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 compo-nents. 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 pol-ishing 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 availabil-ity (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 stud-ies 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^{-1} and phosphorus rose from 125 to 450 µg L^{-1}. Primary production reached its peak at 300 µg C L^{-1} d^{-1} and maximum
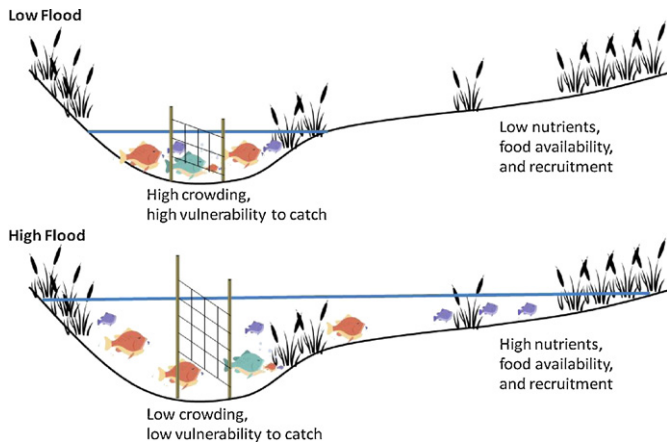
Fig. 1. A diagram of the flood pulse concept, the conceptual model driving this research.

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*,

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

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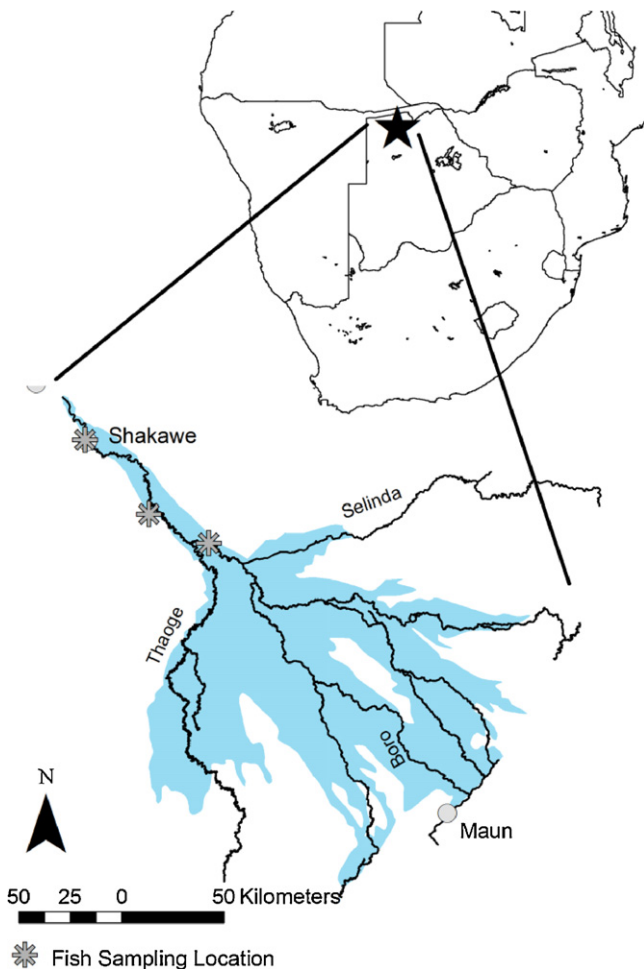
reflected empirical data showing that the hydrology only accounts for 20–40% of the variability in the sampled fish population density.

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 PDF's 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 (PDF's). Therefore, secondly, we used Monte Carlo (MC) filtering (Saltelli et al., 2008) to objectively redefine the prior PDF's 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_i is measured or observed data, P_i 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).

$$E = 1.0 - \frac{\sum_{i=1}^{N}(O_i - P_i)^2}{\sum_{i=1}^{N}(O_i - \bar{O})^2} \tag{1}$$

The fish that were caught in commercial catches were not recorded to the level of species. Instead, tilapias (of the family Chiclidae) 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 yr^{-1}] is the number of recruits per year, α and β 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. α/β describes the maximum recruitment at a high stock and α describes the maximum recruitment/stock at a low stock size.

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

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) [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):

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

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

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

The CR represents the maximum compensatory increase in juvenile survival as the stock size is decreased from unfished to very low levels. Parameters α and β 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 α (Walters and Martell, 2004) (Eq. (5)) such that:

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

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

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

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 dependant 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 [M m^3 yr^{-1}], $\bar{F}$ is the average of the annual maximum inflows [M m^3 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).

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

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

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

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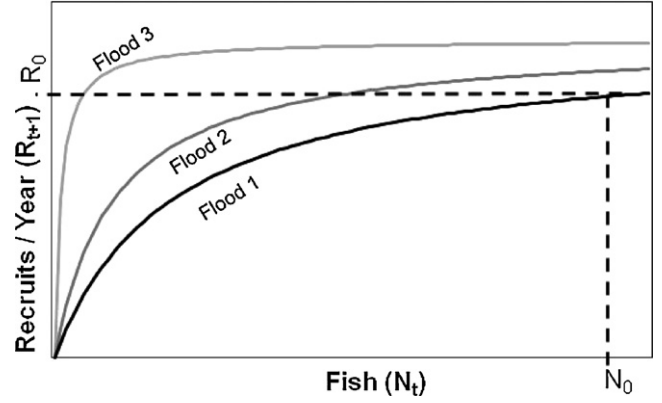

Fig. 3. A demonstration of the response in recruitment as a result of the change in annual maximum flood. The rate of recovery and the carrying capacity increases during smaller floods. Flood$_1$ > Flood$_2$ > Flood$_3$.

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)).

$$M = M_u \alpha^{-0.3} L^{0.3b} \tag{9}$$

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 (yr^{-1}), and L_∞ is the asymptotic length (Eq. (10)).

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

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):

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

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 km^{-2}) and the area of inundation must be known. This was done using in the Okavango
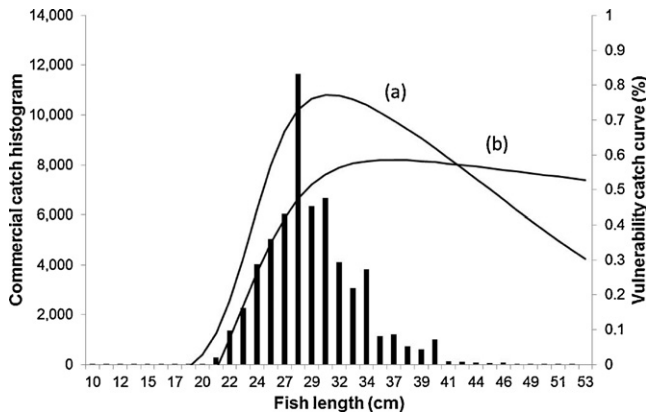
Fig. 4. An example of the dome shaped double logistic curve (Allen et al., 2009) for catch vulnerability. $L_{low} = 2$, $SD_{low} = 2$, $L_{high} = 45$, $SD_{high} = 10$. Histogram data from Mosepele (2009). (a) Shows the dome shaped curve and (b) shows the curve approaching a logistic shape. Both shapes are possible within the bounds of the defined PDF's.

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 PDF's were developed for each parameter based on literature values and data when available. The model was run iteratively sampling parameters from the PDF's 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 PDF's. 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_u	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_∞	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.

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

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_t, were defined as $X_t|B$ or $X_t|\bar{B}$ 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 PDF's $f(X_t|B)$ and $f(X_t|\bar{B})$ were then assigned. The two-sided Smirnov test was performed to check the significance of the difference between the two distributions $f(X_t|B)$ and $f(X_t|\bar{B})$. In the Smirnov test the test statistic $d_{n,\bar{n}}$ is defined by Eq. (13):

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

The null hypothesis for this test is $f(X_t|B) = f(X_t|\bar{B})$. That is, the null hypothesis tests if the distribution of the parameters that created 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, α. A small α 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 $f(X_t|B)$.

2.3.3. Probability density functions

Inherent to these methods is the importance of the selection of the input PDF's. Model parameters and their PDF's 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 tilapiine species.

Species	M	k	Location	Reference
Oreochromis andersonii	1.39	1.0	Okavango Delta, Botswana	Mosepele and Nengu (2003)
O. andersonii	0.67	0.25	Okavango Delta, Botswana	Booth et al. (1995)
Oreochromis macrochir	1.5	1.0	Okavango Delta, Botswana	Mosepele and Nengu (2003)
Oreochromis macrochir	0.95	0.42	Okavango Delta, Botswana	Booth and Merron (1996)
T. rendalli	1.22	0.78	Okavango Delta, Botswana	Mosepele and Nengu (2003)
Serranochromis angusticeps	1.46	1.0	Okavango Delta, Botswana	Mosepele and Nengu (2003)
Serranochromis robustus	1.21	0.83	Okavango Delta, Botswana	Mosepele and Nengu (2003)
Oreochromis niloticus		0.254	Lake Victoria, Kenya	Getabu (1992)
Haplochromis anaphyrmus	1.45	0.671	Lake Malawi, Mozambique	Tweddle and Turner (1977)
Haplochromis molto	0.92	0.55	Lake Malawi, Mozambique	Tweddle and Turner (1977)
Lethrinops longipinnus	1.69	0.571	Lake Malawi, Mozambique	Tweddle and Turner (1977)
Lethrinops parvidens	1.20	0.487	Lake Malawi, Mozambique	Tweddle and Turner (1977)
Tilapia esculenta	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 tilapiine 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 α and β parameters, and asymptotic length (cm), L_∞. 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 α and β for the three indicator species specific to the Okavango Delta. For *O. andersonii* α is given as 0.004 and β is 3.424, for *O. macrochir* α is 0.014 and β is 3.106, and for *T. rendalli* α is 0.026 and β is 2.911. Based on Mosepele and Nengu's (2003) ranges for the von Bertalanffy parameters, PDF's for α and β were established: α Uniform (0.004, 0.026) and β Uniform (2.911, 3.424).

Mosepele and Nengu (2003) also calculated L_∞ for the three indicator species in the Okavango Delta. L_∞ 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_∞ was set to Uniform (40, 53).

A number of studies in southern Africa and the Okavango Delta investigate the growth coefficient (k) for various tilapiine 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 PDF's for each of the parameters. The PDF's 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 PDF's 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
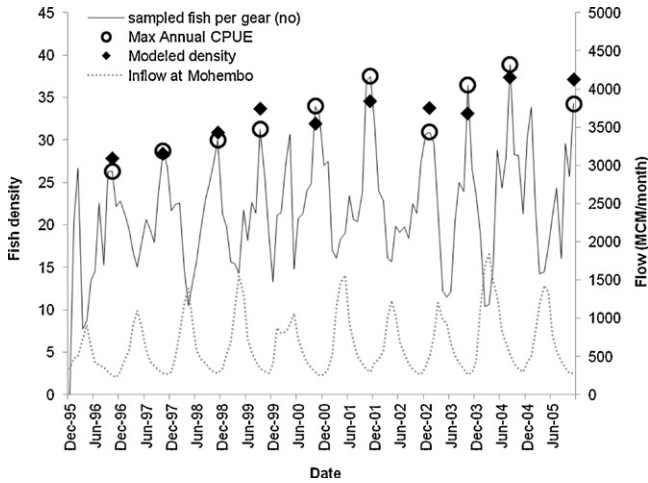
Fig. 5. The best fit model simulation for the initial inverse optimization. Coefficient of efficiency equals 0.64.

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
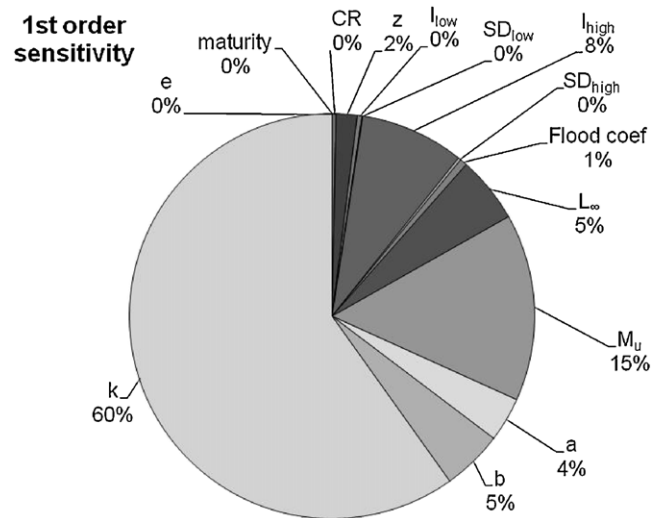

Fig. 6. First order sensitivity for the coefficient of efficiency of the modeled fish density compared to the measured catch per unit effort (CPUE) from the first inverse optimization.

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 PDF's (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
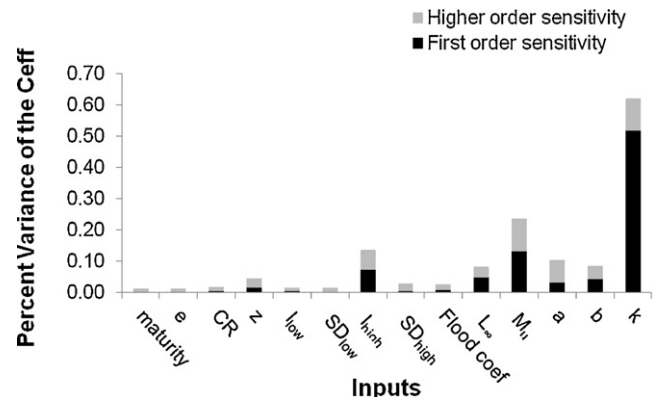

Fig. 7. First and higher order sensitivities for coefficient of efficiency of modeled fish density compared to measured CPUE from first inverse optimization.
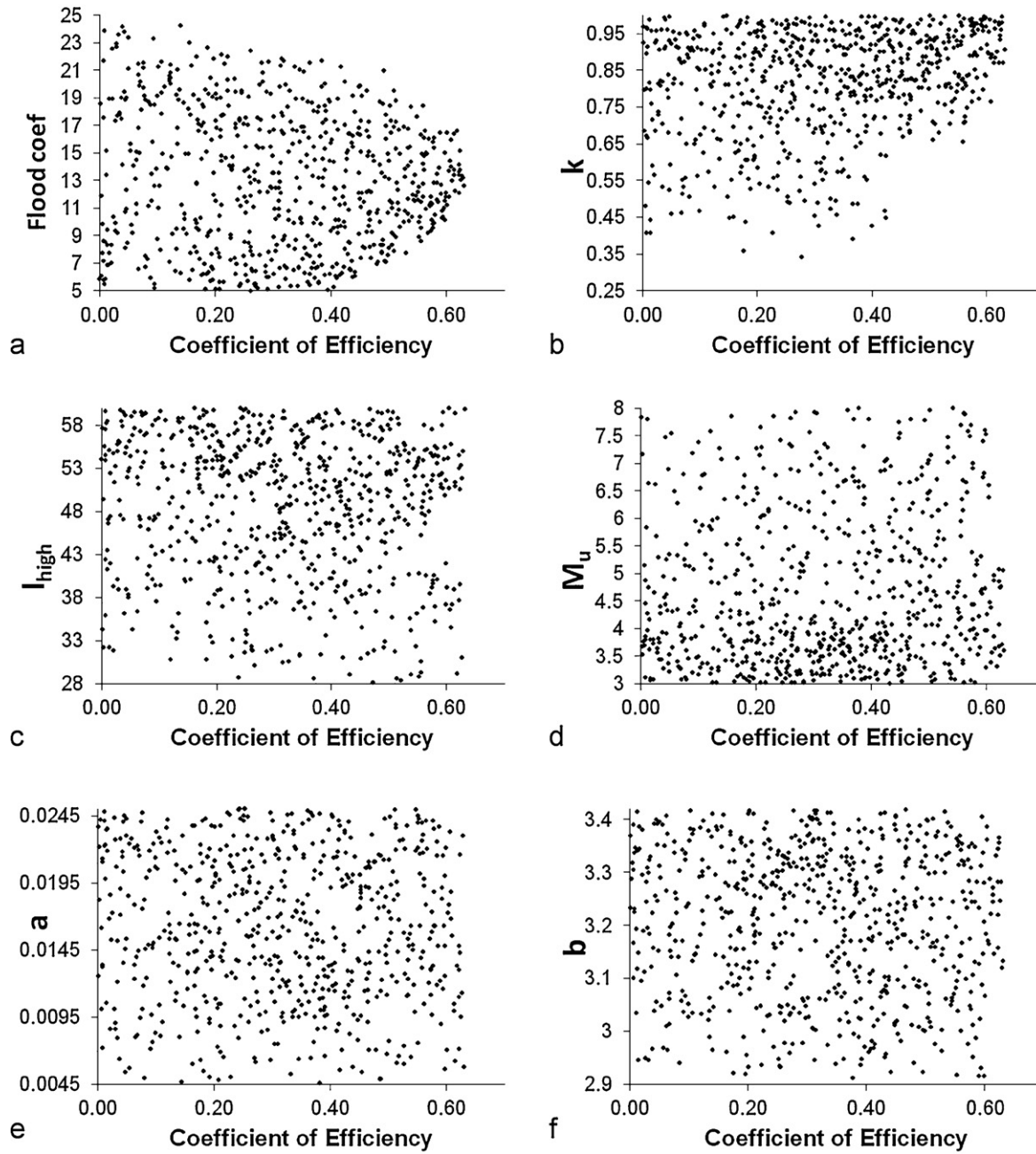
Fig. 8. (a–f) Scatter plots of values for the flood coefficient, k, M_u, L_{high}, a, and b creating behavioral outputs. Note that the flood coefficient converges toward a single value in the highest values for the coefficient of efficiency (best fit model runs). Only simulations with a ceff > 0 are 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: L_{high}, M_u, k, L_∞, and c. When the behavioral parameter distributions were shown to be significantly different from the non-behavioral parameter distributions, new PDF's were assigned to the parameters that matched the behavioral distributions. The behavioral and non-behavioral distributions for five parameters were show to be significantly different. The five significantly different distributions were all skewed and so triangular distributions were chosen to represent these PDF's (Fig. 10). This process truncated the prior PDF's. The GUA was then rerun to understand how this truncation affected the model's uncertainty.
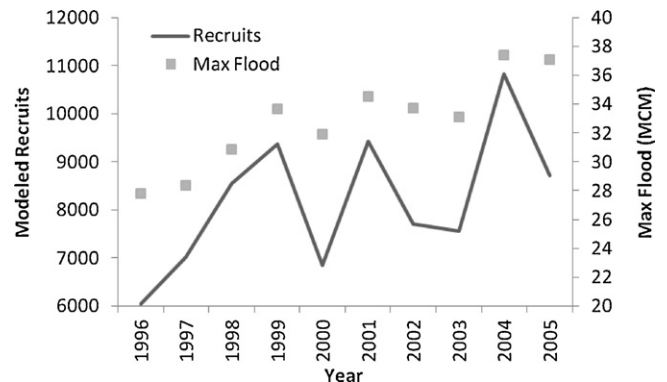

Fig. 9. The effect of the flood coefficient on recruitment (flood coef = 14).
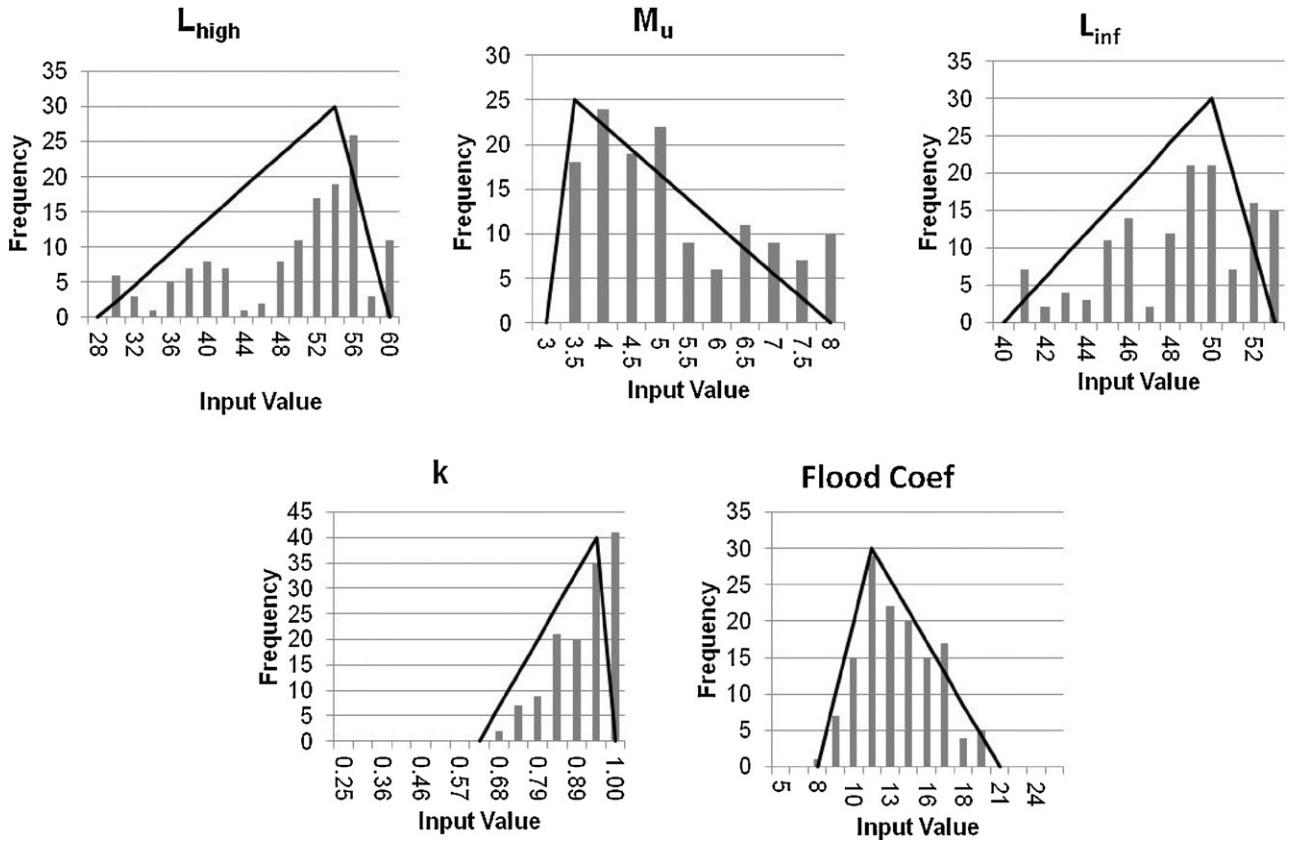
Fig. 10. Important parameters whose behavioral distributions are significantly different from the non-behavioral distributions. These graphs show histograms of the behavioral distributions and their newly defined triangular posterior distributions.

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_∞, 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 the 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
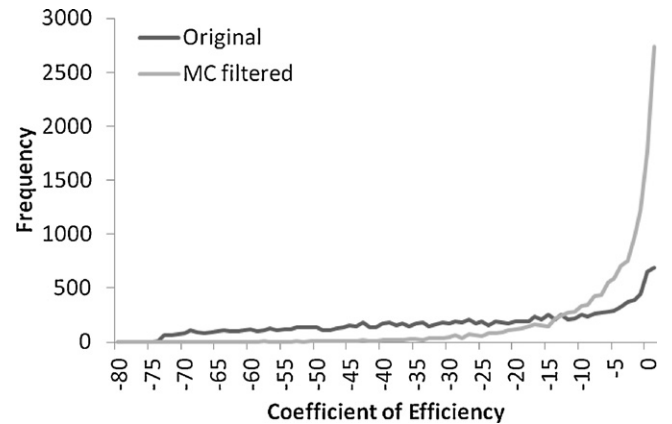

Fig. 11. All GUA results. (a) unfiltered (b) Monte Carlo (MC) filtered. Fig. 12 shows a blowup of results with coefficient of efficiencies greater than 0.
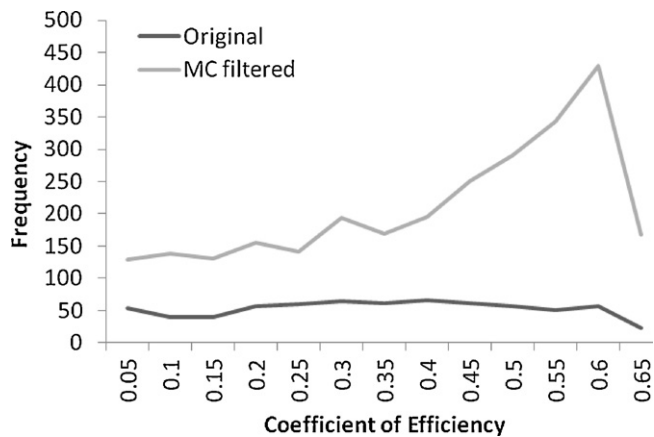
Fig. 12. Uniform and MC filtered GUA outputs with a coefficient of efficiency greater than 0.

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_∞, 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 efficiently 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 PDF's. The modeler can then work in tandem with the biologist to ensure that the new PDF's 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 ceff 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 (ceff 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.

References

Agostinho, A.A., Gomes, L.C., Veríssimo, 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. Prophesy, 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 multi-parameter 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 modelling, 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 (*Sptattus sptattus*). 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.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 Mcilwaine, Rhodesia. J. Fish Biol. 14, 419–424.

Mcgurk, M.D., 1986. Natural mortality of marine pelagic fish eggs and larvae – role of spatial patchiness. Mar. Ecol.-Prog. Ser. 34, 227–242.

Merona, B., Gascuel, 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, G.F., 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), (Pisees, 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., Moyle, 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.

Tweddle, 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 Liamnezimeer in die Oos-Caprivi 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.