

# Variation in Assemblages of Small Fishes and Microcrustaceans After Inundation of Rarely Flooded Wetlands of the Lower Okavango Delta, Botswana

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**Abstract** Water extraction from floodplain river systems may alter patterns of inundation of adjacent wetlands and lead to loss of aquatic biodiversity. Water reaching the Okavango Delta (Delta), Botswana, may decrease due to excessive water extraction and climate change. However, due to poor understanding of the link between inundation of wetlands and biological responses, it is difficult to assess the impacts of these future water developments on aquatic biota. Large floods from 2009 to 2011 inundated both rarely and frequently flooded wetlands in the Delta, creating an opportunity to examine the ecological significance of flooding of wetlands with widely differing hydrological characteristics. We studied the assemblages of small fishes and microcrustaceans, together with their trophic relationships, in temporary wetlands of the lower Delta. Densities of microcrustaceans in temporary wetlands were generally lower than previously recorded in these habitats. Microcrustacean density varied with wetland types and hydrological phase of inundation. High densities of microcrustaceans were recorded in the 2009 to 2010 flooding

season after inundation of rarely flooded sites. Large numbers of small fishes were observed during this study. Community structure of small fishes differed significantly across the studied wetlands, with poeciliids predominant in frequently flooded wetlands and juvenile cichlids most abundant in rarely flooded wetlands (analysis of similarity,  $P < 0.05$ ). Small fishes of  $< 20$  mm fed largely on microcrustaceans and may have led to low microcrustacean densities within the wetlands. This result matched our prediction that rarely flooded wetlands would be more productive; hence, they supported greater populations of microcrustaceans and cichlids, which are aggressive feeders. However, the predominance of microcrustaceans in the guts of small fishes ( $< 20$  mm) suggests that predation by fishes may also be an important regulatory mechanism of microcrustacean assemblages during large floods when inundated terrestrial patches of wetlands are highly accessible by fish. We predict that a decline in the amount of water reaching the Delta will negatively affect fish recruitment, particularly the cichlids that heavily exploited the rarely flooded wetlands. Cichlids are an important human food source, and their decline in fish catches will negatively affect livelihoods. Hence, priority in the management of the Delta's ecological functioning should be centred on minimising natural water-flow modifications because any changes may be detrimental to fish-recruitment processes of the system.

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## Introduction

Inundation of temporary wetlands improves the biological productivity of the associated rivers (Junk et al. 1989;

Bayley 1995; Sparks 1995; Ward 1998; Lewis et al. 2001; Balcombe et al. 2007; Arthington and Balcombe 2011). Because of their high biological productivity—especially regarding macroinvertebrates, which are food resources for early life stages of fish—inundated temporary wetlands are ideal nursery sites for fishes. Inundation of temporary wetlands of river–floodplain systems is thought to improve fish recruitment by stimulating fish spawning and enhancing food availability and diversification of habitats (Coke and Pott 1971; Kwak 1988; Harris and Gehrke 1994; Junk 1999). Merron (1991) suggested that fish recruitment in the Okavango Delta (hereafter referred to as the Delta) predominantly occurs in temporary wetlands. The biological productivity of temporary wetlands is generally influenced by inundation dynamics in which wetlands interact with the timing, magnitude, duration, and frequency of flooding (Power et al. 1995). However, despite the acknowledged importance of inundation of temporary wetlands, we know little in general, and for the Delta in particular, about the linkages between flooding dynamics and biological responses.

The wetlands of the Delta are grouped into two major categories: the permanent wetlands and the temporary wetlands (McCarthy et al. 2005). The permanent wetlands are usually inundated with water, whereas the temporary wetlands experience periodic inundation and drying. The temporary wetlands may be further divided into two major types depending on the average return interval (ARI) of the floods: (1) the frequently flooded wetlands and (2) the rarely flooded wetlands (McCarthy et al. 2005; Murray-Hudson et al. 2011). The least increased frequently flooded wetlands are closer to the active river channels and are inundated every flooding season or once in 2 years, whereas the rarely flooded wetlands receive water only during large floods with an ARI of once or twice in 30 years (Wolski and Murray-Hudson 2006). Large floods are experienced in the Delta during years of high rainfall and high inflows into the system (Mendelsohn et al. 2010). The inundation of these different temporary wetland types may have nonuniform biological responses.

The annual primary production cycle of the Okavango Delta is largely sustained by allochthonous energy mobilised from inundated temporary wetlands (Mendelsohn et al. 2010). When wetlands of the Delta dry, they support a high biomass of terrestrial vegetation that attracts foraging mammals, such as elephants, buffaloes, zebras, giraffes, small antelopes, and hippopotamuses (Bonyongo 2004). These foraging animals deposit large quantities of dung (nutrients) on the temporary wetlands, which supports a boom in aquatic production (algae and microcrustaceans) when inundation occurs (McLachlan 1971; Junk et al. 1989; Bayley 1995; Balcombe et al. 2007; Arthington and Balcombe 2011). Juvenile fish and small-

sized fish species (collectively referred to hereafter as small fishes) capitalise on the high microcrustacean densities (Bayley 1988; Høberg et al. 2002; Lindholm and Hessen 2007a).

Although there is widespread supposition that microcrustaceans are an important food source for early life stages of fish (Brooks and Dodson 1965; May 1974; Cushing 1972, 1990), this has not been validated within the Okavango Delta. The early life history of fish is characterized by high mortality (Trippel and Chambers 1997). Survival of fish during their early life stages affects recruitment success and, in turn, the variable dynamics of fish stocks (Cushing 1972, 1990; Horwood et al. 2000). Possibly as an adaptation to synchronise breeding with the availability of microcrustaceans, Floodplain River fishes spawn before or during inundation of temporary wetlands and raise their juveniles within these habitats (Munro 1990; Merron 1991; Welcomme 2001). Microcrustaceans in temporary wetlands are also preyed on by predatory macroinvertebrates, such as those of the family Chaoboridae (Lewis 1977; Arcifa 2000) and Notonectidae (Gilbert and Burns 1999; Lindholm and Hessen 2007b). Both macroinvertebrates and small fishes are also key food sources for higher-order organisms, such as larger fishes (Merron 1998), crocodiles (Wallace and Leslie 2008), and water birds (Cowx 2007). Therefore, the dependence of small fishes on microcrustaceans may be a critical trophic link allowing the productivity associated with wetland inundation to flow up the food chain (Fernando 1994).

Fish production in the Delta (Merron 1991; Mosepele et al. 2009; Ramberg et al. 2010) and elsewhere (Welcomme 1979; Lowe-McConnell 1987; Agostinho and Zalewski 1995) increases during years of large floods. However, there is debate regarding the causal mechanisms for high fish yield associated with these events. Numerous models, including the flood recruitment model (Humphries et al. 1999), the critical period hypothesis (Hjort 1914; May 1974), and the match/mismatch hypothesis (Cushing 1972, 1990) propose that microcrustacean availability is a key driver of early survivorship and overall fish production (stock size). However, others (King et al. 2009; Ramberg et al. 2010) believe that predation is more important and that poor survivorship during years of limited flooding is caused more by the increased exposure of young fish to greater predation within the main channel, as well as constricted wetland habitats, than by a lack of food. Although different causal mechanisms are proposed, relatively few studies in the Delta have assessed the link between wetland inundation, microcrustaceans, and production of small fishes.

There is a need to better understand the relationship between inundation of temporary wetlands and production of small fishes in the Delta because the natural hydrograph

will be altered by increasing future water abstractions (Ashton 2000; Mbaiwa 2004) and climate change (Andersson et al. 2006; Murray-Hudson et al. 2006; Milzow et al. 2010). Various water developmental projects—such as irrigation, hydropower dams, and expansion of municipal water supplies—have been proposed by Angola, Namibia, and Botswana. These are all expected to decrease water inflows into the Okavango Delta (Ashton 2000). The historically larger floods, evident from the natural hydrograph of the Delta, will be knocked out first, and on the extremes some of the temporary wetlands, such as the rarely flooded patches, will be excluded from the system permanently. The situation is likely to be complicated by climate change; most models within the region are predicting an increase in temperature and a decrease in rainfall (Andersson et al. 2006; Murray-Hudson et al. 2006; Milzow et al. 2010). If the Delta receives less water in the future, the extent of inundation of temporary wetlands will decrease, and fish production may be compromised.

This study examined the community structure of microcrustaceans and small fishes, together with their trophic relationships, in frequently and rarely flooded wetlands of the Okavango Delta. We hypothesized that as a consequence of nutrient and organic matter accumulation during years of no flooding, inundation of rarely flooded wetlands will produce greater densities of microcrustaceans when these patches are inundated, compared with frequently flooded wetlands, and that this will in turn create more suitable habitat for small fishes. An increased understanding of the link between inundation of different temporary wetland types and the associated biological responses will improve our ability to predict the likely consequences of decreased flooding on fish productivity and guide management options.

## Materials and Methods

### Study Area

The study was performed at the Okavango Delta in the Kalahari Desert of northern Botswana (Fig. 1). Rain falling in the highlands of Angola contributes the largest inflows into the Delta, and local rains are also important in determining the extent of inundation of the system (Andersson et al. 2006). Annually, the floods arrive in the upper Delta between February and April and reach the lower parts of the Delta 5 months later (Gieske 1996). The floods are distributed across the system through a series of distributory channels. As water flows through these channels, some of it overflows and inundates surrounding low lands, thus creating temporary wetlands.

### Study Sites

Eight frequently flooded and five rarely flooded wetlands were selected in the lower Delta for the present study (Fig. 1). The vegetation community composition in different wetland types is different with frequently flooded wetlands dominated by wetland grasses (Bonyongo et al. 2000). Thick stands of emergent sedges, as well as leaf-floating and submerged macrophytes, in deep open water habitats are also predominant in frequently flooded wetlands (Meyer 1999; Bonyongo et al. 2000). Rarely flooded wetlands are characterized by terrestrial grasses and thick forests dominated by *Acacia* spp. and *Colophospermum mopane* (Meyer 1999). Macrophytes *Ludwigia stolonifera* and *Lagarosiphon ilicifolius* become established over time within these wetlands (Siziba et al. 2011a).

### Some Hydrological Aspects of the 2009–2010 and 2010–2011 Flooding Seasons

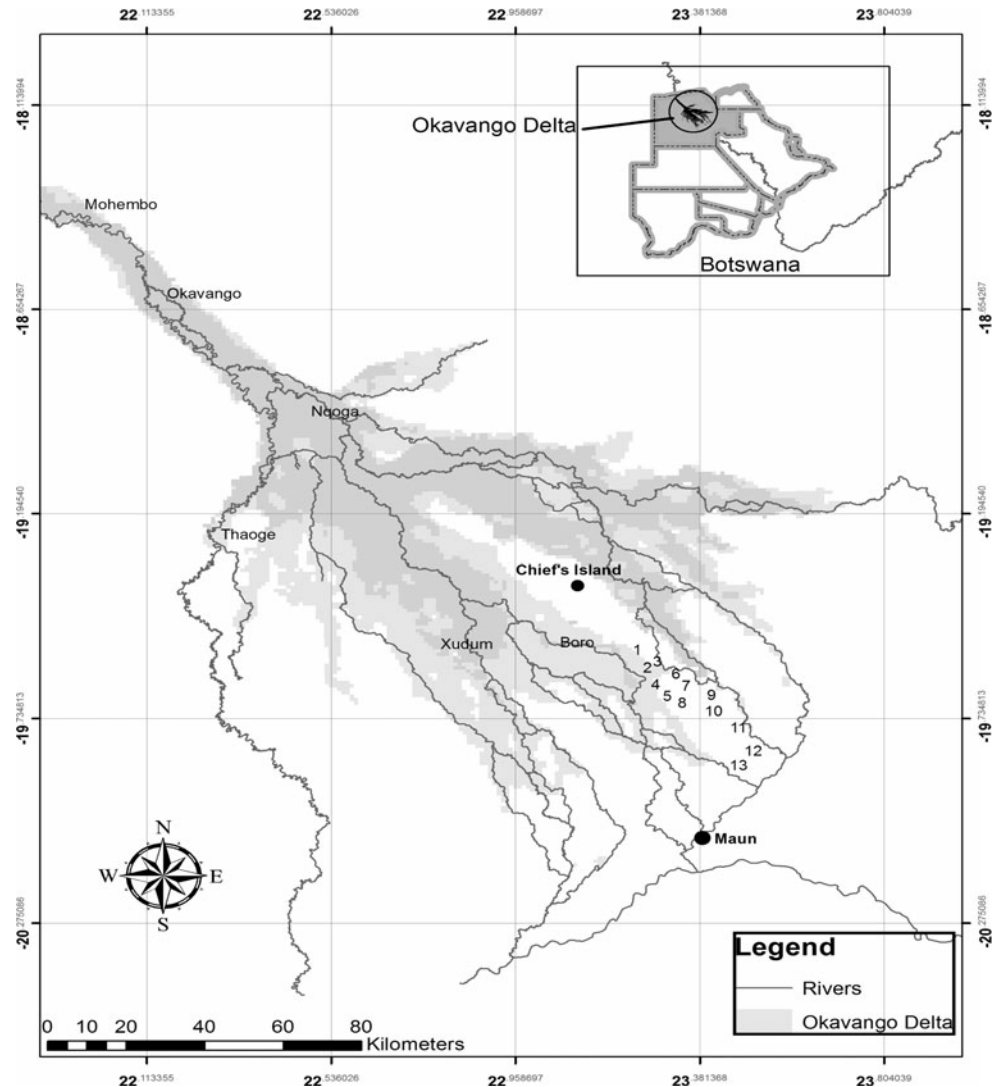
The large floods of 2009–2010 to 2010–2011 were of much greater magnitude than the those received by the Delta in the past 30 years (<http://168.167.30.198/ori/monitoring/water/>). The average monthly discharge from the Okavango River at Mohembo reached estimated peaks of 890 and 898 m<sup>3</sup>/s, respectively, in the 2009–2010 and 2010–2011 flooding seasons (Fig. 2). These peaks recorded in these two seasons were [50 % above the peak of average flooding years shown as 1989 and 1999 (Fig. 2.) During low to average floods, temporary wetlands are usually inundated for 3–4 months, whereas during this study water remained in the wetlands throughout the respective flooding seasons. The study wetlands ranged from 1,000 to 2,000 m long, 200 to 500 m wide, and 1.5 to 3.8 m deep at peak flooding during this study. The wetlands expand at the onset of flooding until peak flooding and then constrict. A detailed description of the studied wetlands is provided in Siziba et al. (2011a, b).

During the two flood seasons of study, water encroached the dry wetlands (rising flood phase) in May 2009 and April through May 2010. The maximum water levels reached within the study floodplains (flood peak) occurred in July 2009 and June through July 2010, and the gradual drying-up of floodplains (flood receding phase) coincided with the following months: October 2009, February through March 2010, September through November 2010, and January through March 2011.

### Field Sampling

Samples of microcrustaceans and small fishes were collected from the shallow inundated terrestrial grasses of the wetlands, referred to as the marginal zone. The choice of the

Fig. 1 Locations of the studied wetlands in the lower Okavango Delta, Botswana, showing frequently flooded (1–8) and rarely flooded (9–13) wetlands



study habitat of the temporary wetlands sites was influenced by previous studies in the Delta (Lindholm and Hessen 2007a; Siziba et al. 2011c) and elsewhere (Bayley 1988), indicating that marginal zones of the wetlands are the most productive and support greater densities of both microcrustaceans and small fishes. Sampling was undertaken on 14 occasions from May 2009 through March 2011 during the rising phase of the hydrograph (May 2009 and April through May 2010), at the flood peak (July 2009 and June through July 2010), and as flood waters were receding (October 2009, February through March 2010, September through November 2010, and January through March 2011).

#### Microcrustaceans

Microcrustaceans were sampled using the tube sampling method (Graves and Morrow 1998) due to the shallowness and high density of vegetation within the marginal zone. At

each site, a plexiglass tube (6 cm in diameter, 0.5 m in length) was pushed through inundated grasses to collect water samples. Microcrustacean samples from each study wetland were collected during the day (0800–1,500 h) from 20 randomly selected points separated by 10 m. A 20-L container was filled with microcrustacean samples to constitute a spatially composited sample representing each study wetland. To concentrate the microcrustaceans, the 20-L samples were filtered through a 45- $\mu$ m mesh net and fixed with Lugol's solution for processing in the laboratory.

During analysis, preserved microcrustacean samples were homogenised by gently mixing to attain an even distribution of organisms before the Utermohl technique (Paxinos and Mitchell 2000) was employed to quantify the microfauna. Depending on the density of microcrustaceans and turbidity, subsamples of 2 or 5 ml were sedimented in counting chambers for at least 4 h before the microfauna were identified and counted under an inverted microscope.



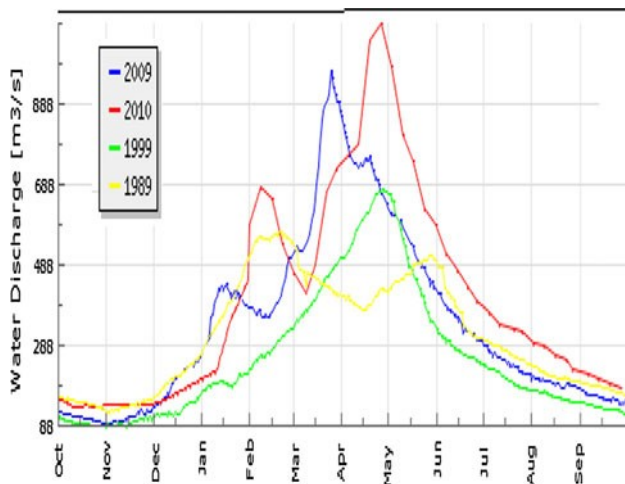


Fig. 2 Hydrographs of water discharge at Mohembo during sampling seasons (2009 and 2010). Hydrographs of years 1989 and 1999 are examples of inflows during small-sized floods to average flooding years (<http://168.167.30.198/ori/monitoring/water/>)

Except for the taxonomically challenging ostracods and nauplii of copepods, which could only be identified to family level, taxonomic keys (Korovchinsky 1992; Smirnov 1992, 1996; Orlova-Bienkowskaja 2001; Fernando 2002) were used to identify microcrustaceans to species level. The actual densities of microcrustaceans in the samples were calculated and expressed as numbers per litre according to the procedures in Masundire (1997). Published length–dry weight relationships (Botrell et al. 1976; Masundire 1994; Kawabata and Urabe 1998) were used to estimate microcrustacean biomass in the samples. For microcrustacean species not included in these publications, we applied length–weight equations of taxa with similar body shapes. Biomass was expressed as average dry weight (dw) per litre.

### Small Fishes

Small fishes were sampled at the same time as microcrustaceans using a throw-trap net design modified from Pelicice et al. (2005). The trap net consisted of a heavy bottom metal ring and a light top ring (see Siziba et al. 2011a for a full description). Separated by a distance of 20 m, the net was deployed five times from the edge of each study wetland. After deployment, the heavy bottom metal ring was pressed against the floor of the wetlands while at the same time suspending the light top ring above water to prevent trapped fish from escaping. The volume of water enclosed in the trap was estimated by multiplying the average water depth and enclosed area. Vegetation and other materials were removed from the trap before fish were scooped out using an aluminium dip net (0.20 × 0.45-m frame, 1-mm mesh) until no fish were captured in ten successive scoops.

Fish were identified as to species level where possible according to Skelton (2001). Fish abundances were expressed as numbers per sampled water volume ( $m^3$ ).

Subsamples of fish for diet assessment were fixed in 10 % formalin soon after capture and then preserved in 75 % ethanol within 24 h. Because it was not possible to assess the gut contents of all sampled species, only the guts of the most abundant tilapia juveniles—*Pseudocrenilabrus philander*, *Barbus haasianus*, and the topminnow *Aplocheilichthys hutereaui*—were examined. Before gut contents were examined, the total length of each sample was measured to the nearest millimetre. The stomach or the whole digestive tract of each fish sample was removed, placed into a Petri dish, and cut open in 20 mL of distilled water. Gut contents were apportioned into different major food types (algae, macroinvertebrates, microcrustaceans, detritus, plant matter, plant seeds, and small fishes) under an inverted microscope at 259 to 1009 magnification. The microcrustaceans present in the fish stomachs were identified to their lowest possible taxonomic level and enumerated. To avoid overestimating the numbers, only heads were counted when only body parts of microcrustaceans were encountered.

### Data Analysis

Data on microcrustacean density and abundance of small fishes was first checked for normality and homogeneity of variances using Kolmogorov–Smirnov procedure and Levene’s test, respectively. To improve on assumptions of normality and homogeneity of variances, both microcrustacean and small fishes data were  $\log_{10}(x + 1)$  transformed. Normalization tests and transformations were performed using SPSS version 19 (IBM, New York, NY, USA).

Trifactorial analysis of variance (ANOVA) was used to analyze the influence of wetland types (frequently flooded and rarely flooded), hydrological phases of inundation (filling phase, peak flooding, and flood recession), and sampling seasons (2009–2010 and 2010–2011) on both microcrustacean density and fish abundance in wetlands (Sokal and Rohlf 1991). Nonmetric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM), based on Bray–Curtis dissimilarity measures, were employed to assess differences in the community structure of microcrustaceans and small fishes between the frequently and rarely flooded wetlands. When significant differences in community structure were detected, similarity percentage procedures (SIMPER) were used to determine which species contributed the highest dissimilarity. Multivariate analyses were performed using Primer version 6.1.5 (Clarke and Gorley 2006).

The relative contribution of each major food type to the diet of individual fish was estimated using Hyslop's (1980) indirect volumetric method. The diet composition of the fish species was summarised by the frequency of occurrence method (Hyslop 1980), which records the percentage of stomachs containing a particular food item of the total stomachs containing food. The index of relative importance (IRI) (Pinkas et al. 1971; Hart et al. 2002) was used to determine the most important microcrustaceans in the fish guts. This index accounts for frequency of occurrence, relative volume of contribution, and relative abundance (in terms of number) according to the following formula:  $IRI = (\% \text{ frequency of occurrence} * (\text{relative } \% \text{ volume} * \% \text{ average number of microcrustaceans}))$ . Significance level in all of these analyses was set at  $\alpha \leq 0.05$ .

## Results

### Microcrustacean Assemblage

There was no significant difference in community structure across the different wetland types (ANOSIM, global  $R = 0.028$ ,  $P = 0.37$ ). Thirty-eight microcrustacean taxa were identified across the study wetlands. Numerically, copepods dominated the assemblage: nauplii (33.2 % of the total count), *Macrocyclus viridis* (1.0 %), *Mesocyclops leukarti* (15.1 %), and *Microcyclus varicans* (10.7 %) (Fig. 3). Other abundant groups by counts were cladocerans: *Alona* spp. (5.1 %), *Chydorus sphaericus*

(8.7 %), *Macrothrix spinosa* (12.5 %), *Simocephalus ser-rulatus* (2.4 %), and unidentified ostracods (3.6 %) (Tables 1, 2). Most of the cladocerans present in relatively large numbers in the samples were periphytic (Tables 1, 2).

The mean densities (all species) of microcrustaceans ranged between 147 and 1,544 individuals/L (Tables 1 and 2). ANOVA results showed that the mean density of microcrustaceans was influenced significantly by wetland type ( $F_{1, 737} = 6.30$ ,  $P = 0.012$ ), by hydrological phase of inundation ( $F_{2, 737} = 12.75$ ,  $P = 0.000001$ ), and by interactions between wetland types and sampling seasons ( $F_{1, 737} = 7.42$ ,  $P = 0.007$ ), between wetland types and hydrological phase of inundation ( $F_{2, 737} = 6.76$ ,  $p = 0.001$ ), and between sampling seasons and hydrological phase of inundation ( $F_{2, 737} = 21.38$ ,  $P = 0.0000001$ ) (Fig. 2a). The highest total density of microcrustaceans was recorded in rarely flooded wetlands during the 2009–2010 flood soon after inundation of these systems (Table 1 and Fig. 5a). The mean total density of microcrustaceans in temporary wetlands decreased in the 2010–2011 flooding season compared with that of 2009–2010 (Tables 1, 2). The average biomass in the 2009–2010 and 2010–2011 flooding seasons was  $4.07 \pm 0.33$  and  $4.7 \pm 0.17$  lg dw/L, respectively (ANOVA  $P \leq 0.05$ ).

### Distribution of Small Fishes

Twenty-three fish species were sampled in frequently flooded wetlands, whereas 15 species were sampled in rarely flooded wetlands. The sampled fish species belonged to six families: Cyprinidae, Distichodontidae,

Fig. 3 Relative abundance (% by counts) of microcrustaceans in inundated grasses of the temporary wetlands of the lower Okavango Delta

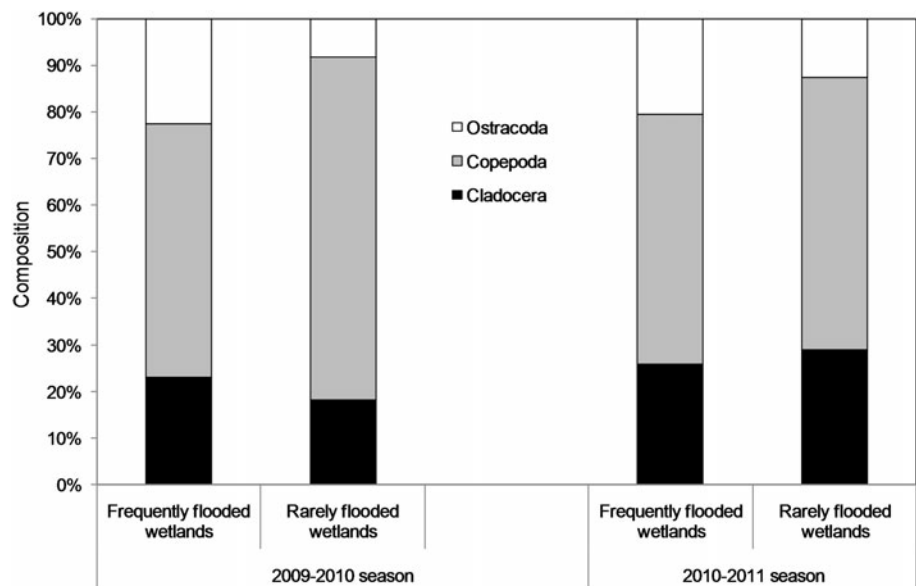


Table 1 Mean density (number per litre and SEM) of microcrustacean in frequently flooded wetlands and rarely flooded wetlands during the May 2009 to March 2010 season

Wetland type	Flood rising	Peak flooding	Flood recession
Frequently flooded			
Copepoda			
Cyclopoid nauplii	56 ± 30	161 ± 116	231 ± 45
<i>M. viridis</i>	2 ± 2	0	12 ± 3
<i>M. varicans</i>	10 ± 9	26 ± 19	84 ± 17
<i>M. leukartii</i>	9 ± 4	79 ± 52	154 ± 25
Cladocera			
<i>M. spinosa</i>	4 ± 2	33 ± 8	177 ± 71
<i>C. sphaericus</i>	10 ± 5	55 ± 28	62 ± 20
Alona	22 ± 13	30 ± 16	43 ± 11
Simocephalus	0	15 ± 2	27 ± 12
Moina	0	0	8 ± 0
Ostracoda			
Ostracods	32 ± 10	138 ± 71	78 ± 8
Mean total numbers/L	147	537	876
Rarely flooded			
Copepoda			
Cyclopoid nauplii	673 ± 326	832 ± 435	165 ± 42
<i>M. viridis</i>	21 ± 9	3 ± 2	0
<i>M. varicans</i>	152 ± 43	210 ± 120	66 ± 28
<i>M. leukartii</i>	13 ± 1	0	153 ± 82
Cladocera			
<i>M. spinosa</i>	4 ± 2	180 ± 158	51 ± 29
<i>C. sphaericus</i>	12 ± 3	225 ± 90	33 ± 14
Alona	0	75 ± 60	66 ± 21
Simocephalus	0	0	27 ± 19
Moina	1 ± 1	0	11 ± 4
Ostracoda			
Ostracods	1 ± 1	19 ± 4	111 ± 8
Mean total numbers/L	877	1,544	681

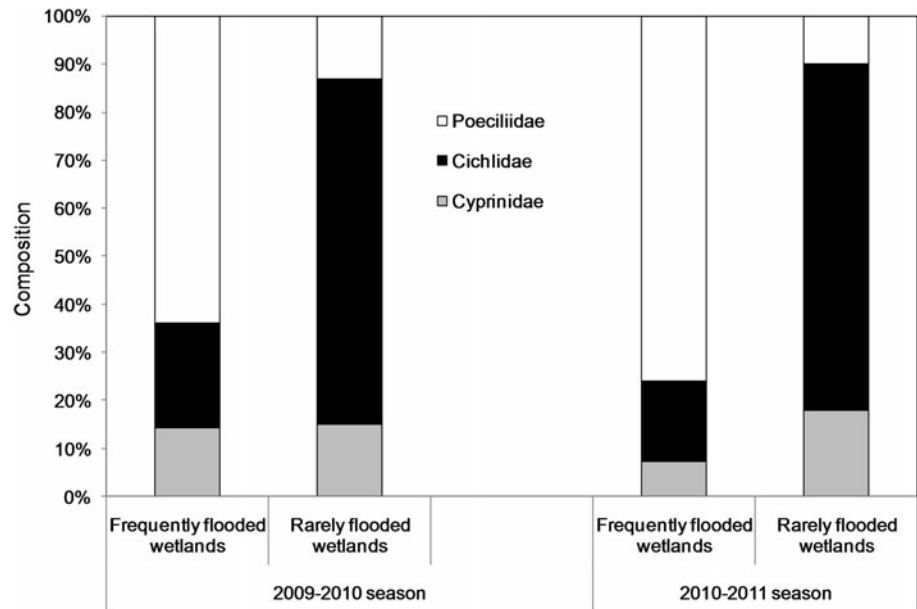
Cichlidae, Poeciliidae, Anabantidae, and Clarridae. Of these families, the poeciliids, cichlids, and small cyprinids were most widely distributed across the studied wetlands. Juvenile cichlids were predominantly collected in rarely flooded wetlands, whereas poeciliids were most abundant in frequently flooded wetlands (Fig. 4). The mean total abundance of fish was high during this study with a maximum of 282 and 260 individuals/m<sup>3</sup> caught in frequently flooded wetlands and rarely flooded wetlands, respectively. Trifactorial ANOVA showed no significant interactions for the main factors (wetland types, hydrological phases of inundation, and sampling seasons) ( $P \geq 0.05$ ). However, the ANOVA results showed a significant influence of sampling season ( $F_{1, 520} = 10.98$ ,

Table 2 Mean density (numbers per litre and SEM) of the most abundant microcrustaceans in frequently flooded wetlands and rarely flooded wetlands during the April 2010–March 2011 season

Wetland type	Flood rising	Peak flooding	Flood recession
Frequently flooded			
Copepoda			
Cyclopoid nauplii	389 ± 142	97 ± 25	167 ± 47
<i>M. viridis</i>		13 ± 5	18 ± 7
<i>M. varicans</i>	91 ± 73	32 ± 7	43 ± 8
<i>M. leukartii</i>	39 ± 11	58 ± 14	105 ± 16
Cladocera			
<i>M. spinosa</i>	29 ± 7	23 ± 7	78 ± 13
<i>C. sphaericus</i>	20 ± 5	17 ± 4	104 ± 53
Alona	45 ± 19	27 ± 10	42 ± 13
Simocephalus	20 ± 4	52 ± 18	17 ± 4
Moina	4 ± 2	13 ± 5	12 ± 4
Ostracoda			
Ostracods	8 ± 3	48 ± 18	32 ± 5
Mean total numbers/L	646	380	618
Rarely flooded			
Copepoda			
Cyclopoid nauplii	81 ± 21	146 ± 123	95 ± 35
<i>M. viridis</i>	42 ± 12	34 ± 26	17 ± 5
<i>M. varicans</i>	89 ± 64	360 ± 292	19 ± 5
<i>M. leukartii</i>	0	117 ± 72	37 ± 9
Cladocera			
<i>M. spinosa</i>	93 ± 67	4 ± 2	116 ± 44
<i>C. sphaericus</i>	43 ± 10	0	30 ± 12
Alona	30 ± 8	4 ± 1	20 ± 6
Simocephalus	4 ± 1	4 ± 2	34 ± 28
Moina	0	0	12 ± 4
Ostracoda			
Ostracods	4	8 ± 3	38 ± 7
Mean total numbers/L	384	676	395

$P = 0.001$ ) and hydrological phase of inundation ( $F_{2, 520} = 3.55$ ,  $P = 0.029$ ) (Fig. 2b) on the abundance of small fishes. In contrast to that of the microcrustaceans, the mean abundance of small fishes increased during the 2010–2011 flooding season compared with that of 2009–2010 (Fig. 5b). ANOSIM showed significant differences in the community structure of small fishes between the rarely and frequently flooded study sites (Fig. 6; global  $R = 0.496$ ,  $P = 0.0001$ ). SIMPER analysis detected a 48.2 % dissimilarity in fish assemblages between the two habitats due to differences in abundances of *Tilapia* and *Oreochromis* and minnows *A. hutereaui*, *A. johnstoni*, *A. katangae*, and *B. haasianus*. Among the

Fig. 4 Relative abundance (% of catches) of small fishes in inundated grasses of the temporary wetlands of the lower Okavango Delta



small-sized fish species, *B. haasianus* was clearly more abundant in rarely flooded wetlands.

#### Fish Gut Contents

Caught fish were categorized into four body size classes: <20, 20–29, 30–39, and ≥40 mm (Table 3). The gut content of all fishes included six major food categories: microcrustaceans, which represented 71.2 % of the overall diet, algae (10 %), detritus (8.4 %), macroinvertebrates (7.5 %), small fishes (1.6 %), and plant materials (1.3 %). The gut contents of small sizes of fishes (<20 mm) was entirely comprised of microcrustaceans (Table 3).

The proportions of microcrustaceans in stomachs of the cichlids (tilapias and *P. philander*) decreased with increasing body size (Table 3). The gut content of tilapias [20 mm in length was mainly detritus, algae, and plant materials. In contrast, the guts of *P. philander* of similar size (20 mm) mostly contained larger prey, such as calanoids; macroinvertebrates, such as shrimps (*Caridina nilotica*); and fish fry, including topminnows (Table 3). The diet of the relatively small-sized *A. hutereaui* and *B. haasianus* was dominated by microcrustaceans (Table 3).

IRI results indicated that *Moina micrura*, *M. spinosa*, *C. sphaericus*, and cyclopoids were the most important microcrustaceans preyed on by tilapias (Table 4). Cyclopoids, calanoids, *M. spinosa*, and ostracods were the most important organisms in the diet of *P. philander* (Table 4). *C. sphaericus*, cyclopoids, and *M. spinosa* were the most important organisms in the stomachs of *A. hutereaui*. The small cyprinid *B. haasianus* mainly fed on larger microcrustaceans, such as the cyclopoids, *M. spinosa*, *M. macrocopa*, and *Daphnia laevis* (Table 4). Nauplii of copepods

that were most abundant in the water column were rarely encountered in fish stomachs.

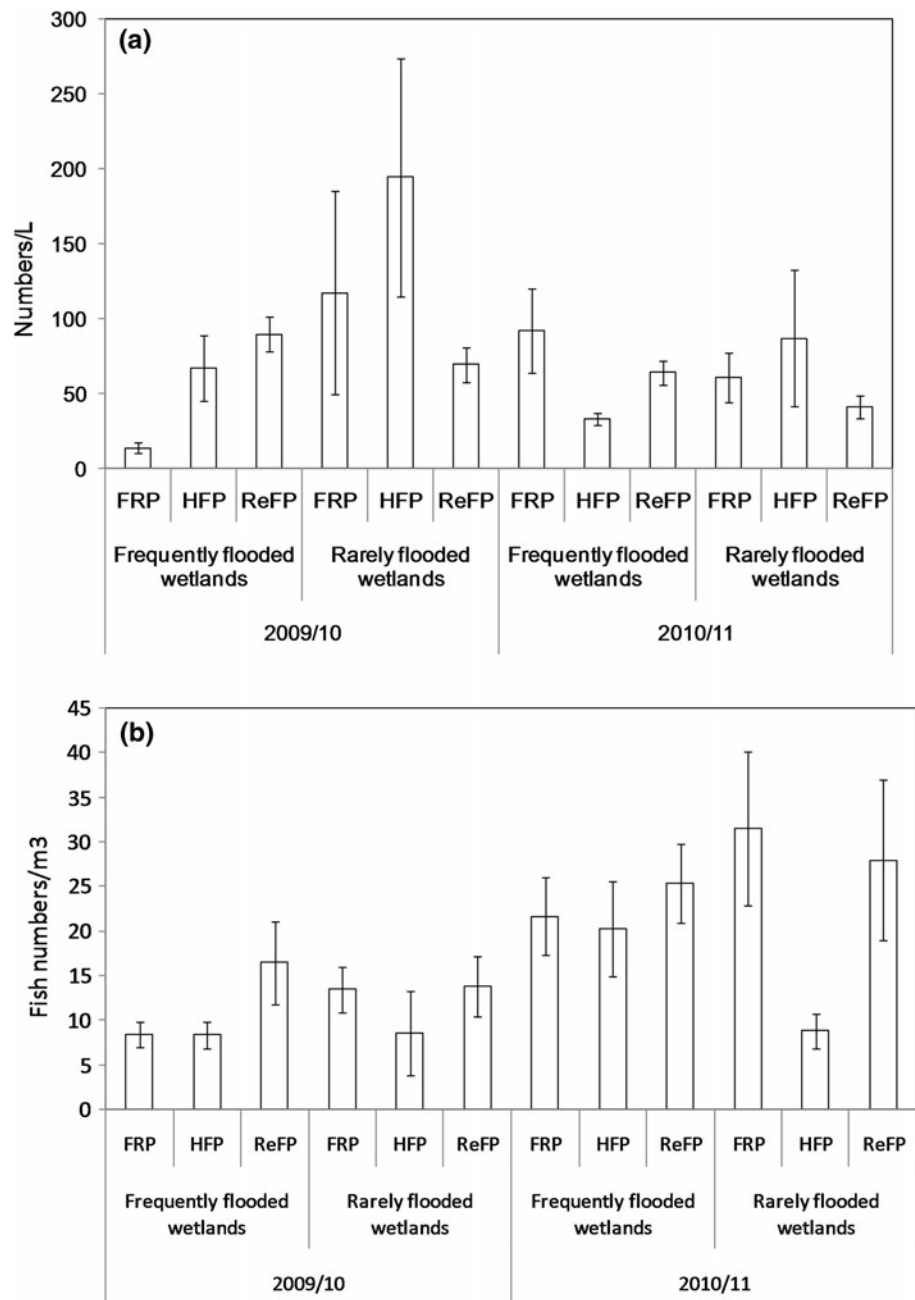
Tilapias sampled from the rarely flooded sites had more microcrustaceans in their guts than those from the frequently flooded sites (Table 5). The number of microcrustaceans counted in the stomachs of juvenile tilapias from rarely flooded sites ranged C143 *C. sphaericus*/fish gut. *M. spinosa*, *C. sphaericus*, and *M. micrura* were predominant (by numbers) in stomachs of tilapia juveniles from rarely flooded wetlands, whereas *C. sphaericus* were predominant (also by numbers [10 organisms/gut]) in stomachs of juvenile cichlids from the frequently flooded wetlands (Table 5).

#### Discussion

High numbers of microcrustaceans that that appeared after inundation of rarely flooded terrestrial patches of the system match the hypothesis of this study. Inundation of habitats rich in organic debris, such as the rarely flooded wetlands, is associated with a boom in aquatic biological activities (Angermeier and Karr 1984; Pusey and Arthington 2003; Rolls and Wilson 2010; Balcombe et al. 2007; Arthington and Balcombe 2011). According to Mosepele et al. (2009), nutrients such as phosphorus and organic carbon accumulate within the temporary wetlands during years of no flooding. The evidence from this study suggests that inundation of rarely flooded patches of the Okavango Delta may create the most suitable nursery habitats, which will in turn support high production of small fishes.



Fig. 5 The averages ( $\pm$ SEM) of a microcrustaceans/L and b small fishes/ $m^3$  across different wetland types during the different hydrological phases of inundation of 2009–2010 to 2010–2011 seasons. FRP filling phase, HFP peak flooding, ReFP flood recession



The large numbers of small fishes observed in temporary wetlands provide evidence of extensive utilisation of these habitats by fish during large floods as previously reported in the Delta by Lindholm et al. (2007). These small fishes were dominated by cichlid juveniles (*T. sparrmanii*, *T. rendalli*, *P. philander*, and *Oreochromis* spp.), topminnows of the genus *Aplocheilichthys*, and small cyprinids of the *Barbus* spp. as previously reported (Høberg et al. 2002; Lindholm et al. 2007; Siziba et al. 2011a). Large numbers of small fishes in temporary wetlands conflicts with Lindholm and Hessen (2007a) who found few small fishes in the same habitats during low floods. It seems that the use of

temporary wetlands in the Delta by fish depends on flood sizes and increases during large floods and decreases during drought years. Our results support findings from elsewhere in the world that large flooding of temporary wetland habitats enhance fish recruitment (Balcombe et al. 2007; Zeug and Winemiller 2008; King et al. 2009; Rolls and Wilson 2010) and support high fish production (Lowe-McConnell 1979; de Graaf 2003) per the flood recruitment model (Harris and Gehrke 1994).

In line with our hypothesis, fish assemblage structure differed between wetland types. Topminnows numerically dominated fish assemblages from frequently flooded sites,

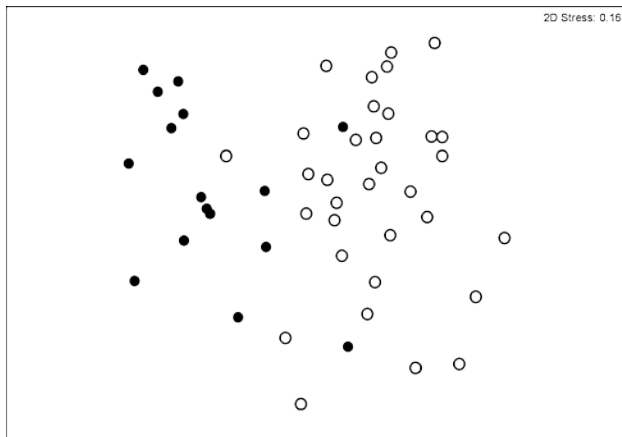


Fig. 6 NMDS ordinations of the 13 studied wetlands based on community structure of small fishes during different phases of flooding. Frequently flooded wetlands (empty circles) and rarely flooded wetlands (filled circles)

whereas juvenile cichlids dominated the rarely flooded sites. We propose that in temporary wetlands of the Delta, dietary requirements of the fish drove this association. For example, adult topminnow diet is known to be based on small-sized invertebrates (Skelton 2001) whereas, in contrast, adult cichlids feed largely on terrestrial detritus and

algae (Merron 1991; Winemiller and Kelso-Winemiller 2003), items that were found in high abundance in the most productive environs of rarely flooded wetlands (Siziba et al. 2011a). High numbers of cichlid juveniles within inundated rarely flooded terrestrial patches was also reported by an earlier study in the Delta (Siziba et al. 2011b). Greater numbers of microcrustaceans in the guts of individuals of cichlid juveniles sampled from rarely flooded wetlands than those from frequently flooded wetlands gives more evidence to our prediction of high productivity of rarely flooded wetlands. Therefore, the human preference for cichlids as a fishery target in the Delta (Merron and Bruton 1995; Mosepele 2000) suggests that large floods are likely to be important if the fishery is to be sustained.

Microcrustaceans were the most abundant food items in the diet of small fishes of the temporary wetlands. These microfauna were relatively more important with a frequency of occurrence of \*100 % in the diet of fishes especially within the size class of  $\geq 20$ -mm TL. The predominance of microcrustaceans in guts of small fishes within the temporary wetlands is in agreement with other studies performed elsewhere (Brooks and Dodson 1965; May 1974; Cushing 1990; Meschiatti and Arcifa 2002; Medeiros and Arthington 2008) and in the Delta (Høberg

Table 3 Contribution by volume (vol%) and frequency of occurrence (% freq) of microcrustaceans and other food types in the stomachs of tilapia juveniles *A. hutereaui*, *P. philander*, and *B. haasianus*

Size class (mm)	Food items	Tilapias (n = 114)		<i>A. hutereaui</i> (n = 80)		<i>P. philander</i> (n = 80)		<i>B. haasianus</i> (n = 80)	
		% Vol	% Freq	% Vol	% Freq	% Vol	% Freq	% Vol	% Freq
\20	Algae	7.4	6.1	7.5	7.7	15.7	33.3	0	0
	Macroinvertebrates	7.3	21.2	20.0	23.1	0	0	0	0
	Microcrustaceans	85.3	100.0	72.5	100.0	84.3	100.0	100.0	100.0
20–29	Algae	14.6	50.0	0	0	0	33.3	0	0
	Detritus	10.4	37.5	0	0	0	0	0	0
	Macroinvertebrates	20.0	45.8	67.8	66.7	23.5	33.3	9.2	10.0
	Microcrustaceans	51.4	97.9	32.7	100.0	76.5	100.0	90.8	100.0
	Plant matter	3.7	2.1	0	0	0	0	0	0
30–39	Algae	29.0	88.2	0	0	0	0	0	0
	Detritus	22.9	82.3	0	0	0	0	0	0
	Macroinvertebrates	11.7	41.1	0	0	0	0	0	0
	Microcrustaceans	28.7	100.0			100.0	100.0	100.0	100.0
	Plant matter	7.8	5.9	0	0	0	0	0	0
[40	Algae	19.4	93.3	0	0	0	0	0	0
	Detritus	28.8	100.0	0	0	0	0	0	0
	Macroinvertebrates	9.8	26.7	0	0	25.2	42.9	0	0
	Microcrustaceans	8.4	53.3	0	0	35.6	71.4	0	0
	Plant matter	27.2	26.7	0	0	0	0	0	0
	Plant seeds	6.4	6.7	0	0	0	0	0	0
	Small fishes	0	0	0	0	39.2	57.1	0	0

Table 4 IRI for invertebrates consumed by small fishes within the temporary wetlands of the Okavango Delta

Invertebrates	Tilapia	P. philander	A. hutereaui	B. haasianus
<b>Cladocera</b>				
M. micrura	2,169.1	97.0	679.9	1,887.1
Macrothrix	1,395.8	1,812.5	1,501.4	2,134.6
Pleuroxus	583.7	31.7	0	864.9
Chydorus	1,190.4	126.1	6,032.9	322.9
Simocephalus	313.6	207.1	205.1	79.5
Dhuvedia	97.8	132.5	0	0
Diaphanosoma	21.3	1,529.0	0	0
Ceriodaphnia	81.9	37.3	85.3	370.8
D. laevis	100.1	0	0	1,865.0
M. macrocopa	0	456.1	0	0
Alona	205.2	208.2	931.0	0
Allonella	26.5	0	0	0
Ilyocryptus	3.5	0	0	0
<b>Copepoda</b>				
Nauplii	3.5	79.2	64.2	0
Cyclopoids	1,264.1	0	2,270.6	5,049.4
Calanoids	0	2,605.5	0	0
<b>Ostracoda</b>				
Ostracods	1,128.1	1,143.5	90.1	793.4
<b>Rotifers</b>				
Lecane	0	0	548.1	0
Asplanchna	0	15.8	179.8	0
Keratella	0	0	90.9	0
<b>Macroinvertebrates</b>				
Mosquito larvae	0	21.4	0	0
C. nilotica	0	683.6	0	0

et al. 2002). The large number of microcrustaceans in the stomachs of small fishes further support the important trophic link of these microfauna in conveying energy to fish, which in turn support other higher-order consumers (Winemiller 1996; Jones et al. 1999; Fisher et al. 2001).

This study showed that with increasing body size, tilapias changed their diet from that dominated by microcrustaceans to one dominated by detritus and vegetative materials, whereas P. philander switched to larger animals, such as calanoids, shrimps (*C. nilotica*), and small fishes. However, the small-sized fish species, A. hutereaui and B. haasianus remained feeding on microcrustaceans even after exceeding the 20-mm size class. According to Medeiros and Arthington (2008), small microphagic planktivores/insectivores, such as minnows, are limited in choice of food items by their small body and small mouth-gape sizes. The shift of tilapias to a detritus-based diet has been observed in the Delta (Høberg et al. 2002), and the progressive shift of P. philanders with increasing body size toward larger animals is in line with other reports (O'Brien 1979; Mhlanga 2004). However, in the Delta, the shift by tilapias from a microcrustacean-based diet to other food

Table 5 Mean counts (number/gut) of microcrustaceans in stomachs of tilapia juveniles in temporary wetlands of the lower Okavango

	Frequently flooded wetlands (n = 57)	Rarely flooded wetlands (n = 57)
<b>Cladocera</b>		
Moina	7 ± 2	21 ± 8
Macrothrix	9 ± 3	48 ± 18
Pleuroxus	1 ± 0.4	15 ± 5
Chydorus	10 ± 2	31 ± 11
Dunhevedia	1 ± 0.6	1 ± 0.5
Simocephalus	3 ± 1	4 ± 2
Diaphanosoma	2 ± 1	4 ± 2
Ceriodaphnia	4 ± 2	1 ± 0.3
D. laevis	1 ± 0.5	4 ± 2
Alona	4 ± 2	6 ± 3
Allonella	4 ± 3	0
<b>Copepoda</b>		
Cyclopoids	5 ± 2	3 ± 1
Nauplii	2 ± 1	1 ± 0.5
<b>Ostracoda</b>		
Ostracods	4 ± 1.5	8 ± 0.5

items seemed to occur earlier in life than what has been reported elsewhere (Balarin and Haller 1982; Moriarty and Moriarty 1973; Lazzaro 1991). Early shifts and inclusion of other food items in their diets by tilapias may be an adaptation to the short-lived nature (3–4 months) of wetland inundation on the Delta. Furthermore, early shifts in diet may be a survival strategy because they decrease the period of dependence on microcrustaceans, which were the key food source for small fishes within the system. Hence, based on the critical period hypothesis (Hjort 1914, 1926; May 1974) and the match/mismatch hypothesis (Cushing 1972, 1990), microcrustacean availability in the Delta is likely to regulate recruitment of juvenile fish into adult fish populations before they exceed the 20-mm size class.

The assemblage structure, density, and size class of microcrustaceans collected during this study differed considerably from previous collections on the Delta. Microcrustaceans collected during years of low flows (i.e., drought) were dominated by large-sized and more planktonic species, such as M. micrura, D. laevis, and M. leukarti (Lindholm and Hessen 2007a). During this study, small-sized nauplii of copepods C. sphaericus and more periphytic cladocerans, such as M. spinosa, dominated the samples. Densities of microcrustaceans were also considerably greater during the drought surveys. For example, 5-fold more M. micrura were recorded by Lindholm and Hessen (2007a) than during the present study. We suggest that the high density of large-sized microcrustaceans during drought was a consequence of concentration effects

during wetland drying and decreased fish recruitment. In contrast, the lower densities and reduced size of microcrustaceans during large-sized flood years suggests that predation is shaping this assemblage. For example, the size efficiency hypothesis (Brooks and Dodson 1965) argues that selective predation leads to the extinction of large microcrustaceans and dominance of microfauna of smaller body sizes (Mehner and Thiel 1999; Shurin and Allen 2001). Intense predation pressure on microcrustaceans also typically results in an assembly of fewer individuals and fewer vulnerable planktonic genera, such as *Daphnia* and *Moina* (Brooks and Dodson 1965; Fernando 2002) such as observed here. Intense predation pressure on microcrustaceans by small fishes within the temporary wetlands of the Delta has been suggested by others (Ramberg et al. 2006; Høberg et al. 2002; Siziba et al. 2011b).

It appears that the magnitude of flooding indirectly shapes the microcrustacean assemblage by affecting the rates and key sources of mortality. We propose that during years of small floods (drought years), microcrustaceans in temporary wetlands are self-regulated by density-dependent mechanisms, such as competition among microcrustaceans for limited resources, which sees the larger individuals survive (Lindholm and Hessen 2007a). Fish predation is relatively unimportant during drought years because low water levels limit fish passage into temporary wetlands (Lindholm and Hessen 2007a). During years of large flood, density-dependent mechanisms are relaxed due to the abundance of available habitat. Fish have good access to the wetlands where they breed and prey heavily on microcrustaceans. Therefore, during large floods, microcrustacean assemblages are likely to be regulated by predation rather than by the density-dependent forces. Therefore, we suggest that manipulative experiments, possibly through microcosms, should be performed to understand the actual predation effect of small fishes on microcrustacean assemblages of the Delta.

## Conclusion

The findings of this study suggest that in the Delta, fish recruitment and production may increase during years of large floods. This is because large floods increase the area of inundated terrestrial patches, including the rarely flooded wetlands, which are nursery habitats for cichlids, an important food source for people in Botswana. The small fishes that dominate the temporary wetland habitats predominantly feed on microcrustaceans, particularly fish of <math>\leq 20\text{-mm}</math> body size. Hence, low availability of microcrustaceans due to no or reduced extent of Delta inundation may negatively affect fish stocks by constraining the production of fish during their early life stages (<math>20\text{ mm}</math>).

This implies that the loss of temporary wetlands may lead to poor recruitment, which will adversely affect higher-order animals, such as fish, aquatic birds, piscivorous fishes, crocodiles, and human beings. Therefore, in the Delta the management challenge lies in striking a balance between water needed for the ecological functioning of the system and that for needed for developmental projects. We suggest that management efforts in the Delta should consider the significance of inundation of temporary wetlands, including the rarely inundated terrestrial patches, on the availability of microcrustaceans and production of small fishes.

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