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#### 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 \%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, CCA revealed a significant ( $p=0.004$ ) association between environmental factors and fish assemblage structure. CCA analyses also showed that spawning for different species is associated with various environmental factors. Annually, results showed that C. gariepinus dominated the fish assemblage during poor flood years while S. intermedius dominated during high flood years. DCA analyses showed that the hydrological gradient had a significant effect on fish assemblage structure at an annual scale, while SIMPER analyses 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.


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## 1. Introduction

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

[^0]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
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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 $9,10 \mathrm{~m}$ long panels of mesh sizes $22-150 \mathrm{~mm}$ stretched; (ii) multifilament, multi-mesh nets made up of 5.5 m long panels of mesh sizes $50-125 \mathrm{~mm}$ 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 $0.8 \mathrm{~ms}^{-1}$ (McCarthy
et al., 1998; Wolski et al., 2006). Lagoons are seasonally connected to the min 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 $49-125 \mathrm{~mm}$. 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 STATISITCA (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 Pasgear (Kolding and Asmund, 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; Oberdoff 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

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