig. 6B) grouped the fish assemblage into five groups along a hydrological scale. SIMPER showed that the top three species contributing to these assemblage shifts were *C. gariepinus*, *H. vittatus* and *S. intermedius*. Furthermore, *C. gariepinus* dominated the fish assemblage during years of low flooded area while *S. intermedius* dominated during high discharge years (Table 7). In fact, %IRI variability for *C. gariepinus* was significantly ( $p = 0.03$ ) related to flooded area while that of *S. intermedius* was significantly ( $p = 0.01$ ) related to discharge (Table 6).



**Table 3**  
Results of regression analysis between two hydrological variables and several fish indices of selected fish species from the delta, where only the significant relationships (at 95% confidence level) are shown. ML - mean length.

Hydrological variable	Fish index	Species	DF	F	P	R <sup>2</sup>	Beta	
Discharge	No/set	<i>C. gariepinus</i>	11	12.27	0.006	0.55	-0.74	
		<i>S. intermedius</i>	11	9.58	0.011	0.49	-0.7	
		<i>C. ngamensis</i>	11	9.84	0.011	0.5	-0.7	
		<i>M. altisambesi</i>	11	10.41	0.009	0.51	-0.71	
		All species	11	16.2	0.002	0.62	-0.79	
	g/set	<i>C. gariepinus</i>	11	16.66	0.002	0.62	-0.79	
		<i>S. intermedius</i>	11	9.89	0.01	0.5	-0.71	
		<i>C. ngamensis</i>	11	13.02	0.005	0.57	-0.75	
		All Species	11	21.72	0.001	0.68	-0.83	
		ML	<i>H. vittatus</i>	11	6.43	0.03	0.39	0.63
	ML	<i>S. intermedius</i>	11	6.46	0.029	0.39	0.63	
		<i>M. altisambesi</i>	11	7.43	0.021	0.43	0.65	
		All Species	11	17.09	0.002	0.63	0.79	
		%IRI	<i>H. vittatus</i>	11	13.45	0.004	0.57	0.76
		<i>C. ngamensis</i>	11	9.65	0.011	0.49	-0.7	
%IRI	<i>M. altisambesi</i>	11	11.34	0.007	0.53	-0.73		
	Flooded area	No/set	<i>C. gariepinus</i>	11	11.82	0.006	0.54	0.74
			<i>H. vittatus</i>	11	11.81	0.006	0.54	-0.74
			<i>S. intermedius</i>	11	22.19	0.008	0.69	0.83
			<i>C. ngamensis</i>	11	6.75	0.027	0.4	0.64
All Species			11	6.34	0.031	0.39	0.62	
g/set		<i>C. gariepinus</i>	11	14.1	0.004	0.59	0.77	
		<i>H. vittatus</i>	11	14.62	0.003	0.59	-0.77	
		<i>S. intermedius</i>	11	17.32	0.002	0.63	0.8	
		<i>C. ngamensis</i>	11	7.1	0.024	0.42	0.64	
		All Species	11	6.22	0.032	0.38	0.62	
ML		<i>S. intermedius</i>	11	34.01	0	0.77	-0.88	
		<i>C. gariepinus</i>	11	22.57	0.001	0.69	0.83	
		%IRI	<i>H. vittatus</i>	11	9.54	0.011	0.49	-0.7
		<i>C. ngamensis</i>	11	5.44	0.042	0.35	0.59	

**Table 4**  
Summary of direct gradient analysis (CCA) results to establish fish distribution pattern and spawning behavior of selected fish species along an environmental gradient in the delta's panhandle. Correlation values in **bold** indicate the key environmental variable in that particular ordination axis. The top four key species are placed in order of importance, starting with those having the highest scores under each axis.

Spawning dynamics	Axis 1			Axis 2			Axis 3		
	Eigenvalue	% variance explained	Pearson correlation	Eigenvalue	% variance explained	Pearson correlation	Eigenvalue	% variance explained	Pearson correlation
<b>Species – environment correlations</b>	<b>Discharge</b>			<b>Area</b>			<b>Temp</b>		
	0.736	-0.323	0.497	-0.835	-0.274	-0.099	0.750	-0.455	0.307
	<b>0.698</b>	0.421	-0.429	0.698	0.421	-0.429	0.634	0.758	-0.094
	0.876	0.139	0.111	0.876	0.139	0.111	0.728	0.207	0.576
	-0.476	0.163	<b>0.623</b>	-0.476	0.163	<b>0.623</b>	pH	<b>-0.481</b>	-0.142
	-0.008	<b>0.419</b>	0.063	-0.008	<b>0.419</b>	0.063	DO	-0.274	0.434
Monte Carlo randomization test (p value) of eigenvalues	0.002	-	-	0.002	-	-	0.004	-	-
Key species	<i>O. macrochir</i>	<i>S. giardi</i>	<i>C. rendalli</i>	<i>H. vittatus</i>	<i>O. macrochir</i>	<i>S. robustus</i>	<i>H. vittatus</i>	<i>O. macrochir</i>	<i>S. robustus</i>
	<i>S. altus</i>	<i>S. macrocephalus</i>	<i>H. cuvieri</i>	<i>S. nigromaculatus</i>	<i>C. rendalli</i>	<i>O. andersonii</i>	<i>S. nigromaculatus</i>	<i>C. rendalli</i>	<i>O. andersonii</i>
	<i>H. vittatus</i>	<i>S. thumbergi</i>	<i>S. intermedius</i>	<i>C. gariepinus</i>	<i>S. woosnami</i>	<i>S. angusticeps</i>	<i>C. gariepinus</i>	<i>S. woosnami</i>	<i>S. angusticeps</i>
	<i>S. codringtonii</i>	<i>S. carlottae</i>	<i>C. gariepinus</i>		<i>S. leopardinus</i>	<i>H. cuvieri</i>		<i>S. leopardinus</i>	<i>H. cuvieri</i>

#### 4. Discussion

Our results show that seasonal changes in the fish assemblage of the Okavango Delta are highly correlated to hydrological variables. Discharge (flood pulse) was the strongest driver of seasonal change, while mean flooded area (contraction and expansion) had a lesser effect. These

results are in accordance to the flood pulse concept by Junk et al. (1989) and consistent with observations from other floodplain systems (Lowe-McConnell, 1987; Arrington et al., 2005).

The observed fish assemblage dynamics are driven by *C. gariepinus*, which dominates the experimental catches at minimum discharge (coinciding with maximum flooded

10

K. Mosepele et al./Ecohydrology & Hydrobiology xxx (2016) xxx–xxx

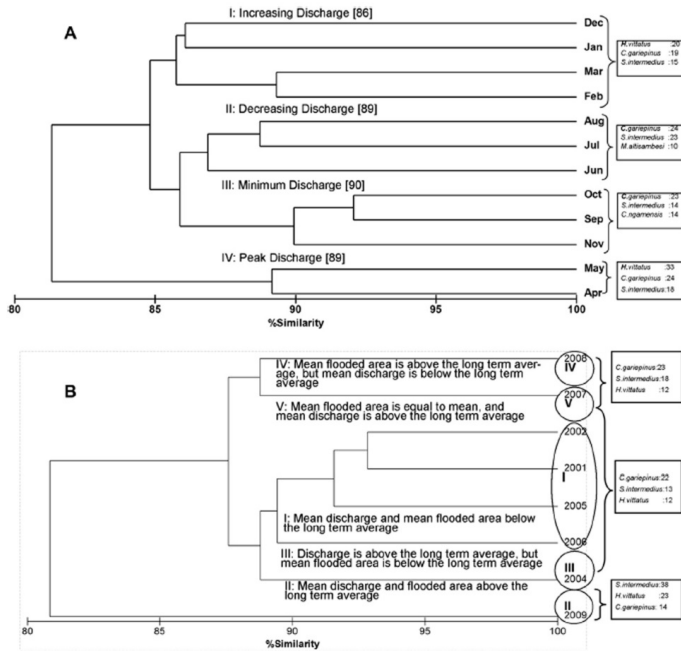


Fig. 6. Cluster analysis illustrating (A) seasonal and (B) annual fish assemblage patterns along a hydrological gradient.

area) and *H. vittatus*, which dominates during peak discharge (coinciding with small flooded area). The low discharge period interfaces with decreasing water levels where fish that were dispersed on the inundated floodplains back-migrate to the main channel and oxbow lagoons. The contraction period (decreasing inundation) results in increased piscivory (Mosepele et al., 2009), where small prey species like *M. altisambesi* become vulnerable to predation from *C. gariepinus* (Merron, 1993). The dominance of the fish assemblage by *C. gariepinus* during the contraction period is perhaps an effect of what Merron (1993) calls the catfish run. Increased activity by *Clarias* during this period (Merron, 1993) is reflected in a higher dominating catch rate in the experimental nets. Conversely, *H. vittatus* is an open water predator which is found predominantly in perennial water habitats (Winemiller and Kelso-Winemiller, 1994). High seasonal fluctuations in the fish assemblage structure (Table 2) are possibly caused by longitudinal migrations (Økland et al., 2005) during increasing and decreasing water levels. There were no significant changes in the density and relative abundance of *H. vittatus* between peak and minimum discharge periods (Fig. 4). Our observations confirm previous findings (Winemiller and Kelso-Winemiller,

1994; Merron and Bruton, 1995) that the local distribution of *H. vittatus* is regulated by the flood regime. *H. vittatus* is primarily a resident channel species (Merron, 1991), where it dominates the fish assemblage at peak discharge.

Floodplains are characterized by shifting mosaics (Ward and Tockner, 2001), driven by dilution (discharge), expansion (flooded area) and contractions (drawdown) which is reflected in the fish assemblage dynamics observed in this study. During maximum inundation (July–September) the habitat is more homogeneous where channels, lagoon and oxbows are connected to create one continuous landscape mosaic, reflected in strong seasonal similarity (Fig. 4). This period also corresponds to high species ( $\alpha$  diversity in the delta (Fig. 3). The low fish assemblage similarity observed between April and August is probably caused by different dispersion and breeding behavior during increasing water levels and subsequent inundation. The flood pulse starting from Mosepele results initially in water level increases within the main channel only (hence no marked changes in habitat or  $\alpha$  diversity) and only longitudinal fish movements. When the river channel is full, water spills over onto the peripheral floodplains and facilitates lateral fish migrations (feeding and breeding) which would then cause variations in  $\alpha$

Please cite this article in press as: Mosepele, K., et al., Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. Ecohydrology. Hydrobiol. (2017), <http://dx.doi.org/10.1016/j.ecohyd.2017.01.005>

Table 5

Summary of spawning seasons of selected species from the Okavango Delta with results of regression analysis where values in the table are partial  $p$  values for each independent environmental factor.  $P$  values in **bold** indicate the environmental factor with the strongest effect while  $p$  values with an \* indicate a significant relationship at the 95% confidence level.

Species	Spawning season	Peak month	Discharge	Area	Temp	pH	DO	R <sup>2</sup>
<i>S. carlotae</i>	Aug–Nov, Jan–Feb	August	<b>0.00*</b>	–	–	–	–	0.67
<i>S. codringtonii</i>	Aug–Nov, Jan–Feb	February	<b>0.05</b>	–	0.06	0.14	0.30	0.79
<i>S. macrocephalus</i>	August–January	September, October	0.04*	0.11	<b>0.01*</b>	–	0.20	0.91
<i>C. ngamensis</i>	August–March	January	–	–	–	0.09	<b>0.01*</b>	0.63
<i>P. okavangensis</i>	December–March	February	–	<b>0.01*</b>	–	–	0.04*	0.76
<i>M. altisambesi</i>	December–April	January	0.24	<b>0.01*</b>	–	–	0.33	0.85
<i>H. cuvieri</i>	July–March	January, November	<b>0.00*</b>	<b>0.00*</b>	–	–	0.03*	0.94
<i>T. sparrmanii</i>	Jun, Aug, Oct–Dec	October	<b>0.04*</b>	–	–	0.27	0.16	0.53
<i>S. angusticeps</i>	June–January	January	<b>0.00*</b>	0.03*	0.15	–	–	0.73
<i>P. acuticeps</i>	June, August–October	June	–	–	<b>0.08</b>	–	–	0.30
<i>B. lateralis</i>	May–November	August	–	–	–	–	0.23	0.62
<i>M. lacerda</i>	Nov– March, August	August	<b>0.44</b>	0.53	0.83	0.48	0.75	0.20
<i>C. gariepinus</i>	November–June	January	0.02*	<b>0.00*</b>	–	–	–	0.85
<i>P. ngamensis</i>	November, January	January	<b>0.01*</b>	0.03*	–	–	0.28	0.73
<i>O. andersonii</i>	Oct–Nov, Jan–Apr, Jun	January	–	<b>0.047*</b>	–	–	–	0.37
<i>S. intermedius</i>	October–February	January	<b>0.00*</b>	<b>0.00*</b>	–	–	–	0.83
<i>S. nigromaculatus</i>	October–March	February	–	–	0.07	0.30	<b>0.05</b>	0.73
<i>S. vanderwaali</i>	October–March	February	–	–	<b>0.01*</b>	–	0.09	0.69
<i>S. thamalakanensis</i>	October–March	January, October	–	–	<b>0.04*</b>	–	0.14	0.55
<i>S. woosnami</i>	October, Jan–February	January	–	–	0.19	0.33	<b>0.02*</b>	0.72
<i>B. poechii</i>	Sep–Dec, August, May	September	0.99	<b>0.00*</b>	<b>0.00*</b>	–	0.13	0.90
<i>S. macrostigma</i>	Sep–Oct, Jan–February	January, October	0.24	–	<b>0.11</b>	–	0.26	0.54
<i>C. rendalli</i>	Sep–Jan, March, May	October	–	0.03*	<b>0.01*</b>	–	–	0.57
<i>S. leopardinus</i>	September–March	January	–	–	<b>0.00*</b>	–	0.01*	0.82
<i>H. vittatus</i>	September–April	January	0.01*	–	–	–	–	0.80

diversity. Flood pulse dynamics in the delta are characterized by a 3–4 month time lag between peak flooding at Mohembo and maximum flooded area expansion (Wolski et al., 2005; Fig. 1) and reflected in the associations with

the two hydrological variables as illustrated in Figs. 4 and 5.

Generally, there is high dissolved oxygen (DO) deficiency in floodplain systems at drawdown periods when decomposition processes outstrip production (Bayley, 1995) but localized hypoxia in the delta also occurs when anoxic water is flushed out from beneath papyrus beds by new floods (Sethebe, 2011). These two processes explain the two low DO periods observed in the delta during April and October/November (Fig. 1). Our results show that DO had a stronger association with species distribution during the latter period (Fig. 5). Two species, *S. macrostoma* (a mochokid) and *Oreochromis andersonii* (a cichlid) were highly associated with the DO gradient (i.e. DO) and have tolerance for hypoxic conditions (Chapman et al., 1994). This confirmed van der Waal's (1998) observation that silurids are not structured along oxygen gradients (see Fig. 5) due to vestigial lungs which allows them to breathe atmospheric oxygen (Lowe-McConnell, 1987). Spawning season for most of the species in this study was also correlated to the hydrological mediated environmental gradient. The high water season in tropical (floodplain) systems creates new micro-habitats, greatly expands the living space, enhances food availability for juvenile fish, and decreases inter-specific competition for food and other resources (Lowe-McConnell, 1987; Chapman and Frank, 2000). Accordingly, this is the period when most floodplain fish species migrate into the marshes for feeding and reproduction (Chapman and Chapman, 2003). Results from our study are consistent with this pattern.

CCA revealed that while the onset of spawning of individual species is lagged, and possibly cued by different environmental factors (Fig. 5), the majority is tied to mean flooded area (Table 5). When water levels rise, terrestrial

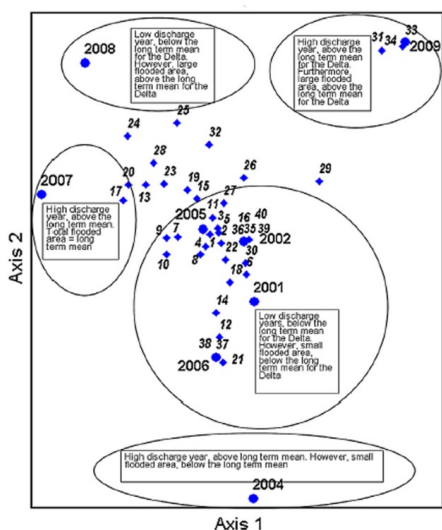


Fig. 7. Results of DCA/DECORANA analysis illustrating inter-annual patterns in fish assemblage shifts in the study area.



**Table 6**

Summary of regression analysis between the two hydrological variables and some indices of selected fish species from the delta based on an annual scale. Significant values (at 95% level) are in bold.

Hydrological Factor	Species	Index	DF	F	p	R <sup>2</sup>	Beta
Area	<i>C. gariepinus</i>	%IRI	7	7.88	<b>0.03</b>	0.57	-0.75
Area	<i>S. intermedius</i>	no/set	7	4.91	0.07	0.45	0.67
Area	<i>M. altisambesi</i>	%IRI	7	4.57	0.08	0.43	0.66
Area	<i>M. altisambesi</i>	g/set	7	3.94	0.09	0.40	0.63
Area	<i>M. altisambesi</i>	no/set	7	6.77	<b>0.04</b>	0.53	0.73
Discharge	<i>S. intermedius</i>	%IRI	7	11.6	<b>0.01</b>	0.66	0.81
Discharge	<i>S. intermedius</i>	g/set	7	39.37	<b>0.00</b>	0.87	0.93
Discharge	<i>S. intermedius</i>	no/set	7	17.61	<b>0.01</b>	0.75	0.86
Discharge	<i>C. ngamensis</i>	g/set	7	4.52	0.08	0.43	0.66
Discharge	<i>H. vittatus</i>	no/set	7	7.50	<b>0.03</b>	0.56	0.75
Discharge	<i>M. altisambesi</i>	g/set	7	4.82	0.07	0.45	0.67

**Table 7**

Summary of assemblage stability values (CV) observed during the study period in the delta of the top four species in the assemblage. Dominant species column refers to the most dominant species in the assemblage based on %IRI with values shown in [].

Year	CV	Description	Dominant species
2001	78	Fluctuating	<i>C. gariepinus</i> [32]
2002	77	Fluctuating	<i>C. gariepinus</i> [31]
2004	87	Fluctuating	<i>S. intermedius</i> [40]
2005	73	Moderately fluctuating	<i>S. intermedius</i> [37]
2006	90	Fluctuating	<i>C. gariepinus</i> [30]
2007	101	Fluctuating	<i>S. intermedius</i> [35]
2008	73	Moderately fluctuating	<i>S. intermedius</i> [33]
2009	70	Moderately fluctuating	<i>S. intermedius</i> [43]

vegetation is submerged and nutrients leaching from decomposing organic matter (dung, terrestrial grass, shrubs and trees), and directly from inflowing water, result in increased plankton production (McLachlan, 1970; Kolding, 1993), which will cascade into fish production. Similar to Chapman and Chapman's (2003) observations, this study also shows that some fish species have discrete breeding seasons that correspond to seasonal flooding (e.g. *P. okavangensis*); other species are multiple spawners that spawn at the onset of the floods until peak flooding (e.g. *M. altisambesi*); while other species spawn throughout the year, with strong seasonal peaks (e.g. *O. andersonii*, a mouth-brooder). Mouth-brooders enhance survivorship as the fry is protected from predation and ventilated to supply sufficient oxygen, which allows them to spawn throughout the year (Corrie et al., 2008). Earlier studies from elsewhere have aggregated fish spawning behavior into a single event driven by either flooding (Duque et al., 1998), oxygen (Chapman and Frank, 2000), temperature (Humphries et al., 1999), or inundated area (Halls et al., 1999). But there are also species that spawn during the low flow period (and high temperatures) like *S. macrocephalus*, *Synodontis thamalakanensis* and *Synodontis vanderwaali* (Table 5). We can conclude that, for the delta, different species spawn at different times and different time spans, cued by different factors which all are likely driven by the hydrological regime. Possibly, these diverse spawning patterns as caused by niche differentiation that reduces inter-specific competition.

According to Kramer (1978), diversity in spawning patterns of tropical freshwater fish can be explained by five hypotheses; spawning is controlled by (i) adult and or

juvenile food availability, (ii) inter-specific competition for food among juveniles, (iii) competition for spawning sites, (iv) a mechanism for reproductive isolation, and (v) is unrelated to local conditions but is a reflection of phylogenetic specialization under particular conditions. While we did not specifically test these hypotheses, our study revealed diverse reproductive strategies that appear consistent with Kramer's hypotheses. As rising water levels successively connects the habitats from channels, through lagoons and oxbows to the floodplains, we can tentatively suggest three kinds of reproductive strategies that describe fish spawning in the delta; (I) channel + lagoon spawners whose spawning season peaks between January and March; (II) floodplain spawners whose spawning season peaks between June and October; and (III) channel + lagoon and floodplain spawners, whose spawning season peaks between (I) and (II) above. Generally, Silurids and Mochokids were strategy (I) species, Tilapia spp. were strategy (II) species, while *Hepsetus cuvieri* was a strategy (III) species.

#### 4.1. Annual dynamics

*S. intermedius* and *C. gariepinus* dominated the delta's fish assemblage between 2001 and 2009. *S. intermedius* is a highly fecund, total spawner (Welcomme, 1985) while *C. gariepinus* is a multiple spawning, fast growing species (van der Waal, 1985). Multiple spawning requires higher annual reproductive effort than single spawning events (Burt et al., 1988), and enhances reproductive success (Cambray and Bruton, 1985). Lowe-McConnell (1987) observed that poor flood years normally resulted in

recruitment failure of total spawners. This suggests that multiple spawning fish (such as *C. gariepinus*) are better competitors during poor flood years than total spawners (such as *S. intermedius*). Agostinho et al. (2000) observed that piscivorous fish species dominate floodplain assemblages during low/poor flood years, which suggest higher survival rates for predators when the fish assemblage is concentrated in the main channels. We argue that since *C. gariepinus* is a large sized predator that sometimes preys on the smaller *S. intermedius* (Winemiller and Winemiller, 1996; Mosepele et al., 2012), its relative survival increases significantly during low/poor flood years. Moreover, *C. gariepinus* has vestigial breathing apparatus which allows it to tolerate adverse environmental conditions (van der Waal, 1998). *S. intermedius* is an opportunistic species with small egg size and high fecundity that takes advantage of optimum conditions (Montcho et al., 2011). In conclusion, we observed that *C. gariepinus* dominated the fish assemblage during low flood year years, while *S. intermedius* dominated the fish assemblage during high flood years. This is in agreement to van der Waal's (1998) observations that *C. gariepinus* usually dominate fish communities at low water levels, while high flood years appears more dominated by *S. intermedius*.

High flood years are normally associated with fast fish growth rates (Dudley, 1974) where fish populations are normally comprised of survivors of the previous year and young-of-year fish (de Graaf, 2003). Therefore, high flood years normally result in a "boom" in fish production, followed by a "bust" during years of low floods (Arthington and Balcombe, 2011; Rayner et al., 2015). We see *S. intermedius* as a typical representative of this phenomenon, being highly fecund (Merron and Mann, 1995; Table 1) and fast growing (Mosepele and Nengu, 2003). The high flood years (2004, 2007–2009) therefore created optimum conditions for "booms" in *S. intermedius* populations, while low flood years (2001, 2002) resulted in a "bust". The residual effect of the high flood years was observed in 2005 where *S. intermedius* still dominated the fish assemblage, though this was a low flood year. This observation is consistent with Welcomme (1985) who highlighted the variable effect of flooding dynamics on fish growth and yield in the Senegal, Niger and Logone rivers.

## 5. Conclusion

Our study has shown that the fish dynamics in the Okavango Delta is strongly influenced by the hydrological regime, which is in accordance with Junk et al.'s (1989) flood pulse concept. However, different fish species in the delta responded differently to variations in discharge, flooded area and water chemistry. Seasonal dynamics appeared more pronounced than inter-annual fluctuations, but overall higher flooding resulted in higher fish production.

One major conclusion from this study is that any future hydrological developments, such as abstraction or regulation in the delta should take into account the effects on the fish assemblages. Consistent low flow regimes resulting from flow releases from upstream developments (e.g. dams in Angola and Namibia) will result in lower fish

production and a fish assemblage dominated by large resilient species such *C. gariepinus*. Conversely, high flood regimes above average will result in higher fish production and a fish assemblage dominated by smaller opportunistic species such as *S. intermedius*. Similar changes will be observed if the flooding regime is altered by future climate change scenarios with either higher or lower precipitation and ensuing flood levels.

## Conflict of interest

None declared.

## Ethical statement

Authors state that the research was conducted according to ethical standards.

## Acknowledgements

This study was funded by the University of Botswana and the Ministry of Environment, Natural Resources Conservation and Tourism. We thank all the field staff of the Okavango Research Institute and the Fisheries Division. We also thank Mrs A. Makati and Mr M. Dhlwayo for their assistance in map production.

## References

- Agostinho, A.A., Thomaz, S.M., Minte-Vera, C.V., Winemiller, K.O., 2000. Biodiversity in the high Paraná River floodplain. In: Gopal, B., Junk, W.J., Davis, J.A. (Eds.), Biodiversity in Wetlands: Assessment, Function and Conservation, vol. 1. Backhuys Publishers, The Netherlands, pp. 89–118.
- Arrington, D.A., Winemiller, K.O., Layman, C.A., 2005. Community assembly at the patch scale in a species rich tropical river. *Oecologia* 144, 157–167.
- Arthington, A.H., Balcombe, S.R., 2011. Extreme flow variability and the 'boom and bust' ecology of fish in arid-zone floodplain rivers: a case history with implications for environmental flows, conservation and management. *Ecohydrology* 4, 708–720.
- Bayley, P.B., 1995. Understanding large river: floodplain systems. *Bioscience* 45 (3), 153–158.
- Burt, A., Kramer, D.L., Nakatsuru, K., Spry, C., 1988. The tempo of reproduction in *Hyphessobrycon pulchripinnis* (Characidae), with a discussion on the biology of 'multiple spawning' in fishes. *Environ. Biol. Fishes* 22 (1), 15–27.
- Cambray, J.A., Bruton, M.N., 1985. Age and growth of a colonizing minnow, *Barbus anoplus*, in a man-made lake in South Africa. *Environ. Biol. Fishes* 12 (2), 131–141.
- Cantu, N.E.V., Winemiller, K.O., 1997. Structure and habitat associations of Devils River fish assemblages. *Southwest Nat.* 42 (3), 265–278.
- Chapman, L.J., Chapman, C.A., 2003. Fishes of the African rain forests: emerging and potential threats to a little known fauna. In: Crisman, T.L., Chapman, L.J., Chapman, C.A., Kaufman, L.S. (Eds.), Conservation, Ecology and Management of African Fresh Waters. University Press of Florida, USA, pp. 176–209.
- Chapman, L.J., Kaufman, L., Chapman, C.A., 1994. Why swim upside down? A comparative study of two Mohokid catfishes. *Copeia* 1, 130–135.
- Chapman, L.J., Frank, C.E., 2000. Breeding seasonality in the African cyprinid *Barbus neumayeri*. *Afr. J. Trop. Hydrobiol. Fish.* 9, 36–48.
- Clarke, K.R., Gorley, R.N., 2001. PRIMER v5 (& v6): User Manual/tutorial. PRIMER-E, Plymouth, United Kingdom.
- Corrie, L.W., Chapman, L.J., Reardon, E.E., 2008. Brood protection at a cost: mouth brooding under hypoxia in an African cichlid. *Environ. Biol. Fishes* 82, 41–49.
- de Graaf, G., 2003. The flood pulse and growth of floodplain fish in Bangladesh. *Fish. Manage. Ecol.* 10, 241–247.



- Dudley, R.G., 1974. Growth of Tilapia of the Kafue Floodplain, Zambia: predicted effects of the Kafue Gorge Dam. *Trans. Am. Fish. Soc.* 2, 281–291.
- Duque, A.B., Taphorn, D.C., Winemiller, K.O., 1998. Ecology of the coporo, *Prochilodus mariae* (Characiformes: Prochilodontidae), and status of annual migrations in western Venezuela. *Environ. Biol. Fishes* 53, 33–46.
- Freeman, M.C., Crawford, M.K., Barrett, J.C., Facey, D.E., Flood, M.G., Hill, J., Stouder, D.J., Grossman, G.D., 1988. Fish assemblage stability in a southern Appalachian stream. *Can. J. Fish. Aquat. Sci.* 45, 1949–1958.
- Gondwe, M., Masamba, W.R.L., 2013. Spatial and temporal dynamics of diffusive methane emissions in the Okavango Delta, Northern Botswana, Africa. *Wetl. Ecol. Manage.*, <http://dx.doi.org/10.1007/s11273-013-9323-5>.
- Grossman, G.D., Dowd, J.F., Crawford, M., 1990. Assemblage stability in stream fishes: a review. *Environ. Manage.* 14 (5), 661–671.
- Halls, A.S., Hoggarth, D.D., Debnath, K., 1999. Impacts of hydraulic engineering on the dynamics and production potential of floodplain fish populations in Bangladesh. *Fish. Manage. Ecol.* 6, 261–285.
- Hart, R.K., Calver, M.C., Dickman, C.R., 2002. The index of relative importance: an alternative approach to reducing bias in descriptive studies of animal diets. *Wildlife Res.* 29, 415–421.
- Humphries, P., King, A.J., Koehn, J.D., 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environ. Biol. Fishes* 56, 129–151.
- Ibarra, M., Stewart, D.J., 1989. Longitudinal zonation of sandy beach fishes in the Napo River Basin, Eastern Ecuador. *Copeia* 2, 364–381.
- Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* 106, 110–127.
- Kolding, J., 1993. Population dynamics and life-history styles of Nile tilapia, *Oreochromis niloticus*, in Ferguson's Gulf, Lake Turkana, Kenya. *Environ. Biol. Fishes* 37 (1), 25–46.
- Kolding, J., Skalevik, A., 2010. Pasgear II, Version 2.3. University of Bergen, Norway.
- Kramer, D.L., 1978. Reproductive seasonality in the fishes of a tropical stream. *Ecology* 59 (5), 976–985.
- Lowe-McConnell, R.H., 1987. *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, United Kingdom.
- McCarthy, T.S., Ellery, W.N., Bloem, A., 1998. Some observations on the geomorphological impact of hippopotamus (*Hippopotamus amphibius* L.) in the Okavango Delta, Botswana. *Afr. J. Ecol.* 36, 44–56.
- McCune, B., Mefford, M.J., 2006. PC-ORD, Multivariate Analysis of Ecological Data. Version 5.10 MjM Software. Gleneden Beach, Oregon, U.S.A.
- McCune, B., Mefford, M.J., 1999. *Multivariate Analysis of Ecological Data, Version 4.24*. Gleneden Beach, OR, USA.
- McLachlan, A.J., 1970. Some effects of annual fluctuations in water level on the larval chironomid communities of Lake Kariba. *J. Anim. Ecol.* 39, 79–90.
- Merron, G.S., 1991. The ecology and management of the fishes of the Okavango Delta, Botswana, with particular reference to the role of the seasonal floods. (PhD thesis Rhodes University, South Africa).
- Merron, G.S., 1993. Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis* in the Okavango Delta, Botswana. *J. Fish Biol.* 43 (4), 575–584.
- Merron, G.S., Bruton, M.N., 1988. The ecology and management of the fishes of the Okavango delta, Botswana, with special reference to the role of the seasonal floods. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. Investigational Report No. 29 291 p.
- Merron, G.S., Bruton, M.N., 1995. Community ecology and conservation of the fishes of the Okavango Delta, Botswana. *Environ. Biol. Fishes* 43, 109–119.
- Merron, G.S., Mann, B.Q., 1995. The reproductive and feeding biology of *Schilbe intermedium* Ruppell in the Okavango Delta, Botswana. *Hydrobiologia* 308, 121–129.
- Mendelsohn, J.M., VanderPost, C., Ramberg, L., Murray-Hudson, M., Wolski, P., Mosepele, K., 2010. Okavango Delta: Floods of Life. RAISON, Namibia.
- Minns, C.K., 1989. Factors affecting fish species richness in Ontario lakes. *Trans. Am. Fish. Soc.* 118 (5), 533–545.
- Montcho, S.A., Chikou, A., Lalèyè, P.A., Linsemair, K.E., 2011. Population structure and reproductive biology of *Schilbe intermedium* (Teleostei: Schilbeidae) in the Pendjari River, Benin. *Afr. J. Aquat. Sci.* 36(2), 139–145.
- Mosepele, K., 2000. Length based fish stock assessment of the main exploited fish stocks of the Okavango delta, Botswana. (MPhil Thesis) University of Bergen, Norway.
- Mosepele, K., Nengu, S., 2003. Growth, mortality, maturity and length-weight parameters of selected fishes from the Okavango Delta, Botswana. In: Pauly, D., Diouf, B., Samb, B., Vakily, M.J., Palomares, M.L.D. (Eds.), *Fish Biodiversity: Local Studies as Basis for Global Inferences*. Brussels, Belgium, pp. 67–74.
- Mosepele, K., Mosepele, B., Wolski, P., Kolding, J., 2012. Dynamics of the feeding ecology of selected fish species from the Okavango River delta, Botswana. *Acta Ichthyol. Piscat.* 42 (4), 271–289.
- Mosepele, K., Moyle, P.B., Merron, G.S., Purkey, D., Mosepele, B., 2009. Fish, floods and ecosystem engineers: interactions and conservation in the Okavango Delta, Botswana. *Bioscience* 59 (1), 53–64.
- Nikolsky, G.V., 1969. *Theory of Fish Population Dynamics as the Biological Background for Rational Exploitation and Management of Fishery Resources*. Olivier and Boyd, United Kingdom.
- Oberdorff, T., Porcher, J., 1992. Fish assemblage structure in Brittany streams (France). *Aquat. Living Resour.* 5, 215–223.
- Økland, F., Thorstad, E.B., Hay, C.J., Næsje, T.F., Chanda, B., 2005. Patterns of movement and habitat use by tigerfish (*Hydrocynus vittatus*) in the upper Zambezi River (Namibia). *Ecol. Freshw. Fish* 14, 79–86.
- Ramberg, L., Wolski, P., Krahl, M., 2006a. Water balance and infiltration in a seasonal floodplain in the Okavango Delta, Botswana. *Wetlands* 26 (3), 677–690.
- Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., van As, J., VanderPost, C., 2006b. *Fish Biodiversity of the Okavango Delta, Botswana*. *Aquat. Sci.* 68, 310–337.
- Rayner, T.S., Kingsford, R.T., Suthers, I.M., Cruz, D.O., 2015. Regulated recruitment: native and alien fish responses to widespread floodplain inundation in the Macquarie Marshes, arid Australia. *Ecohydrology* 8, 148–159.
- Sethebe, K., 2011. Fish dynamics and water quality in the Okavango Delta, Botswana: The case of Guma lagoon. (MSc Thesis) University of The Free State, South Africa.
- Skelton, P.H., 2001. *A Complete Guide to Freshwater Fishes of Southern Africa*. Struik Publishers, Cape Town.
- Smith, P.A., 1976. An outline of the vegetation of the Okavango drainage system. In: *Proceedings of the Symposium on the Okavango Delta and its future utilisation*, Botswana Society, Gaborone, pp. 93–112.
- ter Braak, C.J.E., 1986. Canonical correspondence analysis: a new eigen-vector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.
- Tockner, K., Malard, F., Ward, J.V., 2000. An extension of the flood pulse concept. *Hydrol. Process.* 14, 2861–2883.
- van der Waal, B.C.W., 1985. Aspects of the biology of larger fish species of Lake Liambezi, Caprivi, South West Africa. *Madoqua* 14 (2), 101–1441.
- van der Waal, B.C.W., 1998. Survival strategies of sharp-toothed catfish *Clarias gariepinus* in desiccating pans in the northern Kruger National Park. *KOEDOE* 41 (2), 131–138.
- Ward, J.V., Tockner, K., 2001. Biodiversity: towards a unifying theme for river ecology. *Freshw. Biol.* 46, 807–819.
- Welcomme, R.L., Brummett, R.W., Denny, P., Hasan, M.R., Kagwa, R.C., Kipkemboi, J., Mattson, N.S., Sugunan, V.V., Vass, K.K., 2006. Water management and wise use of wetlands: enhancing productivity. *Ecol. Stud.* 190, 155–180.
- Welcomme, R.L., 1985. *River Fisheries*. FAO Fisheries Technical Paper No. 262. FAO, Rome.
- Welcomme, R.L., 2007. Conservation of fish and fisheries in large river systems. *Am. Fish. Soc. Sympos.* 49, 587–599.
- Winemiller, K.O., Kelso-Winemiller, L.C., 1994. Comparative ecology of the African pike, *Hepsetus odoe*, and tiger-fish, *Hydrocynus forskahlii*, in the Zambezi River floodplain. *J. Fish Biol.* 45 (2), 211–225.
- Winemiller, K.O., Winemiller, L.C., 1996. Comparative ecology of catfishes of the Upper Zambezi River floodplain. *J. Fish Biol.* 49, 1043–1061.
- Wolski, P., Masaka, T., Raditsebe, L., Murray-Hudson, M., 2005. Aspects of dynamics of flooding in the Okavango delta. *Botswana Notes Rec.* 37, 179–195.
- Wolski, P., Savenije, H.H.G., 2006. Dynamics of floodplain-island ground-water flow in the Okavango Delta, Botswana. *J. Hydrol.* 320, 283–301.
- Wolski, P., Savenije, H.H.G., Hudson, M.M., Gumbrecht, T., 2006. Modelling of the flooding in the Okavango Delta, Botswana, using a hybrid reservoir-GIS model. *J. Hydrol.* 331, 58–72.
- Zeug, S.C., Winemiller, K.O., 2007. Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. *Can. J. Fish. Aquat. Sci.* 64, 1291–1301.

Please cite this article in press as: Mosepele, K., et al., Fish community dynamics in an inland floodplain system of the Okavango Delta, Botswana. *Ecohydrology. Hydrobiol.* (2017), <http://dx.doi.org/10.1016/j.ecohyd.2017.01.005>

## 9. Chapter 9

**Paper VIII:** Linhoss, A.C., R. Muñoz-Carpena, M. Allen, G. Kiker, K. Mosepele. (2012). A flood pulse driven fish population model for the Okavango Delta, Botswana. *Ecological Modelling*, 228: 27 – 38

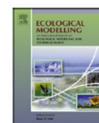
Ecological Modelling 228 (2012) 27–38



Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: [www.elsevier.com/locate/ecolmodel](http://www.elsevier.com/locate/ecolmodel)



### A flood pulse driven fish population model for the Okavango Delta, Botswana

Anna Cathey Linhoss<sup>a</sup>, Rafael Muñoz-Carpena<sup>a,\*</sup>, Micheal S. Allen<sup>b</sup>, Gregory Kiker<sup>a</sup>, Ketlhatlogile Mosepele<sup>c</sup>

<sup>a</sup> Agricultural and Biological Engineering, University of Florida, Frazier Rogers Hall, P.O. Box 110570, Gainesville, FL 32611-0570, USA

<sup>b</sup> Fisheries and Aquatic Sciences, University of Florida, UF P.O. Box 110600, 7922 NW 71st Street, Gainesville, FL 32653, USA

<sup>c</sup> Okavango Research Institute, University of Botswana, Maun, Botswana

#### ARTICLE INFO

##### Article history:

Received 7 November 2011

Received in revised form

23 December 2011

Accepted 24 December 2011

##### Keywords:

Fisheries model

Flood pulse

Okavango

Uncertainty analysis

Sensitivity analysis

Monte Carlo filtering

#### ABSTRACT

The Okavango Delta is a large, remote, and ecologically significant wetland located in Botswana that receives a strong annual flood pulse. Although the hydrology in flood pulsed systems is often theorized to drive fish population dynamics, in the Okavango Delta there are no monitoring or modeling studies that quantify this complex ecological relationship. The objective of this work was to produce and analyze a mechanistic fish population model of the Okavango Delta that is driven by the annual flood pulse in order to corroborate the theory that Delta fish populations are driven by the flood signal. The model tracked age cohorts over time with density dependant recruitment, mortality, and vulnerability components. Global sensitivity analysis identified the parameters that were the most important in determining the model outcome. Monte Carlo filtering truncated prior parameter probability density functions and refined model uncertainty. One of the unique outcomes of this research was the identification of polishing parameters, i.e. model parameters that are essential in obtaining optimal model performance by matching output variability, though they are not important in changing the magnitude of model results. The flood coefficient (a scaling factor that describes how recruitment changes with the magnitude of the flood) was shown to be a polishing parameter, providing quantitative evidence that floods are a driver of fish population dynamics in the Delta. This linkage between the flood pulse and fish population dynamics provides quantitative information that is necessary for making informed decisions regarding the management of hydrologic and ecological resources in the Okavango Delta.

© 2012 Elsevier B.V. All rights reserved.

#### 1. Introduction

The flood pulse concept (Junk et al., 1989) (FPC) is a well known hypothesis that describes an ecological response to flood pulsed hydrology (Fig. 1). In the FPC nutrient availability is linked to the inundation of the floodplain. On an incoming flood, as the water inundates the floodplain, the transition zone where the aquatic environment meets the terrestrial environment has high inputs of nutrients from terrestrial sources such as vegetation and detritus. This leads to high primary productivity in this transition zone. The inputs of nutrients and resulting high primary productivity in the transitional zone iterate with each flood and it is hypothesized that fauna can adapt to take advantage of the increased food availability (Junk et al., 1989). The effect of the FPC is often cited as being a major driver for fish population dynamics in systems that are

regularly inundated (Junk et al., 1989). This theory was originally intended for tropical regions but has been applied to temperate areas as well (Tockner et al., 2000). In general, there are relatively few field studies that quantify this relationship (Bailey et al., 2008; Zeug and Winemiller, 2008) and even fewer modeling attempts to simulate the response (Deangelis et al., 1997; Gaff et al., 2004; King et al., 2003; Merona and Gascuel, 1993).

This study tested the FPC in the Okavango Delta, a large inland delta located in an arid climate that experiences an annual flood pulse from its upstream watershed (Fig. 2). No quantitative studies have been conducted to specifically show how fish respond to the flood pulse in the Okavango Delta. However, there have been studies in the Okavango that show that the annual flood pulse produces a response in other ecological aspects (Hoberg et al., 2002; Merron, 1991). Hoberg et al. (2002) provided a food web conceptual model for ecological responses to the annual flood pulse in the Delta. They measured a 'first flush' effect at the onset of the flood which results in a release of nutrients into the water column. During the rising flood there was a burst in nutrients, primary production, and phytoplankton. Concentrations of nitrogen rose from 1.5 to 3.5 mg L<sup>-1</sup> and phosphorus rose from 125 to 450 µg L<sup>-1</sup>. Primary production reached its peak at 300 µg C L<sup>-1</sup> d<sup>-1</sup> and maximum

Abbreviations: MC, Monte Carlo; GSA/UA, global sensitivity and uncertainty analysis; FPC, flood pulse concept; ceff, coefficient of efficiency; CPUE, catch per unit effort; ORI, Okavango Research Institute; DW, dry weight.

\* Corresponding author. Tel.: +1 352 392 1864x287; fax: +1 352 392 4092.

E-mail address: [carpena@ufl.edu](mailto:carpena@ufl.edu) (R. Muñoz-Carpena).



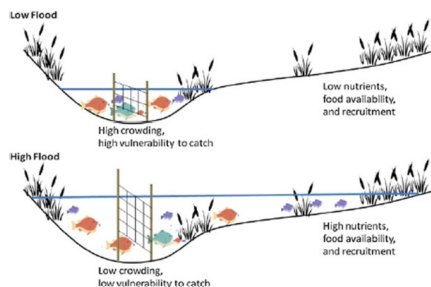


Fig. 1. A diagram of the flood pulse concept, the conceptual model driving this research.

chlorophyll *a* values were  $24 \mu\text{g}$  chlorophyll *a*  $\text{L}^{-1}$  (Hoberg et al., 2002). The authors went on to state that resting zooplankton eggs hatched when they were submerged by the floodwater and fed on the abundant phytoplankton and other food sources provided by the burst in primary production. Peak concentrations of zooplankton went from  $0.1$  to  $10 \text{ mg dry weight per liter (DWL}^{-1}\text{)}$  during the rise of the flood and reached up to  $90 \text{ mg DWL}^{-1}$  at the extreme near-shore edges. In the same study a qualitative analysis of the fishes' response to the flood was also conducted (Hoberg et al., 2002). The tilapiine species *Oreochromis andersonii*,

*Tilapia rendalli*, and *T. sparrmanii* were observed following the rising flood into the study area. Juveniles of the same species were also seen with an increasing frequency just after the peak of the flood. Gut analysis of the fishes showed that smaller fish fed on more zooplankton indicating the importance of the 'first flush' effect for the juveniles. At the end of the flood season very few fry were observed with the conclusion that they migrated out of the area before the connection with the main river system was lost.

In another study, Merron (1991) conceptually related spawning period to the flood pulse in the Okavango Delta. He proposed that the higher the magnitude of the annual flood, the longer the water is retained on the floodplain, leading to a longer spawning period and greater overall production of fish. Additionally, Mosepele et al. (2009) proposed that survivability for smaller fishes is increased in dense floodplain vegetation types because the vegetation provides protection from predators.

Research investigating the influence of the flood pulse on fish populations throughout the world has been conducted with a variety of results (Deangelis et al., 1997; Gaff et al., 2004; King et al., 2003; Merona and Gascuel, 1993). Much of this research showed that these relationships are complex and difficult to quantify. King et al. (2003) investigated floodplain usage by fish in the Murray Darling Basin, Australia where there is annual inundation via snow melt and flood pulse has been theorized to be a major driver for fish populations. Through sampling, these authors noted that floodplain utilization by fish was not as pronounced as expected. They proposed a more complex system and suggested a model based on optimum conditions for floodplain utilization including: temperature, flood pulse predictability, the rate of change in the hydrograph, and inundation duration and area. However, the flood pulse in the Murray Darling Basin may be less predictable than in the Okavango Delta implying that the fish in the Murray Darling may be more opportunistic and less consistent in their behavior.

Merona and Gascuel (1993) showed a statistical relationship between commercial fish catch and the annual flood in the Amazonian floodplain. Among their results they found three relationships of interest to this study. (1) There was a positive correlation between catch and the flood peak three years prior, which they speculated to be associated with recruitment. (2) There was an association between catch and the water level during its rise 2 years prior that was possibly associated with competition. (3) There was an association between catch and severe low water stage 2 years prior that likely due to increased mortality. They were able to produce a statistical model with three variables that explained more than 83% of the variability in the annual fish abundance. Similar to the Okavango, this system experiences a regular and predictable flood pulse.

Deangelis et al. (1997) constructed a mechanistic model, Across Trophic Level System Simulation Landscape Fish model (ALFISH), that spatially predicts fish abundance based on the flood pulse in the Everglades. This fish model was built on top of a spatially explicit hydrologic model that simulates the annual flood pulse. The model simulates seasonal dynamics in production due to the flooding as well as trophic interactions. As the flood rises, modeled fish move into the floodplain in response to increased food availability. Then, as the flood recedes, modeled fish move to find refugia and mortality increases as a result of crowding and predation. Four types of mortality were simulated: background mortality, density dependent mortality, predation by the large fish, and failure to find refugia. Gaff et al. (2004) critiqued ALFISH and concluded that inundation area is not the only driver for fish populations and that other parameters may be just as important. They stated that the best model fit that ALFISH was able to achieve is a coefficient of determination ( $R^2$ ) of 0.88 for water depth and 0.35 for fish density with an inverse relationship between water depth and fish density. However, an  $R^2$  of 0.35 between fish density and water depth

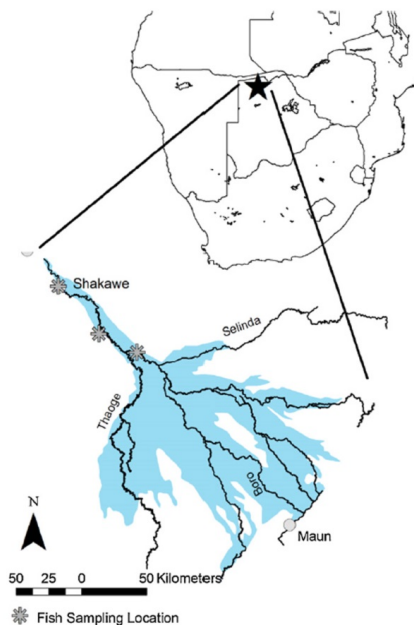


Fig. 2. Site location. The Okavango Delta, with fish sampling sites marked.



reflected empirical data showing that the hydrology only accounts for 20–40% of the variability in the sampled fish population density.

Environmental Flows are criteria that describe the degree to which a natural hydrologic regime must be maintained in order to preserve valuable features of an ecosystem (King et al., 1999; Tharme and King, 1998; Tharme, 2003). Environmental Flows are being developed for the Okavango Delta and a special report was published specifically addressing flows for fish communities (Mosepele, 2009). A major recommendation in the report was for the development of a quantitative relationship between the flood pulse and fish population dynamics in the Delta so that managers can understand feedbacks between hydrology and fish populations. Fish population models are often used to track populations and predict responses to management decisions in other locations (Rogers et al., 2010; Walters and Martell, 2004; Walters et al., 2008). A fish population model has yet to be developed for the Okavango Delta.

Thus, there is a stated management desire for a model that links the flood pulse to fish population dynamics (Mosepele, 2009), quantitative data shows that various aspects of the ecology of the Delta other than fish are driven by the flood pulse (Hoberg et al., 2002; Merron, 1991), and there are qualitative indications that fish population dynamics are affected by the flood pulse (Merron, 1991; Mosepele et al., 2009). Additionally, our summary of the literature demonstrated that there are only a few studies that investigated fish recruitment responses to flood pulsed wetlands and even fewer studies that use models to simulate this relationship. These studies include field research (Bailly et al., 2008; Zeug and Winemiller, 2008; King et al., 2003), statistical models (Merona and Gascuel, 1993), and food web based mechanistic models (Deangelis et al., 1997; Gaff et al., 2004). A benefit of mechanistic models over statistical models is that they can be used to investigate functional relationships. However, over-parameterization, especially in data poor areas, is an important consideration in constructing mechanistic models. In the case of the Okavango, there was not sufficient data to simulate a food web based fish recruitment response to the flood pulse as was done with Deangelis et al. (1997). The objective of this work was to produce a novel simplified mechanistic fish population model of the Okavango Delta that is driven by the annual flood pulse. In addition to this we conducted a global sensitivity and uncertainty analysis to identify the most important parts of the system, simplify the model, and quantify the reliability of the model. We then applied Monte Carlo (MC) filtering to truncate prior parameter probability density functions (PDF), a tool that was especially useful in this data poor area where setting these PDFs can be problematic. The model simulates fish population response to the size of the maximum annual flood. Because of their commercial importance, tilapia and in particular *O. andersonii*, *T. rendalli*, and *Oreochromis macrochir* were used as indicator species.

We used state-of-the-art global sensitivity and uncertainty analysis (GSA/UA) in the development and assessment of the model. GSA was used to identify unimportant parameters that could be set to constants without drastically affecting the outputs, thus simplifying the model (Chu-Agor et al., 2011; Fox et al., 2010; Jawitz et al., 2008; Muñoz-Carpena et al., 2007, 2010). One of the largest critiques of GSA/UA is the rather arbitrary methods for setting the prior probability densities (PDFs). Therefore, secondly, we used Monte Carlo (MC) filtering (Saltelli et al., 2008) to objectively redefine the prior PDFs within their predefined defined physical bounds based on realistic model results and thereby refined model uncertainty.

The model was inverse calibrated to objectively investigate the range of best fit model parameter sets. Traditionally, the goal of inverse optimization techniques is to find the optimal set of parameters for a given model to match some measured data (Mertens et al., 2006). Beven and Binley (1992) and Beven (1993) commented on the limitations of the concept of an optimal

parameter set in complex environmental systems. Beven and Freer (2001) coined the term 'equifinality' to refer to the fact that there may be "many different parameter sets within a chosen model structure that may be behavioral or acceptable in reproducing the observed behavior of that system." As a result, there may be no way to distinguish between these equally acceptable parameter sets. Because of this issue of equifinality in complex ecological models we did not seek an optimal parameter set, but instead looked for evidence of the flood as a driver for fish population dynamics despite signs of equifinality.

## 2. Methods

### 2.1. Fish data

Daily commercial catch data were available from January 1996 to December 2005. All available data were used in this analysis. Fish were caught in gillnets and the daily catch per unit effort (CPUE) was recorded. The CPUE was calculated as the number of fish caught per gillnet per day. Because a relatively standard gear was used throughout the time series, we felt that CPUE could be used as an indicator of fish density using the assumption that a constant fraction of the stock density was captured per gillnet day ( $q$ ) (Fielder, 1992; Hansson and Rudstam, 1995; Hodgkiss and Man, 1977; Borgstrom, 1992). In the model CPUE was calculated only for the lowest flows to protect against changes in  $q$  across seasons.

We produced an annual time step model. The fish data that were available only include fish counts. Since age, weight, and length data, which are necessary for simulating monthly spawning dynamics, were not collected an annual model was deemed to be the most appropriate. This annual time step is also appropriate because we did not seek to simulate seasonal dynamics. Instead we sought to understand if fish populations are influenced by the size of the annual flood. We standardized fish abundance in the model on a per area basis for comparison to the fisheries data from the Okavango Delta. And so, for the purposes of this model, the objective function was the coefficient of efficiency (Nash and Sutcliffe, 1970) between the modeled maximum annual density and the measured maximum annual CPUE.

The coefficient of efficiency (ceff) is a dimensionless index frequently used to assess the goodness of fit of hydrologic models (Eq. (1)) (Nash and Sutcliffe, 1970) where  $O_t$  is measured or observed data,  $P_t$  is modeled or predicted data, and  $\bar{O}$  is the mean of the observed data. It represents one minus the mean square error divided by the variance in the observed data. The ceff provides different information from the coefficient of determination ( $R^2$ ). An  $R^2$  specifies the percent of the variance in the observed data that the modeled data represents. The ceff specifies one minus the percent of the variance in the observed data that is represented in the mean square error (Ritter et al., submitted for publication).

$$E = 1.0 - \frac{\sum_{t=1}^N (O_t - P_t)^2}{\sum_{t=1}^N (O_t - \bar{O})^2} \quad (1)$$

The fish that were caught in commercial catches were not recorded to the level of species. Instead, tilapias (of the family Cichlidae) were lumped as a family. According to Mosepele et al. (2003), Cichlidae is the principal family of fish in both subsistence and commercial gillnet fisheries. The three species with the highest indices of relative importance for the commercial gillnet fishery are all tilapia and include in order of importance: (1) *O. andersonii*, (2) *T. rendalli*, and (3) *O. macrochir* (Mosepele et al., 2003). For the purposes of this work, these three fish species were used as a representative species to base parameters such as maximum age and growth functions, with particular importance placed on *O. andersonii*.

2.2. Model structure

We developed an age-structured, fish population model driven by the flood pulse in the Okavango Delta. The model structure used the Beverton and Holt (1957) stock-recruitment relationship (Eq. (2)) to estimate recruitment, where  $R_t$  [Fish  $\text{yr}^{-1}$ ] is the number of recruits per year,  $\alpha$  and  $\beta$  are Beverton and Holt parameters (1957),  $N_{t,n}$  [Fish] is the number of fish per age class, and  $e$  is the number of eggs produced per year per fish.  $\alpha/\beta$  describes the maximum recruitment at a high stock and  $\alpha$  describes the maximum recruitment/stock at a low stock size.

$$R_t = \frac{\alpha \sum_{n=0}^{n_{\max}} N_{t,n} e}{1 + \beta \sum_{n=0}^{n_{\max}} N_{t,n}} \quad (2)$$

Three constants were required to parameterize the Beverton and Holt equation: one point along the Beverton and Holt curve where recruitment is constant ( $N_{t,n}$ ), survival from natural mortality ( $S$ ) [ $\text{yr}^{-1}$ ], and the Goodyear compensation ratio ( $CR$ ) (Goodyear, 1977). The steady state condition of the Beverton and Holt equation is given as Eq. (3):

$$\sum_{n=0}^{n_{\max}} (N_{t,n}) = \sum_{n=0}^{n_{\max}} (N_{t,n} S + R_t) \quad (3)$$

Thus,  $R_t$  (constant recruitment, used for calibration of the number of fish in the population) can easily be found by Eq. (4):

$$R_t = (1 - S) \sum_{n=\text{maturity}}^{n_{\max}} (N_{t,n}) \quad (4)$$

The  $CR$  represents the maximum compensatory increase in juvenile survival as the stock size is decreased from unfished to very low levels. Parameters  $\alpha$  and  $\beta$  can be derived from  $CR$  from the steady state equation (Eq. 5) at low spawner abundance. The juvenile survival ratio ( $R_t / \sum_{n=0}^{n_{\max}} (N_{t-1,n})$ ) is represented by  $\alpha$  (Walters and Martell, 2004) (Eq. (5)) such that:

$$\alpha_t = (CR) \frac{R_t}{\sum_{n=0}^{n_{\max}} (N_{t-1,n})} \quad (5)$$

and  $\beta$  is the density dependent parameter which can be derived from (Walters and Martell, 2004) (Eq. (6)):

$$\beta_t = \frac{CR - 1}{\sum_{n=0}^{n_{\max}} (N_{t-1,n})} \quad (6)$$

The fish population response to the flood was simulated through recruitment, as floods would be expected to increase both the availability of refuge habitat and food resources (Junk et al., 1989; Bayley, 1991; Tockner et al., 2000; Agostinho et al., 2004; Zeug and Winemiller, 2008). In order to relate recruitment to the flood, a modification was made to the Beverton and Holt density dependent recruitment relationship which assumed that the number of recruits was positively proportional to the annual maximum inflow (Eq. (7)). In this equation,  $F_a$  is the maximum inflow in a given year [ $\text{M m}^3 \text{ yr}^{-1}$ ],  $F$  is the average of the annual maximum inflows [ $\text{M m}^3 \text{ yr}^{-1}$ ], and  $c$  is a scaling flood coefficient. This alteration did not change the actual fish population, but did change the asymptote and the steepness of the stock recruit equation (maximum recruitment possible). The result was a change in the carrying capacity of recruits and rate of recovery between high and low flood years (Fig. 3).

$$\sum_{n=0}^{n_{\max}} (N_{t-1,n}) = \sum_{n=0}^{n_{\max}} (N_{t-1,n}) + (F_a - F)c \quad (7)$$

In each time step, after recruitment is calculated, mortality was calculated. Each age experiences mortality according to:

$$N_{t,n} = N_{t,n-1} \exp^{-Z(\Delta t)} \quad (8)$$

where  $Z$  represents instantaneous total mortality [ $\text{yr}^{-1}$ ] (Beverton and Holt, 1957). The estimate of the total number of fishers in the

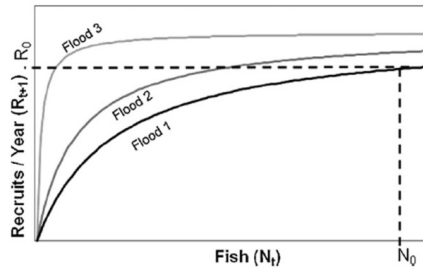


Fig. 3. A demonstration of the response in recruitment as a result of the change in annual maximum flood. The rate of recovery and the carrying capacity increases during smaller floods. Flood<sub>1</sub> > Flood<sub>2</sub> > Flood<sub>3</sub>.

Okavango Delta in the 1990s was approximately 5000 with 300 of those being gillnet fishers, and about 40 total full-time commercial fishers (Kgathi et al., 2005; Mosepele, 2001). Because of the small scale of commercial and subsistence fishing in the Okavango Delta and the low efficiency of the gear, fishing pressure in the Delta is fairly light (Mosepele and Kolding, 2003; Kgathi et al., 2005). Thus, for the purposes of this research mortality from fishing was considered negligible. The exponential function results in an exponential decrease in abundance with age.

Various studies point to an allometric relationship between body weight and mortality (Lorenzen, 1996; MCGurk, 1986; Peterson and Wroblewski, 1984). de Graaf et al. (2005) showed Lorenzen's (1996) allometric weight/mortality relationship can also be related to body length through the von Bertalanffy (1957) length/weight relationship where  $M_u$  is the mortality at unit length,  $L$  is body length in cm, and  $a$  and  $b$  are coefficients (Eq. (9)).

$$M = M_u \alpha^{-0.3} L^{0.3b} \quad (9)$$

Length at a given age was calculated according to the von Bertalanffy equation, where  $L_n$  is the length at age  $n$  and  $k$  is the growth coefficient ( $\text{yr}^{-1}$ ), and  $L_\infty$  is the asymptotic length (Eq. (10)).

$$L_n = L_\infty (1 - \exp^{-k(n-n_0)}) \quad (10)$$

Not all fish are equally vulnerable to catch because of the size selective fishing gear. The vulnerability to catch of each age class was computed using a dome shaped double logistic function (Allen et al., 2009) (Fig. 4):

$$V_n = \frac{1}{1 + \exp(-TL - L_{low})/SD_{low}} - \frac{1}{1 + \exp(-TL - L_{high})/SD_{high}} \quad (11)$$

where  $V_n$  is the vulnerability (unitless) at age  $n$ ,  $TL$  is the average length (cm) at age  $n$ ,  $L_{low}$  is the lower length (cm) at 50% vulnerability,  $SD_{low}$  is the standard deviation of the distribution for  $L_{low}$ ,  $L_{high}$  is the upper length (cm) at 50% vulnerability, and  $SD_{high}$  is the standard deviation of the distribution for  $L_{high}$ .

The measured maximum annual CPUE generally occurred at the annual low flood when the fish were most concentrated in a smaller area. In order to get a similar measure of density, the vulnerable fish were divided by the minimum area of inundation in the Panhandle, where the fish were caught. This measure was considered the modeled annual maximum CPUE. For each year, the modeled annual maximum CPUE was compared to the measured annual maximum CPUE using the  $ceff$  (Nash and Sutcliffe, 1970) which was the objective function of the model.

In order to compute CPUE from the modeled data, the fish abundance had to be expressed as density (fish  $\text{km}^{-2}$ ) and the area of inundation must be known. This was done using in the Okavango



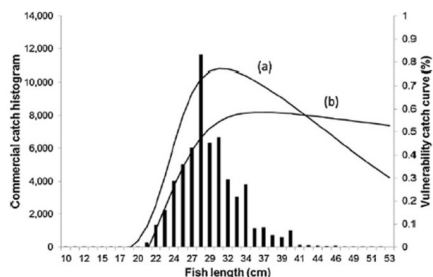


Fig. 4. An example of the dome shaped double logistic curve (Allen et al., 2009) for catch vulnerability.  $L_{low} = 2$ ,  $SD_{low} = 2$ ,  $L_{high} = 45$ ,  $SD_{high} = 10$ . Histogram data from Mosepele (2009). (a) Shows the dome shaped curve and (b) shows the curve approaching a logistic shape. Both shapes are possible within the bounds of the defined PDFs.

Research Institute (ORI) hydrologic model of the Delta (Wolski et al., 2006). The ORI model is a linked reservoir model that simulates flooding extents in the Delta. One of the areas in the model explicitly represents the Panhandle, where the fish data were collected (Fig. 2). The Panhandle is not the area that was the focus for model calibration. This area is also more confined and permanently inundated than the lower Delta which experiences greater dynamics in inundation area. Because of these reasons, in each year the total modeled vulnerable fish population was divided by the average across years of the minimum flooding extents simulated in the Panhandle. This produced an overall better model fit than dividing by the annual minimum flooding extents.

### 2.3. Model optimization

Any parameter into the model has an amount of uncertainty associated with it. To describe that uncertainty PDFs were developed for each parameter based on literature values and data when available. The model was run iteratively sampling parameters from the PDFs using the extended Fourier amplitude sensitivity test (FAST) sampling routine (Cukier et al., 1978; Koda et al., 1979; Saltelli et al., 1999) with SimLab software (SimLab, 2011). This sampling routine is an unbiased method that samples throughout the parametric space and is able to highlight the variety of parameter sets that result in good fit model simulations. Sensitive parameters were identified and uncertainty was measured. Monte Carlo (MC) filtering (Saltelli et al., 2008) was used to filter out unacceptable model simulations as defined by the ceff and prior distributions were refined based on the parameters that generated the acceptable simulations. Insensitive parameters were set to constants. The GSA was rerun with the new posterior distributions and varying only the important parameters.

#### 2.3.1. Global sensitivity and uncertainty analysis

Global sensitivity and uncertainty analysis (GSA/UA) was used to apportion the variation of model outputs onto the model parameters based on input PDFs. The extended FAST GSA/UA method (Cukier et al., 1978; Koda et al., 1979) uses Fourier analysis to decompose the variance of a set of model outputs into first order variances for each parameter. For this method, the model is executed  $C \approx Nk$  times, where  $k$  is the number of parameters and  $N$  is a number that ranges between 100s and 1000s (Saltelli et al., 1999). The extended FAST technique (Saltelli et al., 1999) allows for the additional computation of higher levels of variance which describe the interactions between the parameters (Eq. (12)). Here,

Table 1  
List of parameters and initial distributions.

Abbreviation	Parameter	Distribution
1 $Z$	Natural Mortality	U(0.67, 1.39)
2 $k$	Growth coefficient	U(0.25, 1.0)
3 $M_{10}$	Mortality per unit weight	U(3, 8)
4 $a$	Weight/length parameter	U(0.004, 0.026)
5 $b$	Weight/length parameter	U(2.911, 3.424)
6 $L_{\infty}$	Asymptotic length	U(40, 53)
7 $CR$	Compensation ratio	U(3, 30)
8 $L_{low}$	Lower length at 50% vulnerability	U(1, 3)
9 $SD_{low}$	Standard deviation of $L_{low}$	U(23, 25)
10 $L_{high}$	Upper length at 50% vulnerability	U(28.60)
11 $SD_{high}$	Standard deviation of $L_{high}$	U(10, 30)
12 $Maturity$	Maturity	N(4.25, 0.5)
13 $e$	Eggs $yr^{-1}$	U(350, 1600)
14 $c$	Flood coefficient	U(5, 25)

$V(Y)$  describes the total variance of a single parameter including first and higher levels of variance.

$$V(Y) = \sum_i V_i + \sum_{i/j} V_{ij} + \sum_{i/j/l} V_{ijl} + \dots + V_{123\dots k} \quad (12)$$

FAST also defines  $S_i$  as an index of global sensitivity.  $S_i$  is the ratio of the variance that is ascribed to a single parameter divided by the total model variance. In a model where there are no interactions, the sum of the  $S_i$ 's across all of the parameters is equal to one. In models where there are interactions this sum is greater than one. Note that parameters used in this method must be independent and are assumed so for this work.

#### 2.3.2. Monte Carlo filtering

Sampling throughout the parametric space, as the FAST method does, produced many unrealistic and nonsensical outputs. Using the results of the FAST GSA/UA, MC filtering (Saltelli et al., 2008) was used to filter out those unrealistic outputs or non-behavioral results and redefine the prior parameter distributions based on the realistic outputs. MC filtering divided the outputs into 'behavioral' ( $B$ ) and 'non-behavioral' ( $\bar{B}$ ) based on a threshold that is defined by the user. The  $B$  or  $\bar{B}$  status was mapped back to the parameters and two subsets of each model parameter,  $X_i$ , were defined as  $X_i|B$  or  $X_i|\bar{B}$  based on their behavioral/non-behavioral status. The behavioral subset contained  $n$  elements and the non-behavioral subset contained  $\bar{n}$  elements such that  $n + \bar{n} = N$ , where  $N$  is the number of model simulations. The PDFs of  $f(X_i|B)$  and  $f(X_i|\bar{B})$  were then assigned. The two-sided Smirnov test was performed to check the significance of the difference between the two distributions  $f(X_i|B)$  and  $f(X_i|\bar{B})$ . In the Smirnov test the test statistic  $d_{n,\bar{n}}$  is defined by Eq. (13):

$$d_{n,\bar{n}}(X_i) = \sup ||F_n(X_i|B) - F_{\bar{n}}(X_i|\bar{B})|| \quad (13)$$

The null hypothesis for this test is  $f(X_i|B) = f(X_i|\bar{B})$ . That is, the null hypothesis tests if the distribution of the parameters that created the behavioral outputs was the same as the distribution of the parameters that created non-behavioral outputs. The null hypothesis was rejected at a significance level,  $\alpha$ . A small  $\alpha$  for a particular parameter indicated a high importance of that parameter for driving the behavior of the model (Saltelli et al., 2008). If the null hypothesis was rejected, the prior distribution was reassigned based on  $f(X_i|B)$ .

#### 2.3.3. Probability density functions

Inherent to these methods is the importance of the selection of the input PDFs. Model parameters and their PDFs are shown in Table 1. When the data for the parameters shows no apparent distribution such as normal or triangular, the PDF can be set to uniform

**Table 2**  
Natural mortality ( $M$ ) and growth coefficients ( $k$ ) for selected tilapia species.

Species	$M$	$k$	Location	Reference
<i>Oreochromis andersonii</i>	1.39	1.0	Okavango Delta, Botswana	Mosepele and Nengu (2003)
<i>O. andersonii</i>	0.67	0.25	Okavango Delta, Botswana	Booth et al. (1995)
<i>Oreochromis macrochir</i>	1.5	1.0	Okavango Delta, Botswana	Mosepele and Nengu (2003)
<i>Oreochromis macrochir</i>	0.95	0.42	Okavango Delta, Botswana	Booth and Merron (1996)
<i>T. rendalli</i>	1.22	0.78	Okavango Delta, Botswana	Mosepele and Nengu (2003)
<i>Serranochromis angusticeps</i>	1.46	1.0	Okavango Delta, Botswana	Mosepele and Nengu (2003)
<i>Serranochromis robustus</i>	1.21	0.83	Okavango Delta, Botswana	Mosepele and Nengu (2003)
<i>Oreochromis niloticus</i>		0.254	Lake Victoria, Kenya	Getabu (1992)
<i>Haplochromis anaphymus</i>	1.45	0.671	Lake Malawi, Mozambique	Tweddle and Turner (1977)
<i>Haplochromis molta</i>	0.92	0.55	Lake Malawi, Mozambique	Tweddle and Turner (1977)
<i>Lethrinops longipinnus</i>	1.69	0.571	Lake Malawi, Mozambique	Tweddle and Turner (1977)
<i>Lethrinops parvidens</i>	1.20	0.487	Lake Malawi, Mozambique	Tweddle and Turner (1977)
<i>Tilapia esculenta</i>	1.75	0.28	Lake Victoria, Kenya	Garrod (1963)

(Muñoz-Carpena et al., 2007). The uniform distribution allows for equal probability of selection across the defined range.

The prior distribution for mortality ( $M$ ) was defined based on literature values (Table 2). Values of  $M$  for tilapia species were compiled from a number of studies including the three indicator species in the Okavango Delta. These values range between 0.67 and 1.39 for the indicator fishes in the Okavango Delta. Based on these data, the PDF for  $Z$  was set to Uniform (0.67, 1.39).

The allometric relationship between mortality and fish body length (de Graaf et al., 2005) calculates a decreasing rate of mortality with increasing body length. The four parameters required for calculating mortality according to the allometric relationship are the mortality at unit length ( $M_U$ ), the von Bertalanffy parameters  $\alpha$  and  $\beta$  parameters, and asymptotic length (cm),  $L_\infty$ .  $M_U$  should be estimated for each species (de Graaf et al., 2005; Lorenzen, 2001). de Graaf et al. (2005) used values of  $M_U$  ranging between 1 and 4.5 for species with survival rates between 50 and 80%. Based on the values of  $Z$  chosen for the PDF, survivability for these fishes ranges between 25% and 50%. The PDF for  $M_U$  was set so that ranges similar to the values that were defined for  $Z$  through the literature could be achieved. Based on this analysis the PDF for  $M_U$  was set to Uniform (3, 8).

Mosepele and Nengu (2003) provide values for the weight [g] length [cm] parameters  $\alpha$  and  $\beta$  for the three indicator species specific to the Okavango Delta. For *O. andersonii*  $\alpha$  is given as 0.004 and  $\beta$  is 3.424, for *O. macrochir*  $\alpha$  is 0.014 and  $\beta$  is 3.106, and for *T. rendalli*  $\alpha$  is 0.026 and  $\beta$  is 2.911. Based on Mosepele and Nengu's (2003) ranges for the von Bertalanffy parameters, PDFs for  $\alpha$  and  $\beta$  were established:  $\alpha$  Uniform (0.004, 0.026) and  $\beta$  Uniform (2.911, 3.424).

Mosepele and Nengu (2003) also calculated  $L_\infty$  for the three indicator species in the Okavango Delta.  $L_\infty$  for *O. andersonii* was found to be 53 cm, for *T. rendalli* it was 47 cm, and for *O. macrochir* it was 40 cm. From these values, the PDF for  $L_\infty$  was set to Uniform (40, 53).

A number of studies in southern Africa and the Okavango Delta investigate the growth coefficient ( $k$ ) for various tilapia species including the three indicator species used in this study (Table 2). In these studies,  $k$  varies from 0.25 to 1.0 from. Based on these data, the PDF for  $k$  was set to Uniform (0.25, 1.0).

The Goodyear compensation ratio (Goodyear, 1977) describes the rate at which juvenile survival changes following a depletion in stock. High values of CR allow juvenile survival to increase substantially as the stock declines due to fishing, resulting in high compensation. According to Walters et al. (2008), when recruitment compensation is not especially strong the CR is less than 20. Walters et al. (2007) state that long lived benthic species likely have CR's in the range of 10–50. In Myers et al.'s (1999) meta-analysis of a variety of fish (mostly pelagic species) values for CR

ranged from 1.4 to 123.5 with an average of 18.6. A meta-analysis of stock-recruitment data by Goodwin et al. (2006) showed CR is in the range of 5–100. And Goodwin et al.'s (2006) analysis showed that values for CR in perciformes varied between 3 and 50. Based on these analyses, the PDF for CR was set to Uniform (3, 30).

The vulnerability catch curve (Eq. (11)) was parameterized from inspection of a smaller dataset of commercial catch from the Okavango Delta where fish length was available (Mosepele, 2009). A histogram of caught fish per length was produced and a corresponding vulnerability relationship was developed with PDFs for each of the parameters. The PDFs for the lengths and standard deviation at the upper end of the curve were set to include a wider and higher distribution to account for the mortality that is occurring and also to test for a logistic vulnerability shape versus a dome shape. Based on inspection, the PDFs were set as follows:  $L_{low}$  is Uniform (23, 25),  $SD_{low}$  is Uniform (1, 3),  $L_{high}$  is Uniform (28, 60), and  $SD_{high}$  is Uniform (10, 30).

The model calculates recruitment per time step based on the number of mature fish in that year. Several studies have investigated the age at which cichlids become mature in southern Africa. Dudley (1974) measured the total length and sexual maturity of *O. andersonii* in the Kafue floodplains. He found that that during the years of his study, no fish under 26 cm were mature, three out of 64 fish from 26 to 29 cm were mature, and more than 30% of larger males and 40% of larger females were immature. Dudley (1974) also aged the fish with annual ring formations. He concluded that *O. andersonii* usually spawn after the age of four and very rarely under the age of three. Similarly, Van der Waal (1976) found that in the Zambezi River the minimum size for sexual maturity in *O. andersonii* was 25–27 cm. Hay et al. (2000) also measured the minimum size of for sexual maturity in *O. andersonii* in the Okavango River Namibia which they found to be 13 cm for males and 26 cm for females. Based on these literature values, with emphasis on the ring formation as better measure of age than length, and a PDF for age a sexual maturity was set to Normal (4.25, 0.5).

Fecundity refers to the number of eggs hatched per brood. According to Mortimer (1960) *O. andersonii*, between 17 and 25 cm in length, laid 349–567 eggs in ponds. Additionally, Chandrasoma and Desilva (1981) found intraovarian egg counts in *T. rendalli* ranged between 760 and 6160 in a lake in Sri Lanka. And Marshall (1979) found that *O. macrochir* can produce 1000–5000 eggs within their ovaries and may mouthbrood up to 800 eggs in Lake McIlwaine, Zimbabwe. Several sources state that these indicator species may lay more than one brood per season. Skelton (1993) stated that *T. rendalli* and *O. andersonii* both raised several broods each summer. Naesje et al. (2004) described that *T. rendalli* may lay several broods each season in the Kwando River, Namibia. Mortimer (1960) examined *O. andersonii* for physiological indications of having multiple broods per season. This study did not find physiological



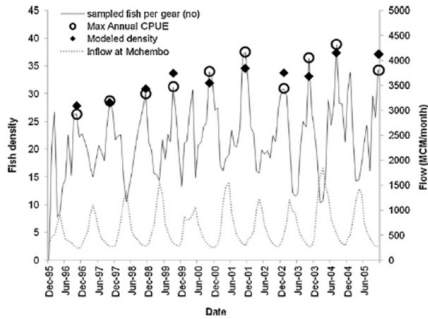


Fig. 5. The best fit model simulation for the initial inverse optimization. Coefficient of efficiency equals 0.64.

indications of multiple broods. However, the same study also observed two instances in ponds where one breeding pair spawned twice in one season. According to these data the PDF for the number of eggs per fish per year ( $e$ ) was set to Uniform (350, 1600).

The flood coefficient ( $c$ ) is a scaling factor that describes how recruitment changes with the magnitude of the flood (Eq. (7)). There were no literature to support values for this coefficient and this research was the first investigation into the quantitative effects of the flood on fish populations in the Okavango Delta. A trial and error investigation into the appropriate ranges for this coefficient was conducted prior to the GSA to get a sense of the values that would drive the model into a behavioral fit. Values for this coefficient ranging between 5 and 25 created acceptable model outputs. Therefore, the PDF for  $c$  was set to Uniform (5, 25). Later MC filtering is used to redefine and truncate this prior distribution. This is shown to be a particularly valuable tool when physical data regarding the parameter is lacking.

3. Results

With 14 parameters, the model was run 13,902 times for the GSA/UA using the FAST Monte Carlo style sampling. From these model runs, the model achieved a maximum ceff of 0.64 (Fig. 5) when comparing annual measured and modeled CPUE. However, achieving the best model fit was not the primary goal of this exercise. We sought also to analyze the results and the functional importance of the flood pulse to corroborate existing conceptual theories that the flood pulse drives fish population dynamics. This was done through GSA/UA and MC filtering.

3.1. Global sensitivity analysis

According to the FAST GSA results (Fig. 6), the most important factors in this model in order of importance, were: the growth coefficient ( $k$ ), mortality at unit weight ( $M_u$ ), and the upper length at 50% vulnerability ( $L_{high}$ ). These were also highly interactive parameters (Fig. 7). Parameters that contributed less than 1% of the total model sensitivity included: maturity,  $e$ , and  $SD_{low}$  (Fig. 7). These three unimportant parameters were set to constants in the next round of MC filtering.

The flood coefficient ( $c$ ), which determines the relationship that flow has on recruitment, was not one of the most sensitive parameters. However, a scatter plot that compares  $c$  to the objective function (ceff) shows that the best model fit converged at a  $c$  of approximately 14 (Fig. 8a). At a  $c$  of 14, the number of recruits

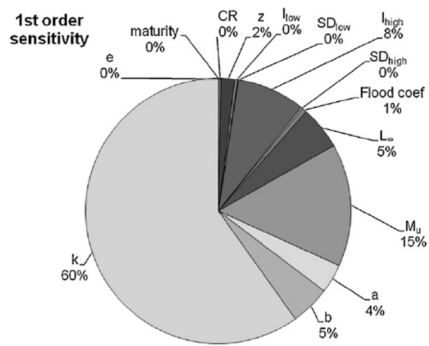


Fig. 6. First order sensitivity for the coefficient of efficiency of the modeled fish density compared to the measured catch per unit effort (CPUE) from the first inverse optimization.

per year varied between 6100 and 10,800, almost doubling their numbers between low and high flood years (Fig. 9) and adding significant variability in the inter-annual population. This was not the case for the other parameters (except for  $k$ ), where there was generally a high degree of equifinality and the model was able to achieve a good fit using parameter values ranging throughout their defined PDFs (Fig. 8c–f). All of the parameters besides  $c$  are related to the baseline size and/or biomass of the population. The flood coefficient ( $c$ ) is the one parameter that is responsible for introducing inter-annual variability in the population dynamics. Without  $c$ , the fish population density would not be dynamic and the model would only be able to simulate a static population between all years divided by the annual flood size.

3.2. Monte Carlo filtering

Through MC filtering, all of the outputs were mapped to their corresponding parameters so that the parameters that created the best fit outputs could be better understood. A threshold of a ceff of 0.50 was set and any model output greater than or equal to 0.50 was defined as behavioral while any output less than 0.50 was defined as non-behavioral. Using this threshold, of the 13,902 runs, 133 were shown to be behavioral. The value of 0.50 was strategically chosen to optimize the solutions that fell into the behavioral

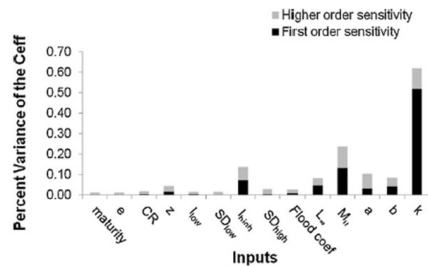


Fig. 7. First and higher order sensitivities for coefficient of efficiency of modeled fish density compared to measured CPUE from first inverse optimization.

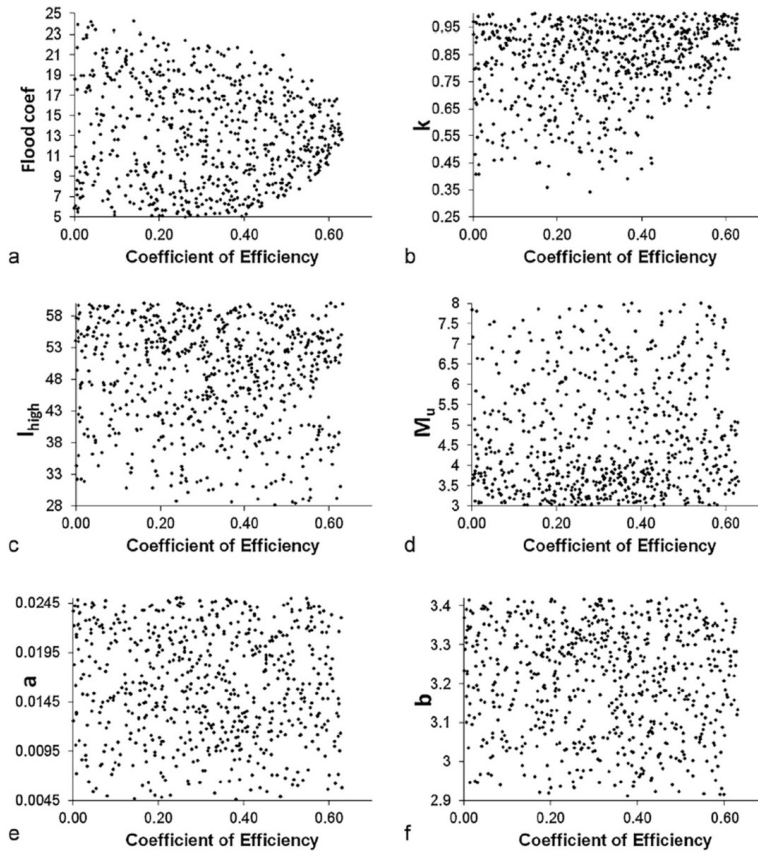


Fig. 8. (a–f) Scatter plots of values for the flood coefficient,  $k$ ,  $M_u$ ,  $I_{high}$ ,  $a$ , and  $b$  creating behavioral outputs. Note that the flood coefficient converges toward a single value in the highest values for the coefficient of efficiency (best fit model runs). Only simulations with a  $ceff > 0$  are shown.

category while at the same time ensured that there were enough values in the behavioral range to employ the two sided Smirnov test. The two sided Smirnov test showed that of the 11 important parameters, 5 had distributions where the behavioral parameters were significantly different from the non-behavioral parameters:  $I_{high}$ ,  $M_u$ ,  $k$ ,  $L_{\infty}$ , and  $c$ . When the behavioral parameter distributions were shown to be significantly different from the non-behavioral parameter distributions, new PDFs were assigned to the parameters that matched the behavioral distributions. The behavioral and non-behavioral distributions for five parameters were shown to be significantly different. The five significantly different distributions were all skewed and so triangular distributions were chosen to represent these PDFs (Fig. 10). This process truncated the prior PDFs. The GUA was then rerun to understand how this truncation affected the model's uncertainty.

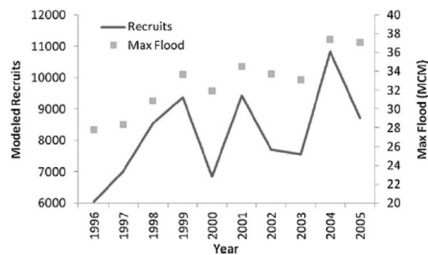


Fig. 9. The effect of the flood coefficient on recruitment (flood coef = 14).

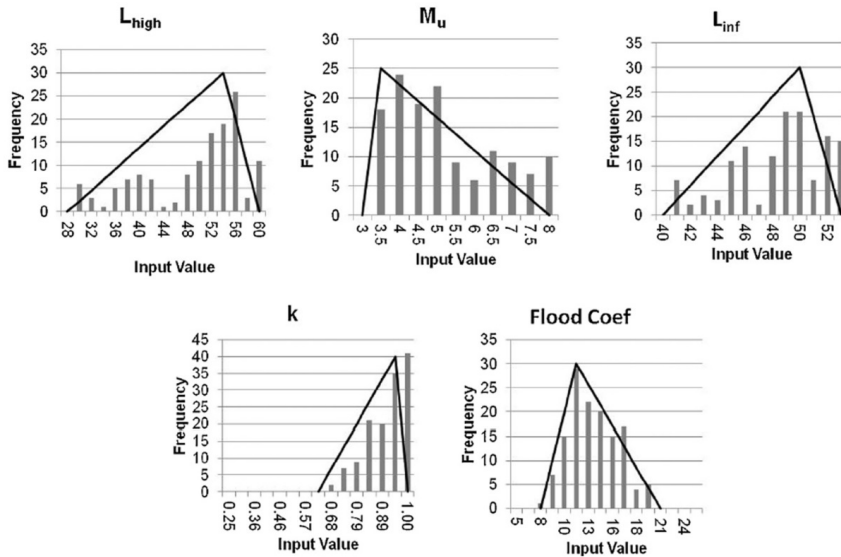


Fig. 10. Important parameters whose behavioral distributions are significantly different from the non-behavioral distributions. These graphs show histograms of the behavioral distributions and their newly defined triangular posterior distributions.

### 3.3. Global uncertainty analysis

After the behavioral distributions were defined, the model was rerun through the FAST GSA/UA with the unimportant parameters set to constants and the posterior triangular PDF's assigned to the parameters:  $L_{high}$ ,  $M_u$ ,  $k$ ,  $L_{inf}$ , and  $c$ . The model results showed similar optimization from before the MC filtering with a maximum  $ceff$  of 0.64 and a maximum  $R^2$  of 0.64. Through MC filtering parameter/output model uncertainty was reduced from an average  $ceff$  in the original uncertainty analysis of  $-26.6$  to  $-7.0$  in the MC filtered uncertainty analysis. The minimum  $ceff$  was also reduced from  $-154.5$  to  $-91.3$ . The 95% confidence interval was reduced from  $(-0.01, -65.8)$  in the original analysis to  $(0.54, -27.1)$  in the MC filtered analysis (Figs. 11b and 12).

### 4. Discussion

Given the ecosystem complexity and lack of data, we did not seek a single optimal solution in the model, but sought the range of parameters that produced the best model fit. The model parameters that produced the best model fit were analyzed in the light of uncertainty and equifinality. There was one parameter in the model, the flood coefficient ( $c$ ), which initiated the inter-annual variability in fish population based on the flood pulse. The flood coefficient's sensitivity was low and could initially be regarded as a relatively unimportant parameter. The most important parameters in the model that were identified through the sensitivity analysis were related to the baseline population size. Depending on the values used for the important parameters the baseline population varied widely between 0 and 80 CPUE. Additionally, all of these important parameters (besides  $k$ ) exhibited major issues of equifinality (Fig. 8 b–f) as they were able to vary throughout their PDF

ranges while still achieving best fit results. Thus, the average population size fluctuated greatly and could also be modeled using a variety of parameters values while still producing good results. For a model to simulate the average population ( $ceff = 0$ ), only the baseline or average population must be correct and it is not necessary to simulate the inter-annual variation; but to get the best model fit, and reach a  $ceff$  above 0, both the baseline population and the inter-annual variability must be modeled. The flood coefficient ( $c$ ) was the only parameter responsible for initiating this inter-annual dynamics in the model. If  $c$  was set to 0, the population in the model would be constant across years. The value for  $c$  actually converged toward a single solution in the best fit model simulations (Fig. 8a). The fact that the model was able to simulate a  $ceff$  of 0.64 only

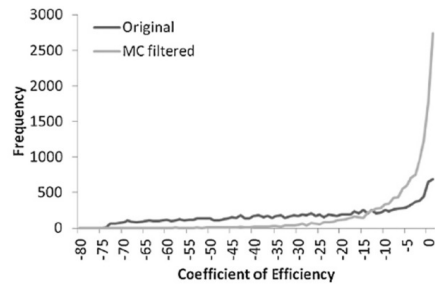


Fig. 11. All GUA results. (a) unfiltered (b) Monte Carlo (MC) filtered. Fig. 12 shows a blowup of results with coefficient of efficiencies greater than 0.



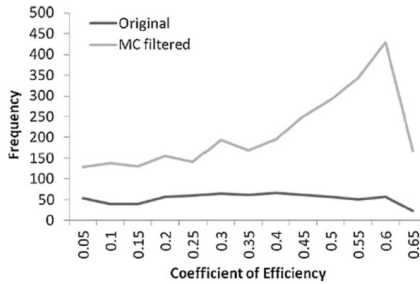


Fig. 12. Uniform and MC filtered GUA outputs with a coefficient of efficiency greater than 0.

through the proper value of  $c$  provides evidence that the flood is an important driver in the system despite the fact that there is equifinality in other portions of the model. This finding also illuminates a gap in existing sensitivity analysis techniques where importance is defined solely on the magnitude of the change in output and does not address how unimportant parameters can be essential for achieving specific objectives such as model optimization (Saltelli et al., 1999; Cukier et al., 1978; Koda et al., 1979).

MC filtering was applied to refine parameter/output uncertainty. The important prior distributions were re-set to triangular distributions where the behavioral parameters were found to be significantly different from the non-behavioral parameters based on the two sided Smirnov test.  $L_{high}$ ,  $M_u$ ,  $k$ ,  $L_{\infty}$ , and  $c$  were all found to have significantly different behavioral parameters and were assigned triangular distributions. This method reduced model parameter/output uncertainty by reducing the 95% confidence interval of the coefficient of efficiency between the modeled density and the measured CPUE from a width of 65.8–27.3. This is useful and allows the modeler in a data poor environment to focus on likely values within the ranges of physically acceptable PDFs. The modeler can then work in tandem with the biologist to ensure that the new PDFs makes sense in a real biological setting providing converging lines of evidence for a more accurate depiction of the system and its interactions.

Thus the results here that achieved a coeff of 0.64 and an  $R^2$  of 0.64 were relatively promising compared to Gaff et al.'s (2004) model of fish populations in the Everglades which achieved an  $R^2$  of 0.35 where fish density was modeled in response to water depth. However, the Okavango fish model is non-spatial and runs on an annual time step whereas Gaff et al.'s study is a spatially explicit model that ran on a monthly time step. Therefore, there were fewer data points simulated in the Okavango model making it perhaps a simpler solution.

Managers must make decisions regarding the use of natural resources in the Okavango Delta. To help ensure the continuation of a healthy system these decisions should be based on an understanding of functional mechanisms and relationships. For example, if spawning is influenced by the flood pulse then ensuring a natural flood regime is an important characteristic to maintain. When monitoring data that informs these decisions is lacking, models can be used to corroborate existing theories on how a system functions. This was the intention of this work. We did not seek an optimal parameter set for calibration or to predict fish responses to changes in hydrology. Instead we sought to provide evidence that fish population dynamics is driven by the flood pulse using a quantitative mechanistic model.

## 5. Conclusion

Several limitations can be identified in this work. The fish data were from commercial catch and not experimental data and so fisherman preferences, knowledge, and other human variables may play into the data (Walters and Martell, 2004). The data came from the Panhandle which is more permanently flooded and is less dynamic than the larger Delta. Additionally, the ORI hydrologic model which simulates the inundation area was not specifically calibrated to the Panhandle reservoir and was more focused on the larger Delta. Finally, the variability of the annual fish population is not exceptionally dynamic; the maximum annual CPUE only fluctuates between 26 and 39. In heavily fished areas, fish populations are often much more dynamic, lending to more variability to model.

Overall, this modeling effort was conducted in an area where data scarcity severely limited model development. Preferably, a model should be based on monitoring data that directly describes the relationship between fish population dynamics and the flood pulse as well as key factors that influence that relationship. In an absence of this data this model was designed to corroborate existing ecological theories but not to replace or negate the need for monitoring data. Therefore, future work in this area should focus on collecting monitoring data that describes the relationship between the flood pulse and fish population dynamics. For example, experimental fish data that included age or size in addition to daily counts would improve our understanding of the system and could be used to assess the performance of the model and inform additional model development.

This model was able to corroborate the existing conceptual theory that the flood pulse drives fish population dynamics in three ways. First, the model was able to simulate fish population dynamics (coeff of 0.64). Second, the model parameter that embodied the flood pulse concept, the flood coefficient, was shown to be important for obtaining the optimal model results. And third, the flood coefficient was shown to converge to an optimal value in the best fit model simulations. Thus, this mechanistic model corroborated conceptual models (Merron, 1991; Mosepele et al., 2009) and qualitative observations (Hoberg et al., 2002) that fish recruitment is positively influenced by the magnitude of the flood pulse in the Okavango Delta. This quantitative linkage between the flood pulse and fish population dynamics is particularly important in this area that lacks monitoring data. This linkage also provides information that is necessary for making informed decisions regarding the management of hydrologic and ecological resources in the Okavango Delta. Managers now have quantitative data that shows a linkage between the hydrology of the Okavango Delta and the ecology of the fisheries resource.

There are few existing mechanistic models that explore flood pulse effects on fish recruitment and none of these models have been developed for the Okavango Delta. This work fills this gap in research by producing a quantitative mechanistic flood pulsed fish population model for the Okavango Delta. Additionally, unexpected outcomes from this work showed that the flood coefficient, and unimportant parameter, drove optimal model solutions. Because of the data gaps, the a priori range for the flood coefficient was unknown. MC filtering was used to revise this range based on behavioral model outputs. This methodology for refining unknown parameter distributions is helpful in any data poor area where there is a lack of information available for defining parameter ranges.

## Acknowledgements

The authors would like to thank the AM-W3 NSF IGERT, Mark Brown, and NASA project 08-LCLUC08-2-0025 for their financial and institutional support of this work. The authors also acknowledge the University of Florida High-Performance Computing Center



for providing computational resources and support that have contributed to the research results reported within this paper. Finally, thanks to the University of Botswana's Okavango Research Institute for all of their onsite assistance.

## References

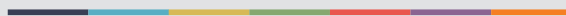
- Agostinho, A.A., Gomes, L.C., Verissimo, S., K. Okada, E., 2004. Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment. *Rev. Fish Biol. Fish.* 14, 11–19.
- Allen, M.S., Brown, P., Douglas, J., Fulton, W., Catalano, M., 2009. An assessment of recreational fishery harvest policies for Murray cod in southeast Australia. *Fish. Res.* 95, 260.
- Bailly, D., Agostinho, A.A., Suzuki, H.I., 2008. Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. *River Res. Appl.* 24, 1218–1229.
- Bayley, P.B., 1991. The flood pulse advantage and the restoration of river-floodplain systems. *Regul. Rivers Res. Manage.* 6, 75–86.
- Beven, K., 1993. Prophecy, reality and uncertainty in distributed hydrological modelling. *Adv. Water Res.* 16, 41–51.
- Beven, K., Binley, A., 1992. The future of distributed models: model calibration and uncertainty prediction. *Hydrol. Process.* 6, 279–298.
- Beven, K., Freer, J., 2001. Equifinality, data assimilation, and uncertainty estimation in mechanistic modelling of complex environmental systems using the GLUE methodology. *J. Hydrol.* 249, 11–29.
- Beverton, R.J.H., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations. 533M. Stationery Office, London, H, 533 p.
- Booth, A.J., Merron, G.S., 1996. The age and growth of the greenhead tilapia *Oreochromis macrochir* (Pisces: Cichlidae) from the Okavango Delta, Botswana. *Hydrobiologia* 321, 29–34.
- Booth, A.J., Merron, G.S., Burton, C.D., 1995. The Growth of *Oreochromis-Andersonii* (Pisces, Cichlidae) from the Okavango Delta, Botswana, and a comparison of the scale and otolith methods of aging. *Environ. Biol. Fish.* 43, 171–178.
- Borgstrom, R., 1992. Effect of population density on gillnet catchability in 4 allopatric populations of brown trout (*Salmo-Trutta*). *Can. J. Fish. Aquat. Sci.* 49, 1539–1545.
- Chandrasoma, J., Desilva, S.S., 1981. Reproductive biology of *Puntius-sarana*, an indigenous species, and *Tilapia-rendalli* (Melanopleura), an exotic, in an ancient man-made lake in Sri Lanka. *Fish. Manage.* 12, 17–28.
- Chu-Agor, M.L., Muñoz-Carpena, R., Kiker, G., Emanuelsson, A., Linkov, I., 2011. Exploring vulnerability of coastal habitats to sea level rise through global sensitivity and uncertainty analyses. *Environ. Model. Softw.* 26, 593–604.
- Cukier, R.I., Levine, H.B., Shuler, K.E., 1978. Nonlinear sensitivity analysis of multiparameter model systems. *J. Comput. Phys.* 26, 1–42.
- de Graaf, G.J., Dekker, P.J., Huisman, B., Verreth, J.A.J., 2005. Simulation of Nile tilapia (*Oreochromis niloticus*) culture in ponds, through individual-based modeling, using a population dynamic approach. *Aquacult. Res.* 36, 455–471.
- DeAngelis, D.L., Loftus, W.F., Trexler, J.C., Ulanowicz, R.E., 1997. Modeling fish dynamics and effects of stress in a hydrologically pulsed ecosystem. *J. Aquat. Ecosyst. Stress Recov.* 6, 1–13.
- Dudley, R.G., 1974. Growth of Tilapia of the Kafue Floodplain, Zambia: predicted effects of the Kafue Gorge Dam. *Trans. Am. Fish. Soc.* 103, 281–291.
- Fielder, D.G., 1992. Relationship between Walleye fingerling stocking density and recruitment in lower Lake Oahe, South Dakota. *N. Am. J. Fish. Manage.* 12, 346–352.
- Fox, G.A., Muñoz-Carpena, R., Sabbagh, G.J., 2010. Influence of flow concentration on parameter importance and prediction uncertainty of pesticide trapping by vegetative filter strips. *J. Hydrol.* 384, 164–173.
- Gaff, H., Chick, J., Trexler, J., DeAngelis, D., Gross, L., Salinas, R., 2004. Evaluation of and insights from ALFISH: a spatially explicit, landscape-level simulation of fish populations in the Everglades. *Hydrobiologia* 520, 73–87.
- Garrod, D.J., 1963. An estimation of the mortality rates in a population of *Tilapia-Esculenta* Graham (Pisces, Cichlidae) in Lake Victoria, East Africa. *J. Fish. Res. Board Can.* 20, 195–227.
- Getabu, A., 1992. Growth-parameters and total mortality in *Oreochromis-Niloticus* (Linnaeus) from Nyanza Gulf, Lake Victoria. *Hydrobiologia* 232, 91–97.
- Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K., Reynolds, J.D., 2006. Life history correlates of density-dependent recruitment in marine fishes. *Can. J. Fish. Aquat. Sci.* 63, 494–509.
- Goodyear, C.P., 1977. Assessing the impact of power plant mortality on the compensatory reserve of fish populations. In: Proceedings of the Conference on Assessing the Effects of Power-Plant-Induced Mortality on Fish Populations. Gatlinburg, Tennessee, p. 185–194.
- Hansson, S., Rudstam, L.G., 1995. Gillnet catches as an estimate of fish abundance: a comparison between vertical gillnet catches and hydroacoustic abundances of Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). *Can. J. Fish. Aquat. Sci.* 52, 75–83.
- Hay, C.J., Naesje, T.F., Breistein, J., Harsaker, K., Kolding, J., Sandlund, O.T. and Zyl, B.v., 2000. Fish populations, gill net selectivity and artisanal fisheries in the Okavango River, Namibia. Recommendations for a sustainable fishery. NINA-NIKU Project Rep. 10, 1–105.
- Hoberg, P., Lindholm, M., Ramberg, L., Hessen, D.O., 2002. Aquatic food web dynamics on a floodplain in the Okavango delta, Botswana. *Hydrobiologia* 470, 23–30.
- Hodgkiss, I.J., Man, H.S.H., 1977. Stock density and mortality assessment of *Sarotherodon mossambicus* (Cichlidae) in Plover Cove Reservoir, Hong Kong. *Environ. Biol. Fish.* 1, 171–180.
- Jawitz, J.W., Muñoz-Carpena, R., Stuart, M., Grace, K.A., 2008. Development, testing, and sensitivity and uncertainty analyses of a transport and reaction simulation engine (TARSE) for spatially distributed modeling of phosphorus in south Florida peat marsh wetlands. U.S. Geological Survey Scientific Investigations Report 2008-5029, 109 p.
- Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. *Can. Spl. Publ. Fish. Aquat. Sci.* 106, 110–127.
- Kgathi, D.L., Mmopelwa, G., Mosepele, K., 2005. Natural resources assessment in the Okavango Delta, Botswana: case studies of some key resources. *Nat. Resour. Forum* 29, 70–81.
- King, J.M., Tharme, R.E., Brown, C.A., 1999. Definition and implementation of instream flows. Thematic Report for the World Commission on Dams. Cape Town, South Africa.
- King, A.J., Humphries, P., Lake, P.S., 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Can. J. Fish. Aquat. Sci.* 60, 773–786.
- Koda, M., Mcrae, G.J., Seinfeld, J.H., 1979. Automatic sensitivity analysis of kinetic mechanisms. *Int. J. Chem. Kinet.* 11, 427–444.
- Lorenzen, K., 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *J. Fish Biol.* 49, 627–647.
- Lorenzen, K., 2001. Using population models to assess culture-based fisheries: a brief review with an application to the analysis of stocking experiments. In: De Silva, S. (Ed.), *Reservoir and Culture-Based Fisheries: Biology and Management*, ACIAR Proceedings 98, 257–265.
- von Bertalanffy, L., 1957. Quantitative laws in metabolism and growth. *Q. Rev. Biol.* 32, 217–231.
- Marshall, B.E., 1979. Observations on the breeding biology of *Sarotherodon macrochir* (Boulenger) in Lake Mchivane, Rhodesia. *J. Fish Biol.* 14, 419–424.
- Mcgurk, M.D., 1986. Natural mortality of marine pelagic fish eggs and larvae – role of size and patchiness. *Mar. Ecol.-Prog. Ser.* 34, 227–242.
- Merona, B., Gascoel, D., 1993. The effects of flood regime and fishing effort on the overall abundance of an exploited fish community in the Amazon floodplain. *Aquat. Living Resour.* 6, 97–108.
- Merron, G.S., 1991. The ecology and management of the fishes of the Okavango Delta, Botswana, with particular reference to the role of the seasonal flood. Unpublished PhD thesis, Rhodes University.
- Mertens, J., Stenger, R., Barkle, 2006. Multiobjective inverse modeling for soil parameter estimation and model verification. *Vadose Zone J.* 5, 917–933.
- Mortimer, M.A.E., 1960. Observations on the biology of *Tilapia andersonii* (Castelnau), (Pisces, Cichlidae), in Northern Rhodesia. Joint Fisheries Research Organization Annual Report. Lusaka 9, pp. 41–67.
- Mosepele, K., 2001. Preliminary description of the Okavango Delta fishery. Unpublished technical report. Fisheries Section, Ministry of Agriculture, Gaborone, Botswana.
- Mosepele, K., 2009. Okavango river basin technical diagnostic analysis: environmental flow module specialist report. Country: Botswana, Discipline: Fish, OKACOM Project Management Unit, Luanda, Angola.
- Mosepele, K., Kolding, J., 2003. Fish stock assessment in the Okavango Delta: preliminary results from a length based analysis. In: Bernard, T., Mosepele, K., Ramberg, L. (Eds.), Proceedings of the Environmental Monitoring of Tropical and Subtropical Wetlands Conference, 4–8 December, 2002. Harry Oppenheimer Okavango Research Centre, University of Botswana, Maun, Botswana, pp. 363–390.
- Mosepele, K., Mmopelwa, T.G., Mosepele, B., 2003. Characterization and monitoring of the Okavango Delta artisanal fishery. In: Bernard, T., Mosepele, K., Ramberg, L. (Eds.), Proceedings of the Environmental Monitoring of Tropical and Subtropical Wetlands Conference, 4–8 December, 2002. Harry Oppenheimer Okavango Research Centre, University of Botswana, Maun, Botswana.
- Mosepele, K., Motye, P.B., Merron, G.S., Purkey, D.R., Mosepele, B., 2009. Fish, Floods, and ecosystem engineers: aquatic conservation in the Okavango Delta, Botswana. *Bioscience* 59, 53–64.
- Mosepele, K., Nengu, S., 2003. Growth, mortality maturity and length-weight parameters of selected fishes of the Okavango Delta, Botswana. *ACP-EU Fish. Res. Rep.* 14, 67–74.
- Muñoz-Carpena, R., Zajac, Z., Kuo, Y.M., 2007. Global sensitivity and uncertainty analyses of the water quality model VFSMOD-W. *Trans. ASABE* 50, 1719–1732.
- Muñoz-Carpena, R., Fox, G.A., Sabbagh, G.J., 2010. Parameter importance and uncertainty in predicting runoff pesticide reduction with filter strips. *J. Environ. Qual.* 39, 630–641.
- Myers, R.A., Bowen, K.G., Barrowman, N.J., 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* 56, 2404–2419.
- Naesje, T.F., Hay, C.J., Nickanor, N., Koekemoer, J.H., Strand, R.L., Throstand, E.B., 2004. Fish populations, gill net catches, and gill net selectivity in the Kwando River, Namibia. NINA project number 27, pp. 1–64.
- Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models part I—a discussion of principles. *J. Hydrol.* 10, 282–290.
- Peterson, I., Wroblewski, J.S., 1984. Mortality-rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* 41, 1117–1120.
- Ritter, A., Muñoz-Carpena, R., Regalado, C.M. Prediction ability of mathematical models: objective assessment of goodness-of-fit with statistical significance. *Water Resour. Res.*, submitted for publication.

- Rogers, M.W., Allen, M.S., Brown, P., Hunt, T., Fulton, W., Ingram, B.A., 2010. A simulation model to explore the relative value of stock enhancement versus harvest regulations for fishery sustainability. *Ecol. Model.* 221, 919–926.
- Saltelli, A., Tarantola, S., Chan, K.P., 1999. A quantitative model-independent method for global sensitivity analysis of model output. *Technometrics* 41, 39–56.
- Saltelli, A., Ratto, M., Andres, T., Campolongo, F., Cariboni, J., Gatelli, D., Saisana, M., Tarantola, S., 2008. *Global Sensitivity Analysis: the Primer*. John Wiley & Sons, Ltd., Sussex, England.
- SimLab, 2011. Software Package for Uncertainty and Sensitivity Analysis. Joint Research Centre of the European Commission. Downloadable for free at: <http://simlab.jrc.ec.europa.eu>.
- Skelton, P.H., 1993. *A Complete Guide to the Freshwater Fishes of Southern Africa*. Southern Book Publishers, Halfway House, South Africa.
- Tharme, R.E., 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *River Res. Appl.* 19, 397–442.
- Tharme, R.E., King, J.M., 1998. Development of the building block methodology for instream flow assessments, and supporting research on the effects of different magnitude flows on riverine ecosystems. Water Research Commission Report No. 576/1/98.
- Tockner, K., Malard, F., Ward, J.V., 2000. An extension of the flood pulse concept. *Hydrol. Process.* 14, 2861–2883.
- Twedde, D., Turner, J.L., 1977. Age, growth and natural mortality-rates of some cichlid fishes of Lake Malawi. *J. Fish Biol.* 10, 385–398.
- Van der Waal, B.C.W., 1976. 'n Visekologiese studie van die Liamezimeer in die Oos-Capryvi met verwysing na visontginning deur die Bantoebevolking. PhD Thesis. Rand Afrikaans University, South Africa. 192 p. (In Afrikaans).
- Walters, C.J., Hilborn, R., Christensen, V., 2008. Surplus production dynamics in declining and recovering fish populations. *Can. J. Fish. Aquat. Sci.* 65, 2536–2551.
- Walters, C.J., Hilborn, R., Parrish, R., 2007. An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. *Can. J. Fish. Aquat. Sci.* 64, 1009–1018.
- Walters, C.J., Martell, S.J.D., 2004. *Fisheries Ecology and Management*. Princeton University Press, Princeton, NJ, p. 399.
- Wolski, P., Savenije, H.H.G., Murray-Hudson, M., Gumbricht, T., 2006. Modelling of the flooding in the Okavango Delta, Botswana, using a hybrid reservoir-GIS model. *J. Hydrol.* 331, 58–72.
- Zeug, S.C., Winemiller, K.O., 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Res. Appl.* 24, 90–102.





Graphic design: Communication Division, UIB / Print: Skjipes Kommunikasjon AS



[uib.no](http://uib.no)

ISBN: 9788230842034 (print)

9788230863169 (PDF)