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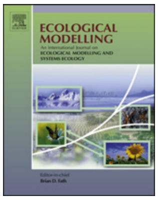

A flood pulse driven fish population model for the Okavango Delta, Botswana

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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.

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 (Bailly 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 $\mathrm{mg\,L^{-1}}$ and phosphorus rose from 125 to 450 $\mu\mathrm{g\,L^{-1}}$. Primary production reached its peak at 300 $\mu\mathrm{g\,C\,L^{-1}\,d^{-1}}$ and maximum

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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.

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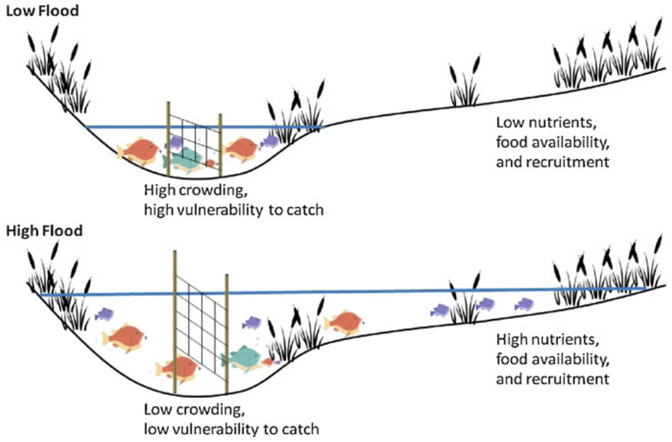

Fig. 1. A diagram of the flood pulse concept, the conceptual model driving this research.

chlorophyll *a* values were 24 μg chlorophyll $a\,L^{-1}$ (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 mg dry weight per liter ($DW\,L^{-1}$) during the rise of the flood and reached up to 90 mg $DW\,L^{-1}$ 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.

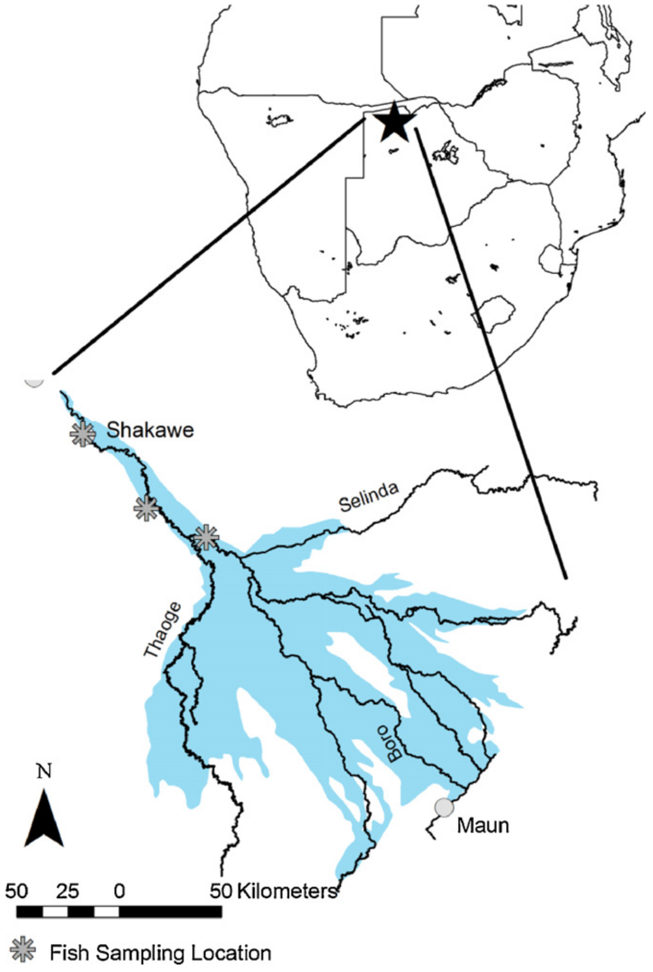

Fig. 2. Site location. The Okavango Delta, with fish sampling sites marked.

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 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