

FISH COMMUNITY STRUCTURE AND FOOD WEB ECOLOGY IN THE LOWER
OKAVANGO DELTA, BOTSWANA

A Dissertation

by

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ABSTRACT

Alteration of the flow regime may affect species distributions, mechanisms of community assembly, and patterns of energy flow within and between fluvial ecosystems. Changes in the periodicity and predictability of flows may reduce a river's capacity to produce ecosystem services affecting human welfare. This dissertation assesses how periodic wetting and drying influence fish assemblage structure and food web dynamics in rivers of the lower Okavango Delta, Botswana. This information should aid in the development of appropriate management interventions that balance biodiversity conservation with sustainable use of ecosystem services.

During low-flow periods, ephemeral aquatic habitats had higher α diversity and higher species turnover compared to permanent habitats, indicative of fish aggregation and random changes in species abundance at a local scale as habitat patches became smaller and more isolated. Assemblage nestedness was higher in permanent habitats, suggesting fish had dispersed non-randomly among patches in that habitat type as water levels fell. During high-water periods, fish assemblages were homogenized both at local and regional scales, suggesting a greater influence of mass effects. Controlling for the influence of season and habitat type on species abundance showed most negative species co-occurrences involving predators and potential prey, suggesting that predation mortality or predator avoidance could be a primary driver of species segregation. Most aggregations involved intra-guild interactions among non-predatory species, suggesting species affinity to similar habitats. The biomass of most fish populations was supported

by food chains originating from either seston or C4 grasses. The degree of dependence on a single source was positively related to trophic position during the dry season in the Boro River (a highly ephemeral river), suggesting that species higher in the food web assimilated material disproportionately from one source during this period. During the same period, the degree of dependence on a single source was inversely related to trophic position in Boteti River (a more permanent river), suggesting that fish foraging habits shift in response to seasonal patterns of connectivity and habitat availability. I infer from these findings that maintenance of a relatively natural flow regime will be necessary for conserving aquatic ecosystem structure and function in this system.

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CHAPTER I

INTRODUCTION

River-floodplain ecosystems are complex, with diverse biota, high environmental heterogeneity that is dynamic in response to hydrological fluctuations (Dittrich et al. 2016). Consequently, ecological communities in these systems may experience changes in species richness and composition over variable scales of space and time (Fernandes et al. 2014). Changes in the periodicity and predictability of flows may reduce a river's capacity to produce ecosystem services affecting human welfare. For example, reduced flows may cause an alteration or reduction in aquatic habitats available for fish reproduction or reduce inputs of food resources from the terrestrial environment that support aquatic food webs (Junk et al. 1989, Tockner et al. 2000). Alteration of the flow regime usually affects the physical and chemical dynamics of the river, including nutrient cycling and sediment transport (Roelke et al. 2006, Winemiller et al. 2006). Identification of biodiversity patterns river-floodplain systems and the processes that sustain it is an essential step towards better ecological understanding and natural resource management. This dissertation aims to contribute to our understanding of river-floodplain ecology by examining several aspects of fish assemblages in the lower Okavango Delta.

The Okavango Delta is situated in the northwestern region of Botswana in Southern Africa. It is the largest natural water body in Botswana and contributes about

80% to the national fish production (FAO 2007). Moreover, the Okavango Delta contributes significantly to Botswana's tourism industry of which more than 90% is wildlife and fisheries based (Mbaiwa 2005). Botswana contains only the downstream portion of the Okavango River, which originates in Angola and flows through Namibia. This places the country's tourism industry and the livelihoods of riparian communities in a precarious situation due to potential severe threats to biodiversity from proposed water extraction schemes upstream, climate change, and the impending growth of mining activities (Mitchell 2013). All of these factors may alter the magnitude and timing of the annual flood pulse, thus exacerbating flow intermittence and habitat fragmentation, especially in the terminus region of the delta.

At present, the Okavango Delta has a natural flow regime and is described as a relatively pristine ecosystem with high spatial and temporal environmental heterogeneity and biodiversity, including native megafauna. The floodplains are submerged during the annual flood pulse, thus forming a homogeneous aquatic environment that subsequently becomes fragmented when flows decline during the dry season. During low flows in the lower Okavango Delta, fragmented aquatic habitats include isolated pools in floodplains and river channels that sustain assemblages of fishes and other aquatic organisms. Cycles of inundation and desiccation of these pools are believed strengthen the influence of stochastic factors operating on relatively short timescales on local assemblage structure (Hortal et al. 2014). Therefore, the lower Okavango Delta provides an excellent model system for testing ecological hypotheses to improve our theoretical understanding of complex and dynamic ecosystems.

Isolated pools may be used to address ecological questions pertaining to island biogeography, geographical gradients of biodiversity, metacommunities, species' trait variations and community structure on a relatively short ecological time scale (Jackson et al. 2013, Hortal et al. 2014). Hortal et al. (2014) discussed that fragmented pools and lakes may be seen as islands within a sea of terrestrial landscapes, because they can be clearly defined spatially, and they have biota that can be distinguished from those of surrounding areas in the landscape. The fish diversity in pools may be evaluated in relation to their age (i.e., duration of water retention), habitat diversity, and the influence of area or isolation on species richness (March and Bass 1995; Rolon et al. 2008; Bagella et al. 2010). Moreover, pool depth may serve a role similar to that of elevation in islands in terms of its influence on species diversity (Hortal et al. 2014).

Prior investigations of fish assemblages in the Okavango Delta have focused on permanent reaches of the upper Okavango Delta (Mosepele et al. 2011, Mosepele et al. 2017). A study by Merron and Bruton (1995) that surveyed fishes from intermittent rivers of the lower Okavango Delta and compared fish α -diversity between upper and lower regions of the delta (Merron and Bruton 1995). The food web ecology and fish community assembly in the intermittent rivers of the lower Okavango Delta have not been documented previously. The complex and dynamic food webs of river-floodplain systems are poorly understood (Winemiller 2004, Layman et al. 2012), and this is especially the case for intermittent rivers of sub-Saharan Africa. Generalizations about carbon sources that support river food webs are elusive, because sediment load, dissolved organic matter, primary productivity, transparency and densities of aquatic

organisms may vary from one system to the other, or from one time period to another (Roach 2013, Winemiller et al. 2014).

The aim of this dissertation was to improve our understanding of fish assemblage structure and food web dynamics in seasonally flooded rivers in the lower Okavango Delta and in so doing, contribute to sustainable management of biodiversity in this region. The rivers in the terminus of the Okavango Delta are facing environmental threats from human activities, including climate change, water diversion and pollution for mining. The following chapters provide an initial assessment of multiple components of fish diversity, community assembly mechanisms, and food web ecology in a poorly studied region of the Okavango Delta.

Chapter II addresses the role of hydrology in structuring fish communities in intermittent rivers of the lower Okavango Delta. Hydrology is particularly crucial in intermittent rivers because it has a temporal dimension (Ward 1989) that shifts distributions of lotic, lentic and terrestrial habitat types (Larned et al. 2010, Datry et al. 2016). During the wet season, high flows increase connectivity in three dimensions (longitudinal, lateral, and vertical) which facilitates dispersal of aquatic biota, nutrients and other material among locations in the riverscape (Fullerton et al. 2010). However, the dry season results in fish habitat loss and community disassembly, even to the point of local extirpation in ephemeral habitats (Benton et al. 2003, Fahrig 2003, O'Neil 2016). Therefore, to improve biodiversity conservation in intermittent rivers, it is imperative to understand how biota respond to changes in flow conditions.

Chapter III also compares fish assemblage structure in relation to hydrology, but goes further by addressing the potential influence of interspecific interactions by using joint species distribution modeling (JSDM). The idea that community assembly is governed by a set of rules was proposed by Diamond (1975). Connor and Simberloff (1979) critiqued this idea and pointed out that it lacked formal tests. Since then, ecologists have relentlessly sought evidence for deterministic causes of community assembly with particular emphasis on interspecific interactions (Ovaskainen et al. 2010, Morales-Castilla et al. 2015, Tulloch et al. 2018). Generally, abiotic factors may have a strong influence on species establishment and persistence at larger spatial scales (Heino et al. 2015, D'Amen et al. 2018) and they determine species fundamental niches (Kraft et al. 2015). At more local scales where biotic interactions may assume greater importance, organism fitness may be influenced by the restriction of the fundamental niche into a narrower realized niche (Chase and Leibold 2003, Stachowicz 2001, Ovaskainen et al. 2017). Despite these expectations, general assembly patterns are elusive (Scherrer et al. 2019). Joint Species Distribution Models (JSDMs) provide a means to infer the relative importance of different assembly mechanisms under varying environmental conditions. While sophisticated tools have improved our ability to detect non-random patterns of species co-occurrence, it is still difficult to infer the underlying mechanisms that produce these patterns (Dorman et al. 2018). This chapter shows that combining JSDMs with other data, such as species traits and trophic guilds, can facilitate inferences about cause and effect from statistical results.

Chapter IV investigates the food web ecology of seasonally flooded rivers in the lower Okavango Delta. I used stable isotope tracers of carbon and nitrogen to estimate the major energy pathways that support fish biomass in this river-floodplain system. The magnitude of the annual flow regime, which determines subsequent water retention time in fragmented pools, plays a pivotal role in determining changes in fish community structure in the Okavango Delta (Mosepele et al. 2009). This implies that food web pathways may be continuously changing both spatially and temporally depending on the magnitude of the flood pulse. Due to the complexity of the Okavango Delta, food web pathways are intricate and fragile with high sensitivity to human interference (Mosepele et al. 2009). Since natural flow variability ensures a periodic connection between aquatic and terrestrial subwebs, water extraction may negatively affect critically important food web pathways supporting fish production (Mosepele et al. 2009). In addition to water extraction, livestock grazing, floodplain recession (molapo) farming and invasions of alien species threaten biodiversity and fish production in the lower Okavango Delta (Ramberg et al. 2006, Motsumi et al. 2012). This chapter provides baseline data and preliminary results on consumer-resource interactions that will aid in the development of appropriate management interventions that balance biodiversity conservation with optimal use of ecosystem services.

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CHAPTER II

EPHEMERAL HABITAT SUPPORTS HIGH FISH ALPHA AND BETA DIVERSITY DURING DROUGHT IN A SUBTROPICAL SEMIARID WETLAND

Introduction

Shifts between flowing water, standing water, and terrestrial habitats in intermittent rivers lead to increased habitat complexity such that community diversity may result from multiple processes acting jointly across space and through time. During the dry season, when the habitat is fragmented into standing pools of water, dispersal limitation may increase diversity and allow coexistence of ecologically similar species (Leibold and Chase 2018). However, desiccation of intermittent river reaches often causes local extirpation of some species. After flow resumption, species recolonize these patches from their dry-season refugia, either by active or passive dispersal (Winemiller et al. 2010). Recruitment may also occur within-patches as a result of complex life-cycles (Lancaster and Belyea 1997, Winemiller et al. 2010) such as estivation (Johnels and Svensson, 1955, Fishman et al. 1986) and embryonic diapause (Watters 2009, Polačik and Podrabsky, 2015) that allow organisms to withstand complete desiccation. However, periodic cycles of wetting and drying over long periods may lead to enhanced functional acclimatization due to legacy effects that in turn may result in unexpected responses to local environmental variation (Hawkes and Kitt 2015, Vass and Langenheder 2017).

Within a river reach, total biodiversity (γ diversity) depends on average biodiversity within habitats (α diversity) and differences in biodiversity composition among habitats (β diversity) (Pelaez and Pavanelli 2018). Depending on the strength of local ecological filters, variation in species composition within similar habitats may result from deterministic factors such as priority effects, competition, and predation, or stochastic factors including random dispersal and random changes in species abundance (ecological drift) (Chase 2007, O'Neil 2016, Leibold and Chase 2018). In intermittent rivers, α , β , and γ diversity may exhibit dynamic variation along spatial hydrological gradients (Datry et al. 2017). For example, α diversity may significantly vary between permanent habitats and ephemeral habitats (Stromberg et al. 2005, Beesley and Prince 2010, Katz et al. 2012, Datry et al. 2017). Therefore, biodiversity conservation in intermittent rivers requires a further understanding of how communities respond to disturbances, such as flooding and drying.

β diversity is affected by compositional heterogeneity due to different species identities within and among sites (turnover) and ordered species loss where the species present in sites with poor species richness are proper subsets of the species in sites that have higher species richness (nestedness) (Baselga 2010, Anderson et al. 2011, Legendre 2014). In intermittent rivers, compositional heterogeneity and differences in species richness within and among aquatic habitats are higher with increasing fragmentation and environmental harshness (Bogan et al. 2013, Miyazono and Taylor 2015, Datry et al. 2014a, Ruhi et al. 2015). For example, fish and invertebrate assemblage composition may show significant turnover during the last stages of drought, and spatial

heterogeneity often declines during and immediately after flooding (Fernandes et al. 2009, Buendia et al. 2014). Species nestedness may dominate along intermittence gradients owing to a greater loss of species in reaches with short water residence time when compared to perennial reaches due to physiological and environmental constraints (Datry et al. 2014b). In addition to being influenced by the temporal dynamics and spatial scale of habitat disturbance, species turnover or nestedness are both influenced by interspecific variation in mobility (Tonkin et al. 2015) and landscape features (Datry et al. 2017).

Here, I provide additional insights into the drivers of fish community diversity in naturally functioning intermittent rivers. Flows in the Boro, Thamalakane, and Boteti rivers in the lower reaches of the Okavango Delta are intermittent in response to a sustained flood pulse that occurs each year from mid-winter (June) to mid-autumn (March). Part of the delta's fluvial network flows through the town of Maun, a rapidly growing human population that depends on water and aquatic resources from the delta. I obtained fish samples from four sites representing two different habitat types (ephemeral and permanent).

Surveys were conducted during the dry and wet seasons. I tested four hypotheses. (1) Fish α diversity was expected to be relatively lower during the flood peak compared with the falling-water phase of the annual hydrologic cycle. The lower α diversity results from high dispersal and low densities of most species within expanded and well-connected channel habitats. (2) Within aquatic habitat types, assemblage nestedness was expected to be greater among patches in the permanent habitat type

compared to the ephemeral habitat type, and species turnover was expected to be higher in the ephemeral habitat type compared to the permanent habitat type during the dry season. (3) Similarly, species turnover between aquatic habitat types was expected to be higher during the dry season due to habitat fragmentation and isolation that increase the strength of environmental filtering and ecological drift. (4) Fish assemblages were expected to be homogenized during the high-water period due to increased aquatic habitat connectivity and greater fish dispersal resulting in higher between-habitat similarity of assemblage structure.

Methods

Study area

The Okavango Delta (19°17' S, 22° 54' E) in northern Botswana is an inland delta comprised of a complex network of channels that creates habitat heterogeneity and supports ecosystem productivity within an arid subtropical region. The total area of the delta varies between 12, 000 km² during the wet season and 3, 000 km² during base flow conditions (Gumbrecht et al. 2004). The delta is classified as a natural ecosystem with relatively high biodiversity, especially for large mammals (Mladenov et al. 2005). Species richness in the Okavango Delta is estimated to include multiple taxonomic groups. Among them are 71 fishes, 33 amphibians, 64 reptiles, 444 birds, 122 mammals, and approximately 1300 plants (Ramberg et al. 2006). The magnitude and duration of the annual flood pulse depend on the amount of rain falling in the Angolan highlands where headwaters originate. The flood pulse in the lower delta is not correlated with

local rainfall (Ringrose et al. 1988) and peaks typically between August and October (McCarthy et al. 1998).

Sampling scheme

I conducted surveys at four sites in intermittent rivers (Boro, Thamalakane, and Boteti) of the lower reaches of the Okavango Delta (Figure 1). One site (Borojunction, BJN; 19° 55' 01.0"S; 023° 30' 52.0"E) was located where the Boro River joins the Thamalakane River. Approximately 4 km upstream of the junction on the Boro River was a second survey site (Botswana Defence Force Camp, BDF; 19° 52' 28.1"S; 023° 26' 45.0"E). Two additional sites were located downstream; on the Thamalakane River at Dikgathong (DKN) (20° 08' 27.9"S; 023° 22' 38.5"E) and on the Boteti River at Chanoga (CHN) (20° 10' 02.4"S; 023° 39' 33.6"E). At DKN, the river branches. One channel flows southwest towards Lake Ngami, and the other channel forms Boteti River that flows southeast through CHN, terminating in Makgadikgadi salt pans.

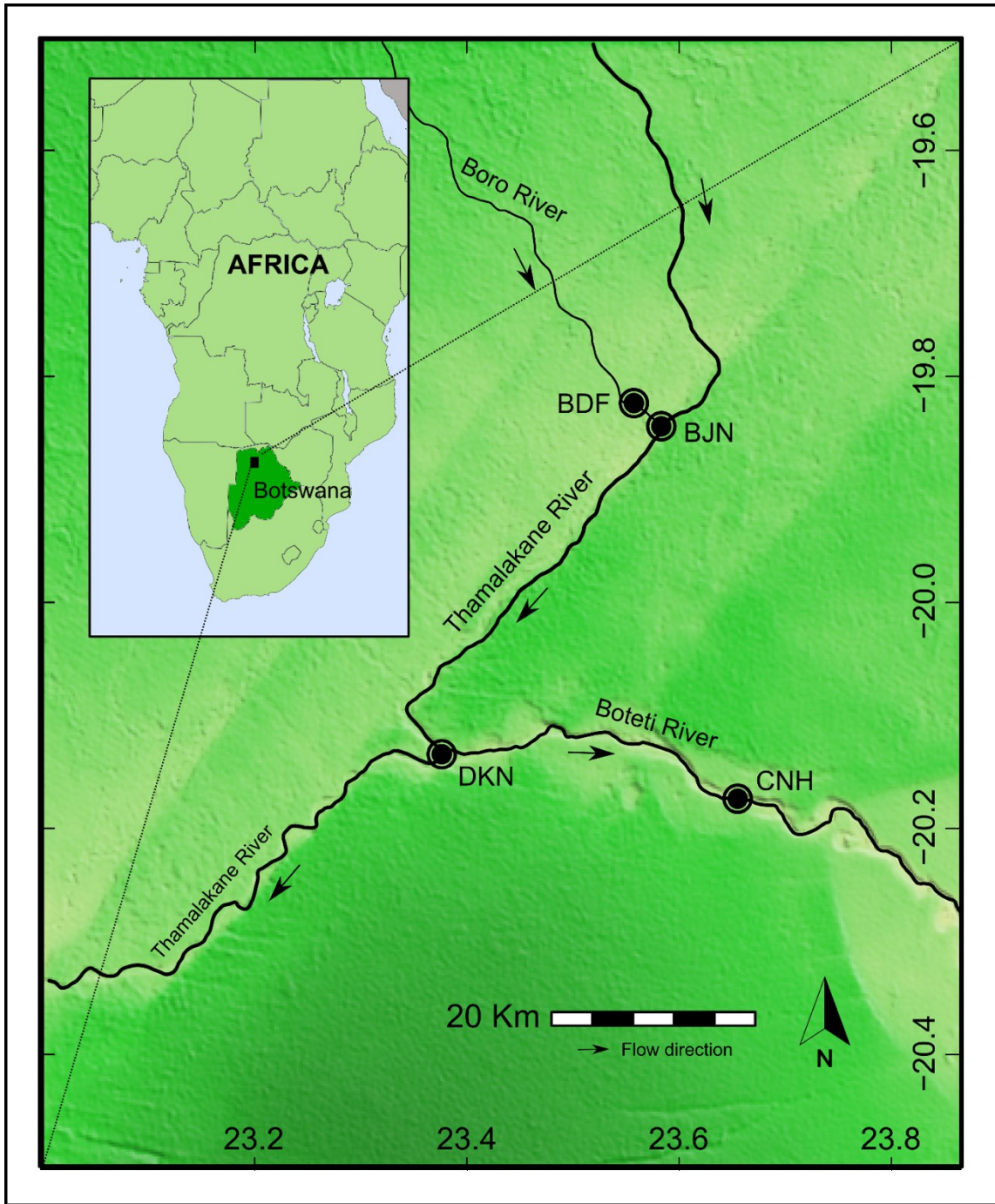


Figure 1. A map of the study sites in the lower Okavango Delta. BDF and BJN are located upstream, and BJN is a confluence between the Boro River and the Thamalakane River. Downstream, Thamalakane River branches at DKN to form the Boteti River on which CHN is located. The direction of water flow is shown with arrows.

Water levels were high at all sites from August to November, and this period was classified as the *high-water* season (Figure 2). From December to February, water levels had fallen, and this survey period was classified as the *low-water* season. During the low water season, the four sites encompassed a range of hydrological conditions. Compared to other sites, CHN and DKN retained water for extended periods. These sites remained wet and connected even after nearby river reaches had dried and therefore, I classified them as *permanent habitat*. CHN maintained a sizeable deep pool (ca. 400 m length, 50 m width, 2.5 m depth) throughout the dry season (named Chanoga lagoon in Merron and Bruton, 1995). Dikgathong had a vast floodplain that was inundated during high water (Figure 3d). Phragmites and hippos were always spotted at the site. BDF and BJN completely dried out and became isolated by the end of the low water season, and therefore I classified them as *ephemeral habitat*. During February, the site at BDF only retained water in a small stretch of aquatic habitat (ca. 5 m x 70 m, 0.6 m depth) along the channel margin, and the site at BJN was mostly dry except for some shallow areas (<20 cm depth) and a moderately deep stretch of aquatic habitat (ca. 10 m x 90 m, 0.9 m depth) within the Thamalakane channel.

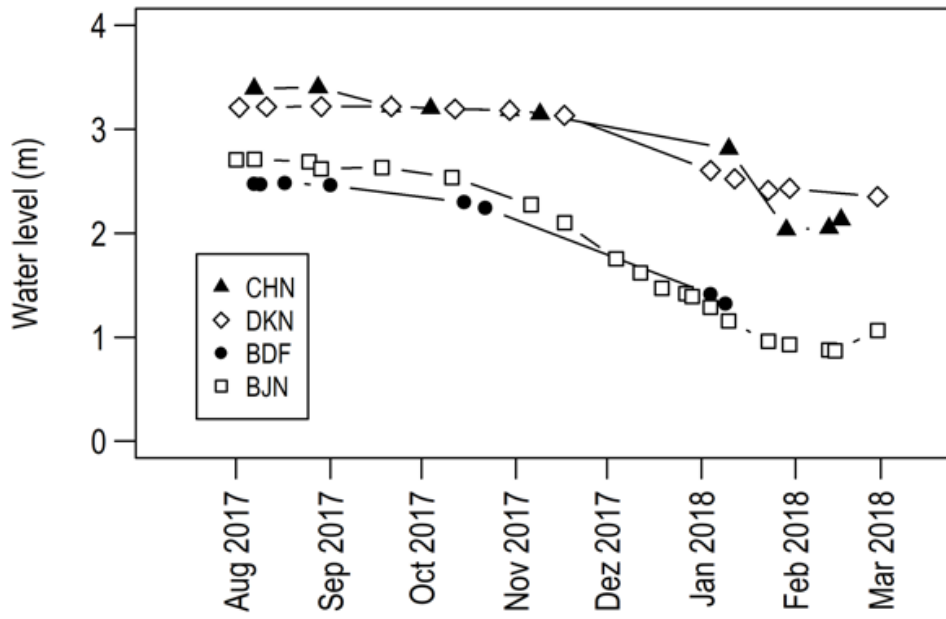


Figure 2. Variation in monthly mean water level at the four sampling sites during the study period. Permanent habitat had higher water level than ephemeral habitat.

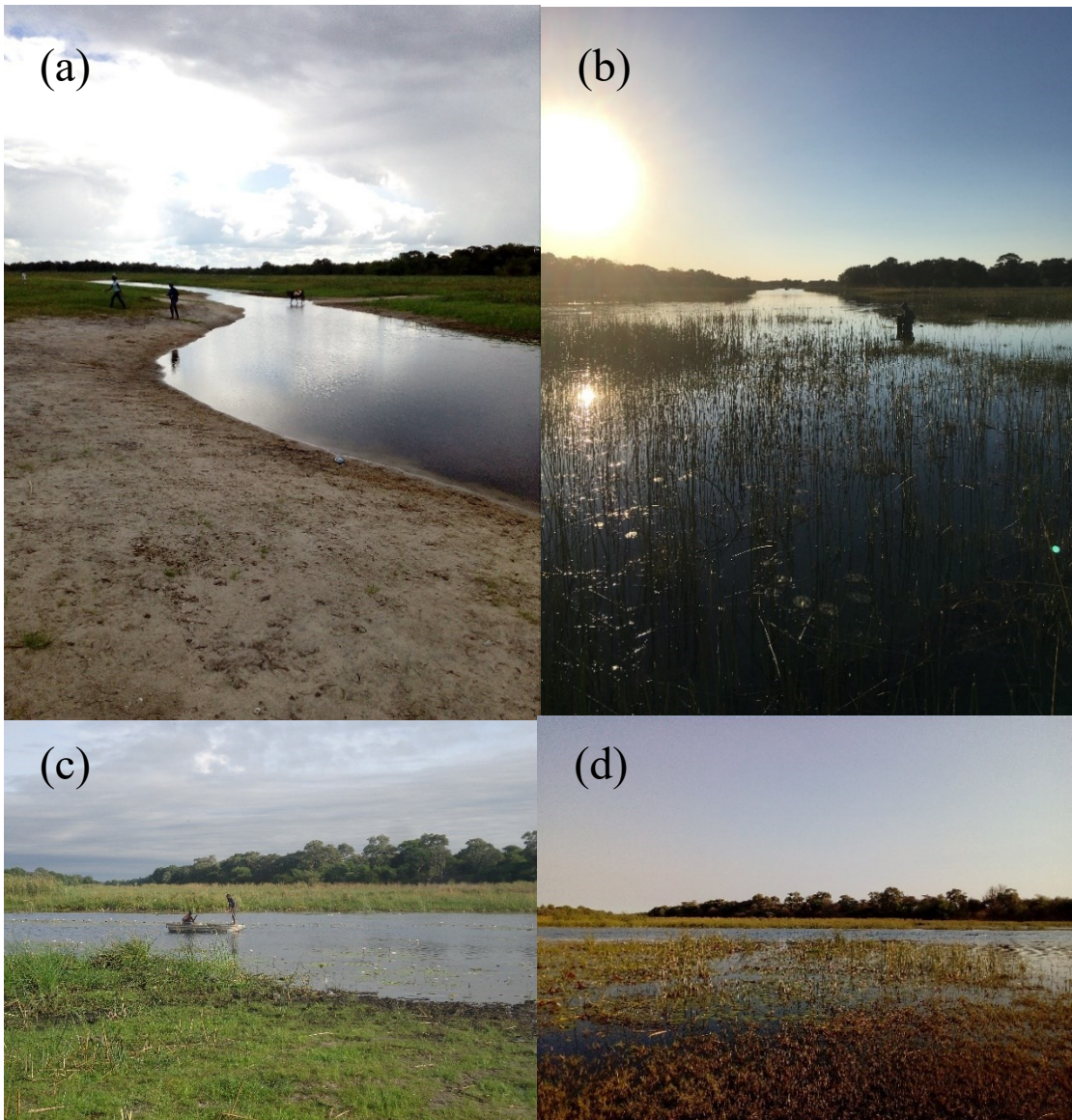


Figure 3. Two of the four sites that were sampled in this study representing the two habitat types. The top two pictures show Boro Junction, an ephemeral habitat, during low water (a) and high water (b). During low water, a cow is seen crossing in ankle-deep water at the same location where the gill net was set during high water. The bottom two pictures show Dikgathong, a permanent habitat, during low water (c) and high water (d).

I sampled fish bi-monthly between August 2017 and February 2018 using a nylon multifilament gillnet. The gillnet consisted of eleven panels. Each panel had a length of 10 m and a depth of 2.4 m. The panels comprised of different mesh sizes: 12 mm, 16 mm, 22 mm, 28 mm, 35 mm, 45 mm, 57 mm, 73 mm, 93 mm, 118 mm, and 150 mm. I randomly ordered the panels to form one multipanel gill net. I set the gill net once at each site during each survey period for approximately 12 h between 1800 hr and 0600 hr the following day. I surveyed each site four times (two times during the high-water season and two times during the low water season), resulting in a total of 16 gill net samples comprising of 176 panel settings. Although gillnets are passive gears that can select for fishes with specific morphologies and behavioral tendencies, the long duration of sets and multiple mesh sizes was effective in capturing a multitude of sizes, from small (<5 cm Total length, TL) to large (>80 cm TL) individuals of the species that are documented to be common in this system (Merron and Bruton 1995). I identified specimens to species level based on keys and illustrations in Skelton (2001) and measured them for total length to the nearest 1 mm. Voucher specimens (TAMU AUP IACUC 2017-0069) were euthanized, fixed in formalin, and preserved in ethanol for archiving in the Biodiversity Research and Teaching Collection at Texas A&M University, College Station.

Data analysis

To test my hypotheses, I investigated three diversity aspects of the fish assemblage. I used α diversity to describe the number of species at a local scale by

characterizing the number of species in a gillnet sample. I used two different approaches to characterize β diversity. First, I quantified variation in species composition within a distinct season x habitat type (β_{within}). Contrasting β_{within} between seasons x habitat types provided insights on whether species composition was more homogeneous in one season x habitat type compared to another. Second, I quantified overall variation in species composition among all sites (β_{across}). Evaluating β_{across} between seasons x habitat types provided insights on whether species composition varied when contrasting one season x habitat type to another. I calculated each metric as follows:

α diversity

Because differences in the number of sampled individuals can bias estimates of α diversity, I rarefied the data (*sensu* Gotelli and Colwell 2001) before comparing seasons and habitats. I estimated α diversity after bootstrapping the data: a resampling procedure that allows for generation of samples with equal number of individuals. I generated a pooled sample of species abundance by summing the abundance of each species in all gillnet samples in each season x habitat type. From the pooled sample, I randomly resampled and replaced 93 individuals. This sample size represented the smallest number of fish captured by a gill net from all seasons and habitats during the study period. I repeated this procedure to produce a collection of 9,999 bootstrap samples and calculated α diversity in each of them. This generated a sampling distribution of 9,999 α -diversity values for each season x habitat type which were used for hypotheses testing. Using sampling distributions for statistical inference is more appropriate than using raw data if the number of samples is small, but the size of each sample is large and

representative of the population (e.g., Bickel and Freedman, 1984). This was the case with my data set, which had a total of 8,289 fishes distributed in 16 gillnet samples. This data set represented the diversity of the sampled sites with species accumulation curves approaching horizontal asymptotes.

However, using sampling distributions does not allow for the application of conventional tests like ANOVA due to violation of the assumption of independence. For this reason, I chose to use bootstrapping techniques to test if α diversity differed between pairs of seasons x habitat types. From two continuous distributions of α diversity positioned along the x-axis, I randomly and repeatedly sampled a pair of samples and subtracted the sample of the first distribution from the sample of the second distribution. This produced a sampling distribution of differences (*SDD*) comprising of 9999 differences in α diversity. I tested if *SDD* differed from zero (Chernick and LaBudde 2011; Dixon et al. 1987). *SDD* comprised of exclusively positive differences when the two distributions did not overlap, and this indicated that all α -diversity values sampled from the first distribution were smaller than values sampled from the second distribution. Negative differences occurred when samples from the first distribution were larger than samples from the second distribution, indicating that the distributions overlapped. To estimate the P value, I calculated the proportion of negative differences in *SDD* and doubled this proportion to comply with a two-tailed test (Chernick and LaBudde 2011). The null hypothesis was that the two distributions were similar. I did not reject the alternative hypothesis that α diversity differs between two seasons x habitat types if P values were less than or equal to 0.05.

β_{within} (Nestedness and turnover within aquatic habitat types)

I estimated turnover and nestedness within a season x habitat type using resampling procedures. I obtained a pooled sample from each season x habitat type as previously described for α diversity. From the pooled sample, I randomly resampled and replaced a pair of samples comprising of 93 individuals each. Resampling was repeatedly executed to produce a collection of 9,999 pairs of simulated samples which I used to calculate species turnover and nestedness following Podani et al. (2013). These metrics were favored because they tend to outperform other methods that may produce biased results (Schemera and Podani 2011). Turnover was based on the Ružička dissimilarity index as described in Podani et al. (2013) and was calculated as $2 \min (B, C) / (A + B + C)$, where A is the sum of species abundances shared by sites 1 and 2, B is the sum of abundances for species collected only at site 1, and C is the sum of abundances for species collected only at site 2. This index maximized turnover when two bootstrap samples had the same total abundance and did not share species. Nestedness was described as $(A + |B - C|) / (A + B + C)$ when $A > 0$, otherwise it equals 0, and its maximum value was achieved when one sample was a perfect subset of the other (Podani et al. 2013). The collection of bootstrap turnover or nestedness values generated sampling distributions for each season x habitat type. I tested if turnover or nestedness differed between pairs of seasons x habitat types using the bootstrap method.

From two continuous sampling distributions positioned along the x-axis, I repeatedly resampled and replaced pairs of bootstrap samples and calculated the difference between their turnover or nestedness. Differences in turnover or nestedness

were obtained by subtracting the sample of the first distribution from the sample of the second distribution. This produced a sampling distribution of differences (*SDD*) comprising of 9,999 differences in turnover or nestedness. *SDD* comprised of exclusively positive differences when the two distributions did not overlap, and this indicated that all β_{within} values sampled from the first distribution were smaller than values sampled from the second distribution. Negative differences occurred when samples from the first distribution were larger than samples from the second distribution, indicating that the distributions overlapped. To estimate the P value, I calculated the proportion of negative differences in *SDD* and doubled this proportion to comply with a two-tailed test (Chernick and LaBudde 2011). The null hypothesis was that the two distributions were similar. I did not reject the alternative hypothesis that β_{within} differs between two seasons x habitat types if P values were less than or equal to 0.05.

β_{across} (Turnover and nestedness across aquatic habitat types)

I tested for variation in β diversity across seasons and habitat types using resampling procedures. I generated a pooled sample for each season x habitat type and performed bootstrapping by repeatedly resampling and replacing 93 individuals from the pooled sample. This produced a collection of 9, 999 bootstrap samples for each season x habitat type. I combined all seasons x habitat types to form a large collection of 39, 996 bootstrap samples. From the large collection, I generated a dissimilarity matrix using turnover and nestedness metrics described in Podani et al. (2013). I used the dissimilarity matrix in metric multidimensional scaling (MDS) and produced ordinations containing 39,996 scores (i.e., 9,999 scores for each season x habitat). The first two axes of the

ordination accounted for most of the variation in turnover and nestedness. Therefore, I only considered these axes for further analysis. I used scores from these axes to produce bidimensional sampling distributions that were used to test for species turnover and nestedness across seasons x habitat types. I tested if there was turnover or nestedness between pairs of seasons x habitat types by evaluating the overlap between two bidimensional distributions. This was performed using a bidimensional extension of the bootstrap method used in the previous analysis. From two sampling distributions positioned along the x- and y-axis, I repeatedly resampled a pair of bootstrap samples and calculated the differences in the MDS scores. Differences were calculated by subtracting x- and y-scores of the first distribution from the x- and y-scores of the second distribution. This produced a collection of 9,999 differences constituting a bidimensional distribution of the differences in MDS scores (*dMDS*). I plotted *dMDS* and described its major direction by fitting a vector starting at the origin and cutting across the cloud of points (a no-intercept regression line).

I rotated *dMDS* by radially moving it around the origin to align its direction with the x-axis and tested if it comprised of differences that differed from the origin. All differences were positive along the x-axis if all the MDS scores sampled from the first distribution were closer to the origin than all the MDS scores sampled from the second distribution. Positive differences indicated no overlap between the two distributions. Differences in MDS scores were negative along the x-axis when the following conditions were met: (i) Samples from the two distributions had a similar direction from the origin to the MDS plot and (ii) the MDS scores sampled from the first distribution

were farther from the origin than the MDS scores sampled from the second distribution. Negative differences indicated that the two distributions overlapped. To estimate the P value, I calculated the proportion of negative differences in *dMDS* and doubled the proportion to comply with a two-tailed test (Chernick and LaBudde 2011). The null hypothesis was that the two distributions were similar. I did not reject the alternative hypothesis that β_{across} differs between two seasons x habitat types if P values were less than or equal to 0.05. All analyses were carried out in R (R Core Team 2019).

Results

α diversity

A total of 8,289 fishes representing 30 species were collected during the study (Table 1). Species accumulation curves approached horizontal asymptotes for individuals sampled from different habitat types and seasons (Figure 4), indicating high sampling sufficiency for documenting α diversity. Generally, α diversity was higher during the low water season when compared to the high-water season (Figure 5a). The permanent habitat type had approximately three more species during the low water season when compared to the high water season ($P = 0.04$) and the ephemeral habitat type had approximately five more species during the low water season when compared to the high water season ($P = 0.002$). α diversity was marginally insignificant among habitat types during the low water season, with the ephemeral habitat type having approximately four more species compared to permanent habitat type ($P = 0.06$). α

diversity was not significantly different among habitat types during the high-water season ($P = 0.13$).

Table 1. Total number of species caught and the percent contribution of each species to the total abundance of the sampled fish population. *Brycinus lateralis* and *Schilbe intermedius* contributed more than 50 (%) to the total abundance of the sampled fish population.

Species	Number	(%) of total
<i>Brycinus lateralis</i>	3307	39.90
<i>Schilbe intermedius</i>	2285	27.57
<i>Petrocephalus okavangensis</i>	971	11.71
<i>Marcusenius altisambesi</i>	784	9.46
<i>Hepsetus cuvieri</i>	223	2.69
<i>Enteromius paludinosus</i>	122	1.47
<i>Tilapia sparrmanii</i>	118	1.42
<i>Synodontis spp</i>	103	1.24
<i>Enteromius poechii</i>	72	0.87
<i>Clarias gariepinus</i>	50	0.60
<i>Sargochromis carlottae</i>	40	0.48
<i>Sargochromis codringtonii</i>	33	0.40
<i>Coptodon rendalli</i>	32	0.39
<i>Pseudocrenilabrus philander</i>	24	0.29
<i>Serranochromis macrocephalus</i>	21	0.25
<i>Mormyrus lacerda</i>	20	0.24
<i>Serranochromis angusticeps</i>	18	0.22
<i>Oreochromis andersonii</i>	11	0.13
<i>Serranochromis altus</i>	11	0.13
<i>Enteromius radiatus</i>	11	0.13
<i>Oreochromis macrochir</i>	7	0.08
<i>Clarias ngamensis</i>	7	0.08
<i>Serranochromis thumbergi</i>	6	0.07
<i>Hippopotamyrus ansorgii</i>	3	0.04
<i>Pharyngochromis acuticeps</i>	2	0.02
<i>Parauchenoglanis ngamensis</i>	2	0.02
<i>Enteromius bifrenatus</i>	2	0.02
<i>Enteromius spp</i>	2	0.02
<i>Clarias theodorae</i>	1	0.01
<i>Enteromius barnardi</i>	1	0.01
Total	8289	100

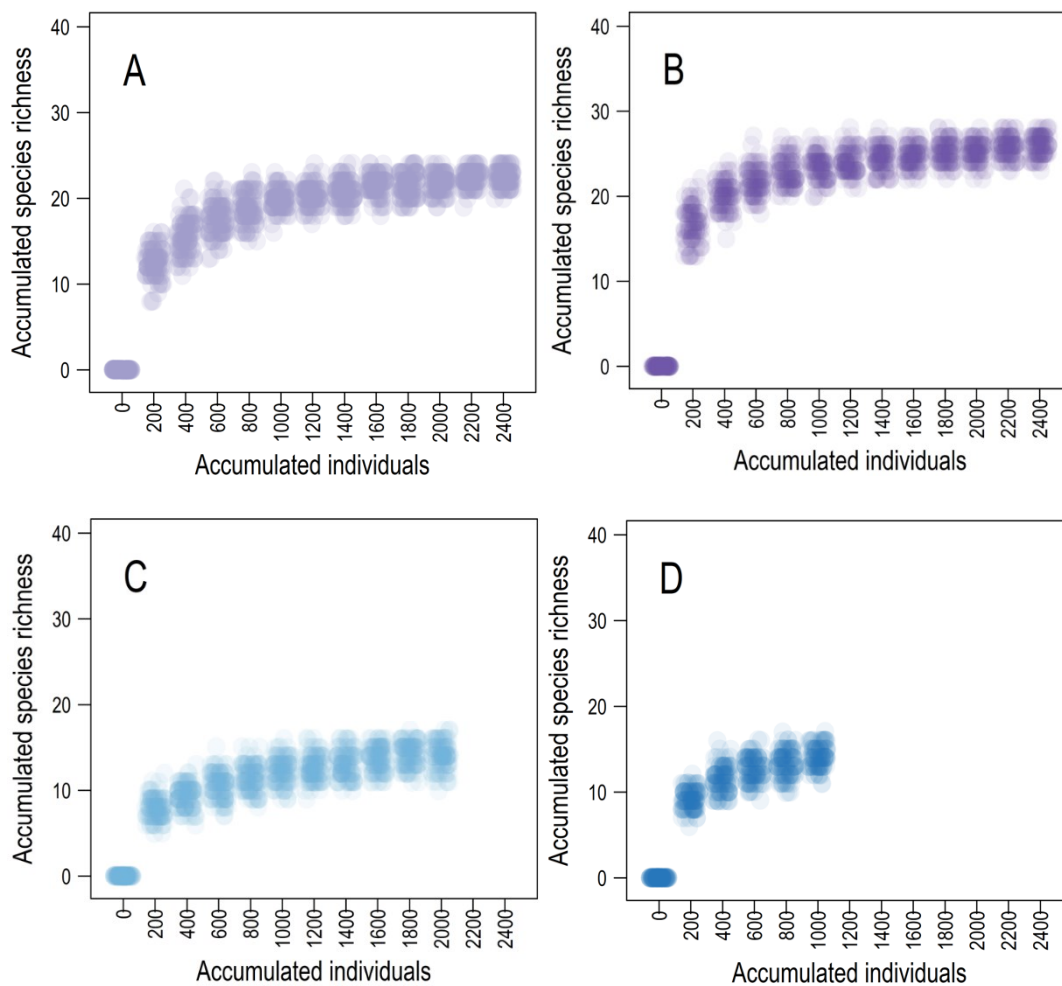


Figure 4. Species accumulation curves for fish samples taken during low water in permanent (A) and ephemeral habitat (B) and during high water in permanent (C) and ephemeral habitat (D).

$$\beta_{within} (\text{Turnover})$$

During the low water season, heterogeneity was significantly higher within the ephemeral habitat type compared to the permanent habitat type with a turnover difference of 0.31 ($P = 0.01$; Figure 5b). Heterogeneity within the ephemeral habitat type

was not significantly different from that within the permanent habitat type during the high-water season ($P = 0.15$) and there was no significant difference in heterogeneity among seasons in both the permanent ($P = 0.42$) and ephemeral habitat types ($P = 0.20$).

β_{within} (Nestedness)

During the low water season, nestedness was significantly higher among patches within the permanent habitat type compared to the ephemeral habitat type with a nestedness difference of 0.31 ($P = 0.02$; Figure 5c). During the high-water season nestedness within the ephemeral habitat type was not significantly different from that within the permanent habitat type ($P = 0.15$). Nestedness was not significantly different among seasons within permanent ($P = 0.42$) and ephemeral habitat types ($P = 0.20$).

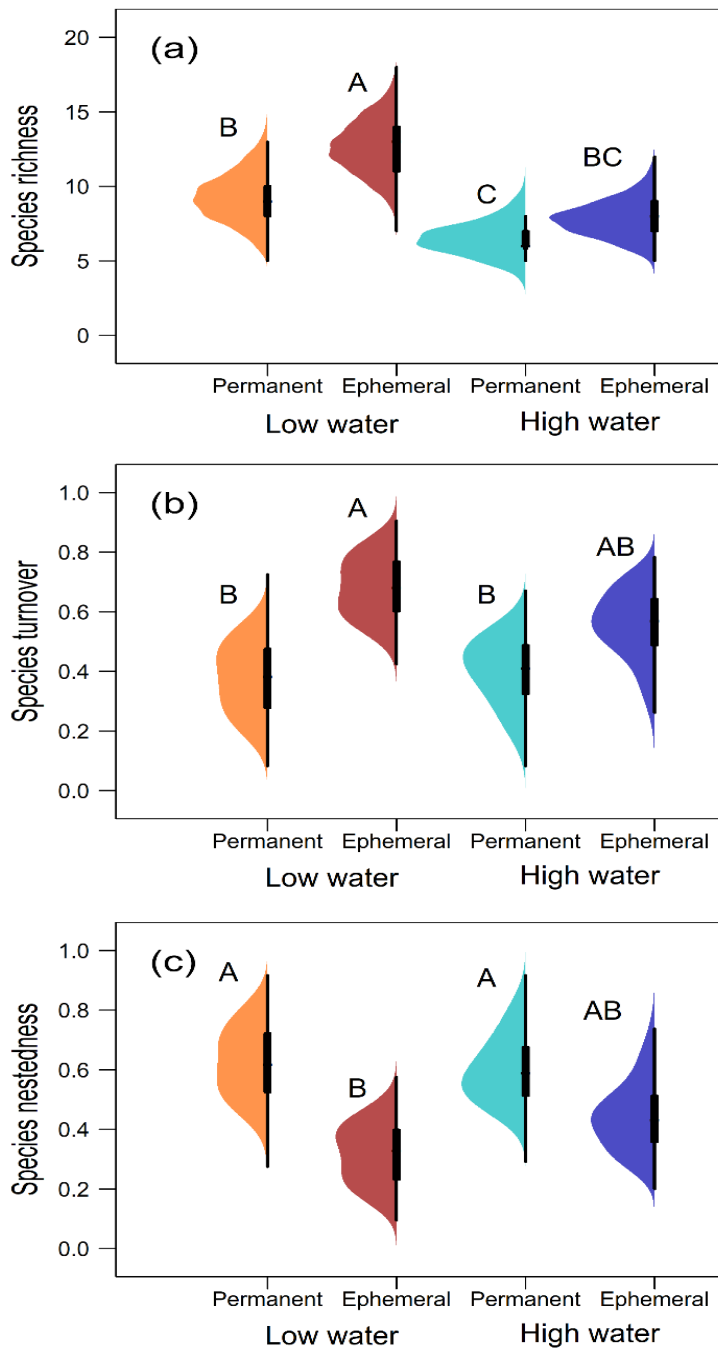


Figure 5. Bootstrap distributions of α -diversity (a), β_{within} (turnover) (b), and β_{within} (nestedness) (c) for fish samples from permanent and ephemeral habitat types during low and high water periods. Different letters indicate significant statistical differences.

β_{across} (Turnover and nestedness)

Regionally, assemblage composition significantly differentiated among habitat types during the low water season ($P = 0.02$). Turnover in the ephemeral habitat type occupied a region of assemblage ordination space distinct from other groups during the low water season (Figure 6). Turnover did not differ significantly among habitat types during the high-water season ($P = 0.07$), and among seasons in both permanent ($P = 0.40$) and ephemeral habitat types ($P = 0.22$). There was no species nestedness among habitat types and seasons (Figure 7).

Discussion

Analysis of α and β diversity showed that hydrology and habitat type play critical roles in maintaining biodiversity in intermittent rivers of the lower Okavango Delta. Within habitat types, α diversity was lowest during the high-water period, and highest during low flows suggesting that greater connectivity enhanced fish dispersal during the wet season, while habitat loss resulted in crowding with shrinking habitats during the dry season. This partially agrees with Merron and Bruton's (1995) finding that water persistence and hydroperiod stage were significant determinants of fish diversity patterns in the Thamalakane and Boteti river systems. However, Merron and Bruton (1995) were concerned only with species richness at a broader scale, and they found higher α diversity in the permanent swamps of the upper delta, compared to the intermittent rivers in the lower delta. By analyzing multiple components of fish diversity, I provide additional insights into diversity-disturbance relationships in the lower Okavango Delta.

My results showed that β diversity was generally higher during the dry season compared to the wet season, as expected. This suggests greater potential for demographic stochasticity within and among habitat types during this period.

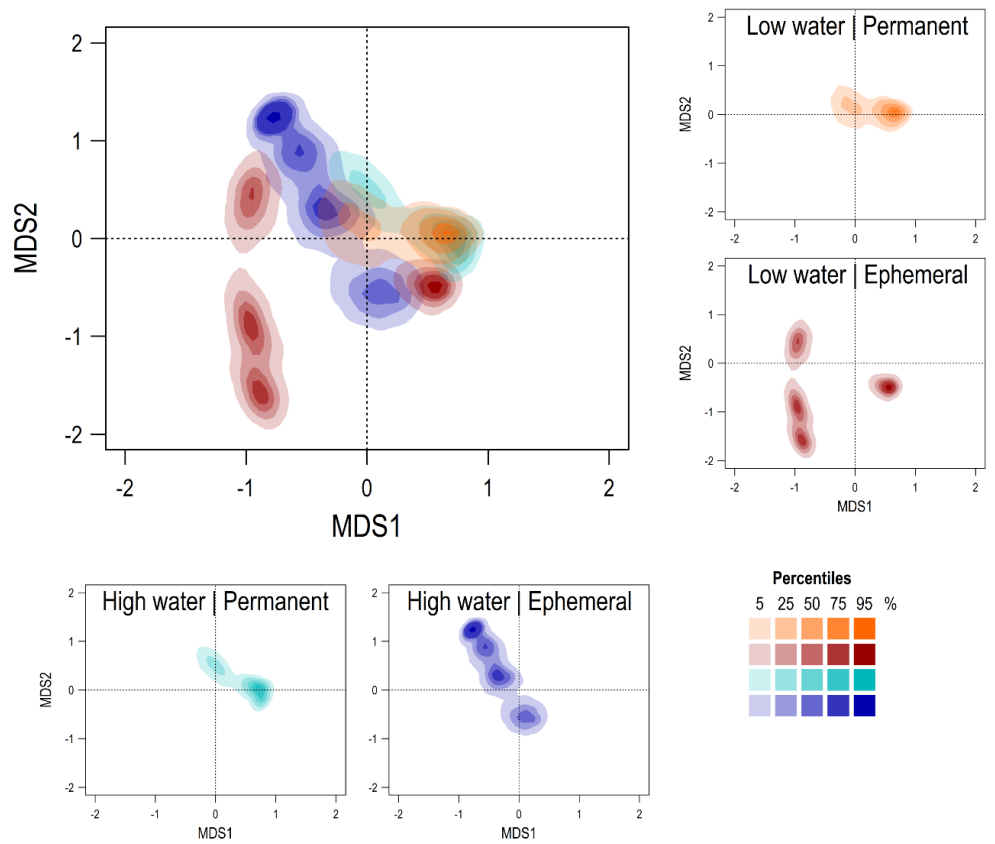


Figure 6. MDS plots showing differences in fish assemblage structure across seasons and habitat types (β_{across}). Different colors represent different seasons x habitat types (green = high-water permanent, blue = high-water ephemeral, orange = low-water permanent and brown = low-water ephemeral).

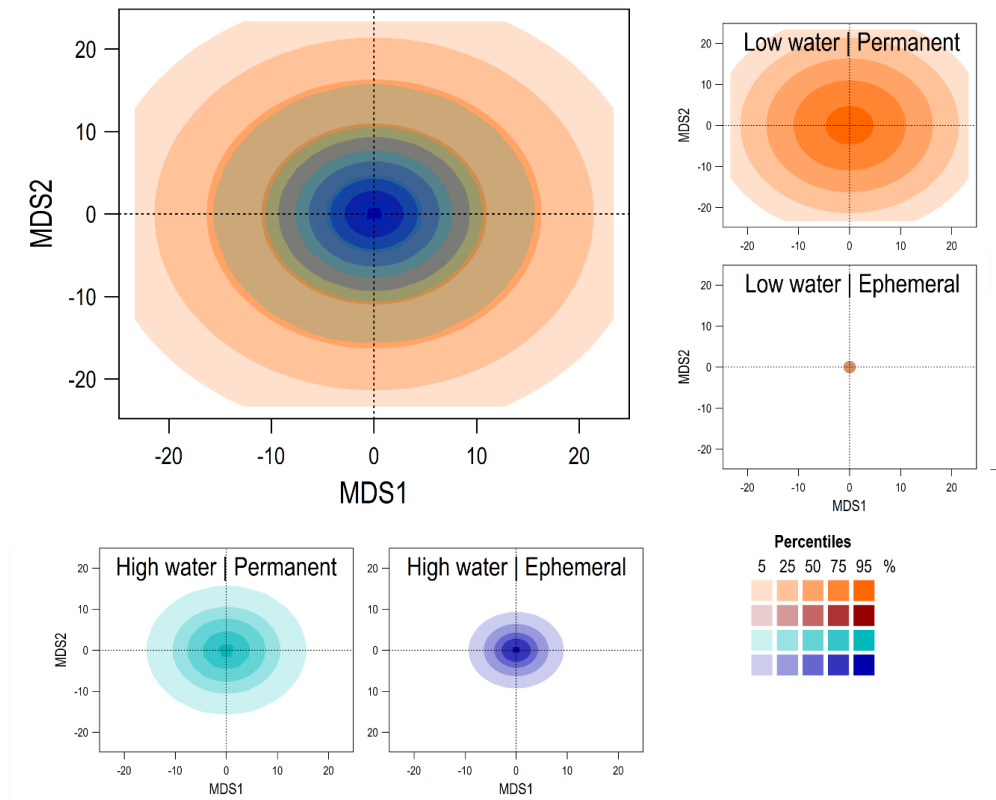


Figure 7. Plots showing degrees of nestedness of fish assemblages across seasons and habitat types.

During the wet season, river-floodplain systems are characterized by increased connectivity in three dimensions (longitudinal, lateral, and vertical) which facilitates dispersal of biota, nutrients and other material among habitats (Fullerton et al. 2010). Fish dispersal allows species to exploit newly available resources and to escape competition and predation in newly created habitat that has low fish densities (Junk 1999, Winemiller and Jepsen 1998, Shimadzu et al. 2013, Bokhutlo et al. 2016). In the Okavango Delta, species such as *Schilbe intermedius*, *Clarias gariepinus* and

Marcusenius altisambesi usually leave the main river channel during the flood to seek prey and spawn in the flooded area (Merron 1993, Merron and Mann 1995). Low per-unit-area densities of fishes in newly expanded habitats may partially explain the lower richness of samples during the high-water period.

In perennial river-floodplain systems, during the initial stages of drying, aquatic habitat shrinks in the floodplains, resulting in higher fish densities within the main river channel, and high α diversity may be encountered within restricted habitat (Merron 1993, Winemiller and Jepsen 1998, Grubh and Winemiller 2018). This could explain the relatively high α diversity in permanent habitats during low flows. In ephemeral habitats, drying generally is accompanied by a rapid decline in species richness due to deterioration of abiotic environmental conditions and strong biotic interactions, such as competition and predator-prey interactions that prevail in shallow aquatic habitats that are relatively smaller in size, even to the point of local extirpation (Benton et al. 2003, Fahrig 2003, O'Neil 2016). Therefore, sustained high α diversity in ephemeral habitats during low flows suggests a legacy effect whereby species persist under suboptimal environmental conditions for a limited time, but these levels of α diversity would not be sustainable if these conditions were chronic (Vass and Langenheder 2017).

Centuries of seasonal wetting and drying might promote the evolution of adaptive traits that allow fish to cope with environmental stress or disperse within a dynamic habitat mosaic. Physiological and behavioral adaptations might lessen the influence of species sorting during community assembly (Brendonck 1996, Chase 2003, Loeuille and Leibold 2008, Boersma et al. 2014). Such historical contingencies influence

demographic responses to disturbances at local scales (Hawkes and Keitt 2015). In ephemeral habitats, legacy effects may be strongest during the early portion of the dry season when communities are in a transitional stage. With a prolonged drying and habitat degradation, local fish assemblages are strongly influenced by current conditions. Consequently, greatest changes in community structure should be observed during late stages of the dry season (Boersma et al. 2014, Bogan et al. 2017). Except for species that estivate during drought conditions, aquatic organisms must disperse or else perish when their aquatic habitat dries entirely (Bonada et al. 2006, O'Neil 2016).

Ephemeral and permanent habitat showed contrasting patterns of within-habitat β diversity during the low water period. Ephemeral habitat had significantly higher species turnover, and permanent habitat had higher assemblage nestedness. Because permanent patches remained connected during low water while ephemeral patches became isolated, dispersal limitation among ephemeral patches may have resulted in higher turnover, while dispersal among permanent patches led to increased nestedness. Moreover, ecological drift resulting from the stochastic fate of species may be more pronounced during the low-water period in ephemeral patches. Increased ecological drift reduces the strength of niche selection (Vellend et al. 2014) and leads to increased heterogeneity within habitats (Myers et al. 2015). However, within-habitat assemblage composition was more homogeneous during the high-water period, likely due to extensive fish dispersal under conditions of high aquatic habitat connectivity.

Assemblage composition across the regional landscape revealed high species turnover during the low-water period. This means that during the dry season, fish in

different habitats were subjected to different selection pressures or local filters, leading to the divergence of local assemblages and increased β diversity (Myers et al. 2015, O'Neil 2016). This is consistent with the patch dynamics metacommunity paradigm (Winemiller et al. 2010) and may indicate the importance of dispersal limitation due to habitat fragmentation (Arrington and Winemiller 2006, Chase 2010, Datry et al. 2016, O'Neil 2016, Tonkin et al. 2017). It could also be due to increased effects of species sorting as a result of intermediate levels of dispersal as the water gradually dried up before complete loss of connectivity (Leibold et al. 2004, Heino et al. 2015, Leibold and Chase 2018). On the other hand, biodiversity was homogenized across habitats during the wet season due to increased connectivity among habitats, suggesting a strong mass effect in community assembly (Amoros and Bornette 2002, Leibold et al. 2004, Thomaz et al. 2007, Ng et al. 2009, Leibold and Chase 2018, Bower et al. 2019).

Analysis of fish diversity patterns in the lower reaches of the Okavango Delta supports the idea that hydrology plays a crucial role in structuring aquatic communities in intermittent rivers. However, it is important to note that my findings could be a result of sampling artefacts resulting from use of gill nets within small, isolated habitats during the dry season. Gillnets are passive gears that may not obtain a representative sample of local fish assemblages in large flooded areas compared to small, isolated habitats where fishes have a greater chance of encountering the net. Therefore, I cannot discount the possibility that some of the variation in my response variables could have been influenced by sampling bias. This could partially explain the markedly higher α diversity

in the ephemeral habitat type when compared to the permanent habitat type during low-water periods.

Fish in intermittent rivers are threatened by habitat fragmentation, invasion by alien species, groundwater extraction, and climate change (Kerezszy et al. 2017). Potential large-scale water abstraction for irrigation schemes, hydropower generation, and human consumption coupled with climate change are significant threats to the biodiversity of the Okavango Delta (Mitchell 2013). These threats may lead to declines in commercial and subsistence fisheries, resulting in reduced food security as well as diminished social and recreational services with negative consequences on the tourism industry and the economic security of riparian communities. Therefore, annual flow pulses of sufficient magnitude and duration are essential for the maintenance of ecosystem services in this system. This study expands our understanding of intermittent river ecology during a time when the hydrology of these ecosystems is being altered by climate change and water use by humans (Acuna et al. 2014, Ruhí et al. 2016). To further understand the mechanisms that structure aquatic communities in intermittent rivers, future research should examine species functional traits and methods capable of revealing the role of biotic interactions.

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CHAPTER III

INFERENCE OF FISH ASSEMBLY MECHANISMS IN THE OKAVANGO DELTA USING JOINT SPECIES DISTRIBUTION MODELS AND TROPHIC GUILDS

Introduction

Non-random patterns of species co-occurrence often reflect both environmental filtering (Heino et al. 2015, Kraft et al. 2015, D'Amen et al. 2018) and biotic interactions (Stachowicz 2001, Ovaskainen et al. 2017). However, there is less agreement on the relative importance of these processes across multiple spatial scales (Spasojevic and Suding 2012, Price et al. 2017), and in heterogeneous environments, the processes may synergistically affect species co-occurrence patterns (D'Amen et al. 2018). For example, plant species may negatively associate under favourable abiotic environmental conditions, reflecting competitive exclusion, and positively associate under less suitable conditions when fitness is more strongly influenced by tolerance limits to abiotic factors (Barrio et al. 2013, Milazao et al. 2013, Bar-Masada and Belmaker 2017). In animal communities, predation can result in reduced co-occurrence of predators and prey when prey populations become depleted during times and in places where predators are abundant, or when prey are able to avoid areas with predators (Englund et al. 2009), whereas positive species associations may occur when predators are attracted to areas where prey are abundant (Chase et al. 2002, Finke and Denno 2004).

Fish community assembly in rivers varies seasonally with the magnitude, duration, and timing of flood pulses. Biotic interactions tend to be stronger during low-

water periods when fishes are concentrated within shrinking aquatic habitats (Arrington and Winemiller 2006, Montaña et al. 2014, Fitzgerald et al. 2017). For example, top-down control of basal resources by benthivorous fish is much stronger during the annual low-water period in piedmont and lowland rivers in Venezuela (Flecker 1996; Winemiller et al. 2014). Arrington et al. (2005) observed increasingly non-random patterns of species co-occurrence when species density was higher in a tropical lowland river. The mechanisms that drive species co-occurrence remain poorly documented for rivers in semiarid regions. These ecosystems harbor unique biodiversity and support many ecosystem services (Larned et al. 2010, Boulton et al. 2017). Intermittent rivers experience extremes in discharge, ranging from flooding to desiccation. During dry periods, aquatic habitat is reduced and disconnected, resulting in a mosaic of habitat types with wide variation in physicochemical characteristics and food resource availability (Rolls et al. 2012). Isolated habitats within a given reach may differ in water residence time, depending on channel geomorphology and bed material (Godsey and Kirchner, 2014).

Traditionally, evaluation of non-random patterns of community structure relied mostly on comparisons of empirical data with distributions generated by null-models (e.g., Connor and Simberloff 1979, Brown et al. 2002, Gotelli and McCabe 2002, Cordero and Jackson 2019). Some ecologists have begun using Joint Species Distribution Models (JSDMs) with species abundance and environmental data as a means to infer mechanisms of community assembly (Hui 2016; Inoue et al. 2017, Radinger et al. 2019). A particularly appealing feature of this approach is the capability

to separate environmental filtering from biotic interactions within one model fit (Warton et al. 2015, D'Amen et al. 2018).

When a JSDM is fitted without environmental covariates, the model resembles unconstrained ordination (Warton et al. 2015). If environmental variables are included in the model, the resulting residual species correlations may represent species co-occurrences without the direct influence of species responses to measured environmental covariates (Hui et al. 2015). This means that in a constrained JSDM, the influence of environmental covariates on species occurrence is removed/controlled for (Ovaskainen et al. 2017). However, residual species correlations may be either a result of biotic interactions or species responses to other covariates that were not included in the model (Hui et al. 2015, Warton et al. 2015, Ovaskainen et al. 2017). Therefore, it is not possible to determine the ecological mechanisms that drive residual species associations from these models alone (Warton et al. 2015). Interspecific associations depend on several limiting factors and trade-offs, such as traits of prey and predators that influence encounters and capture success and the manner in which environmental variation influences habitat and resources (Kneitel and Chase 2004). For this reason, ecologists often analyse species co-occurrence in conjunction with additional species information such as habitat preferences, migratory patterns, phylogenies, and guild membership (Peres-Neto 2004, Kohli et al. 2018). This approach to analyzing species co-occurrence facilitates inferences about the mechanisms driving non-random patterns of co-occurrence (Mouchet et al. 2013).

Designation of guild membership in conjunction with JSDMs can facilitate the inference of probable drivers of co-occurrence patterns in heterogeneous environments. For example, a negative correlation between two species within the same trophic guild could suggest avoidance of interspecific competition (Stachowicz 2001, Kneitel and Chase 2004). Similarly, a negative correlation between a predator and potential prey species could suggest either predator depletion of local prey (e.g., within an isolated aquatic habitat) or prey avoidance of predators (e.g., within a refugium when prey are capable of dispersal and habitat selection) (Englund et al. 2009). Conversely, positive co-occurrence of predatory species and potential prey may indicate predators select areas with abundant prey. Further, the use of guild membership may help with inferences pertaining to those interspecific interactions that are due to unmeasured environmental covariates. For example, a negative co-occurrence involving non-predatory species from different trophic guilds could arise from species differences in tolerance to abiotic conditions. Similarly, inter-guild positive co-occurrence involving non-predatory species could be a result of species aggregating within suitable habitat (Stachowicz 2001). Therefore, using trophic guilds in conjunction with JSDMs may help to disentangle the residual correlations and tease apart putative biotic interactions from those interactions that may be influenced by unknown environmental factors.

In this study, I used JSDMs to infer the relative roles of environmental filtering and biotic interactions in the assembly of fish communities from intermittent rivers in the lower Okavango Delta. A previous study in these rivers suggested that the magnitude of the annual flood pulse has a pervasive influence on the structure of local fish

assemblages (Merron and Bruton 1995). However, that study did not investigate the influence of hydrology on interspecific associations. Here, I assessed patterns of covariation in species responses to seasonal variation in hydrology, habitat type, and water quality. At the landscape scale, hydrology varies along longitudinal, lateral, and vertical dimensions. I measured and compared water quality at the mesohabitat scale during multiple stages of the annual flood pulse in the lower Delta. To infer mechanisms influencing species co-occurrence, I used JSDMS to factor out correlations with abiotic environmental variables and then analyzed residual correlations to interpret patterns of species co-occurrence in relation to fish trophic guilds. Patterns of species co-occurrence were expected to depend on trophic guild and degree of tolerance to stressful abiotic conditions.

First, I modeled species responses to stages of the annual flood pulse and habitat type and assumed that species per-unit-area densities would increase as the water level fell. Most positive residual species correlations from the model that included seasonal variation in hydrology and habitat type were expected to be primarily intra-guild, suggesting species aggregation within preferred mesohabitats. Negative species co-occurrence was expected between predators and their potential prey during low-water periods, an indication of prey depletion within isolated ephemeral habitats. Second, I modeled species responses to water depth and quality and expected that species abundance would vary widely in relation to environmental conditions. Most positive residual correlations from the model that included water depth and quality were expected to be between species from different trophic guilds, reflecting greater densities of

potential prey within aquatic refugia during the early dry season. Negative species correlations were expected to be primarily between species from the same guild, suggesting competitive exclusion when drought severity increased, and resources became limiting for most fishes.

Methods

Study area

The Okavango Delta is located in the semi-arid northwestern region of Botswana. It is characterized by low annual rainfall, which averages around 490 mm (Gumbricht et al. 2004). After entering Botswana at Mohembo, the Okavango River forms a relatively narrow perennial channel in the panhandle, which extends for approximately 100 km. In the lower panhandle, the channel branches out to form an alluvial fan comprising a myriad of channels and swamps that cover approximately 13 000 km² during high floods (Gieske 1997). Most of the outflow (2%) from the delta into the intermittent rivers occurs through the Boro channel, which forms a confluence with the Thamalakane River at Matlapaneng, eventually draining into Lake Ngami and the Makgadikgadi salt pans (Gieske 1997). Electrical conductivity and water temperature increase down the fluvial gradient from Mohembo to the lower delta while pH, dissolved oxygen, turbidity and total suspended solids decrease (Gondwe and Masamba 2016).

Fish sampling and environmental descriptors

Fishes were sampled from four sites in the lower Okavango Delta: Borojunction (BJN; 19° 55' 01.0"S; 023° 30' 52.0"E) a site near the Botswana Defence Force Camp

(BDF; 19° 52' 28.1"S; 023° 26' 45.0"E), Dikgathong (DKN; 20° 08' 27.9"S; 023° 22' 38.5"E) and Chanoga (CHN; 20° 10' 02.4"S; 023° 39' 33.6"E) (Figure 8), using a multifilament gillnet comprising of eleven panels that were 10 m long with different mesh sizes. The mesh sizes used were 12 mm, 16 mm, 22 mm, 28 mm, 35 mm, 45 mm, 57 mm, 73 mm, 93 mm, 108 mm and 150 mm. Fish were sampled during the wet (August 2017 to November 2017) and dry (December 2017 to February 2018) seasons. During each survey, the gill net was set once at each site for approximately 12 h between 1800 h and 0600 h the following day. Fish sampling resulted in a total of four gill net samples from each site (two from the low-water season and two from the high-water season) which produced a total of 16 gill net samples that were used for analysis. Water residence for CHN and DKN persisted throughout the sampling period, and these sites were classified as *permanent habitat*. BDF and BJN dried out completely by the end of the dry season, and they were classified as *ephemeral habitat*.

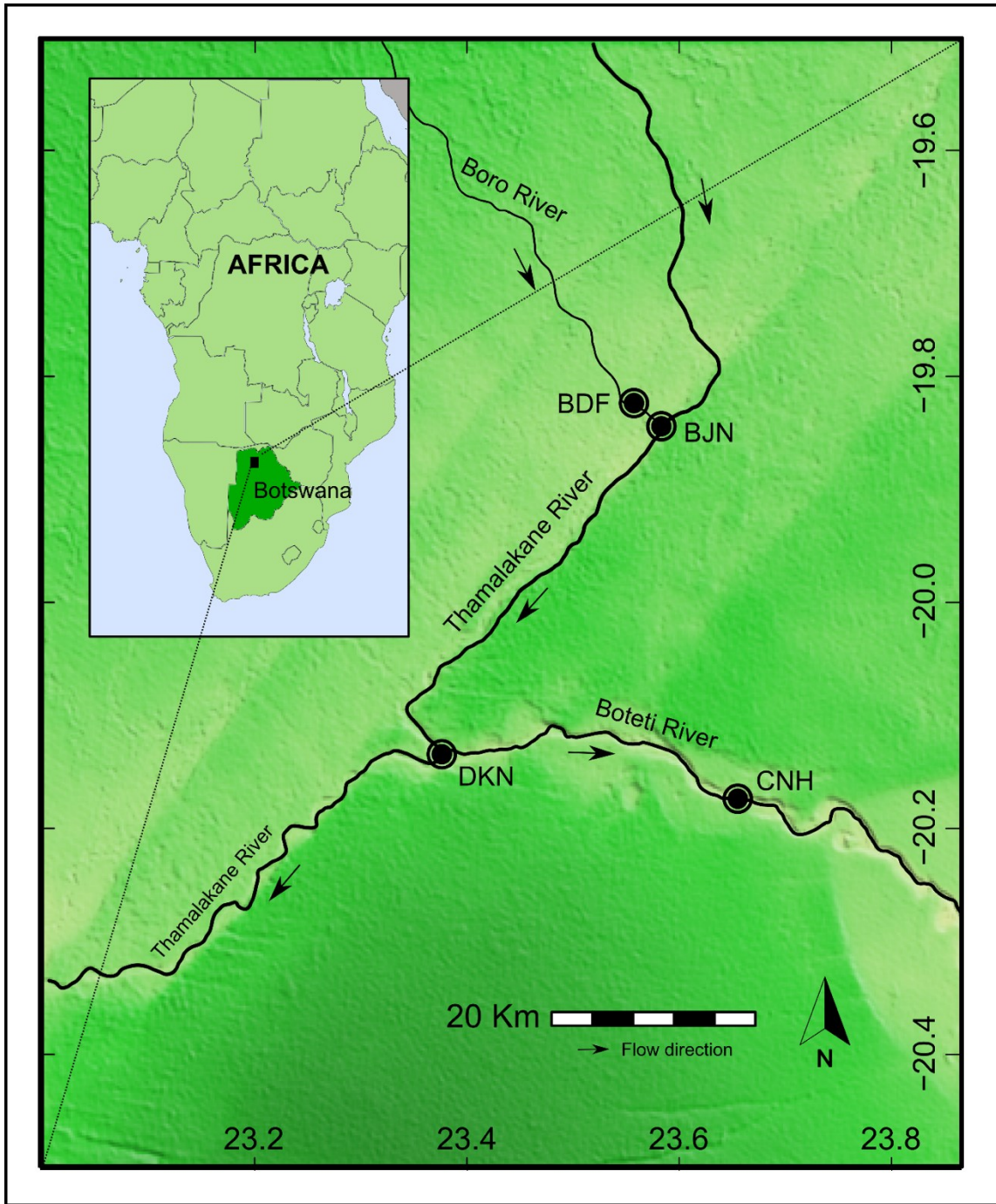


Figure 8. Map showing locations of the study sites in the lower Okavango Delta. BDF and BJN are located upstream, and BJN is a confluence between the Boro River and the Thamalakane River. Downstream, Thamalakane River branches at DKN to form the Boteti River where CHN is located. The direction of water flow is shown with arrows.

To facilitate analysis of potential interspecific variation in response to abiotic environmental conditions at the survey sites, I measured several water physicochemical parameters using a handheld water quality meter at approximately 0600 h. Measured physicochemical parameters were: dissolved oxygen (measured to the nearest 0.01 mg/l), pH (measured to the nearest 0.1), conductivity (measured to the nearest 0.1 $\mu\text{S}/\text{cm}$) and temperature (measured to the nearest 0.1 $^{\circ}\text{C}$). Following Haak et al. (2020), I accounted for temporal fluctuations in species abundance by including season as a covariate. Season was a binary categorical variable (wet vs dry). I also included the covariate habitat type as a binary variable (ephemeral vs permanent). I obtained water-level data (measured to the nearest 0.01 m) for each site from the Department of Water Affairs in Maun, Botswana.

Physicochemical water parameters

I used Principal Coordinate Analysis (PCoA) to model the major abiotic environmental gradients in the dataset. Variables included in the analysis were water depth, temperature, dissolved oxygen (DO), pH, and conductivity. Prior to inclusion in analyses, environmental variables were standardized by taking the Z-score to achieve the same range of variation. To identify variables with strongest influence on abiotic environmental variation, I correlated each variable with the scores of the first and second axes of the PCoA. I retained environmental variables with a correlation coefficient > 0.6 for further analyses.

To reveal the association of water physicochemical parameters with seasonal variation in hydrology and habitat type, I used Redundancy Analysis (RDA). RDA was

conducted using a subset of the most influential variables from the PCoA (DO, depth, and temperature) as response variables, and season and habitat type were used as explanatory variables. Statistical effects of season and habitat type were tested using permutation tests after 9999 randomizations.

Joint species distribution modeling

I used JSDMs to investigate species interactions and individual species responses to seasonal change in hydrology, habitat type, and water physicochemical parameters. I applied correlated response models that regressed separate Bayesian generalized linear models for each species against environmental covariates and latent variables at the same time. Latent variables are random variables that define the underlying gradients in the data, and they are estimated during model fitting (Hui et al. 2015). Therefore, the model simultaneously estimates relationships between multiple species and environmental covariates while approximating species responses to latent variables. This makes it possible to partition the observed correlation into that which is due to species responses to known environmental covariates and that which is unexplained and may be interpreted as indicative of species interactions (Warton et al. 2015, Hui 2016). The interpretation of species responses to latent variables is not always straightforward because species may respond to unknown environmental covariates or those that were not measured during the study (Kissling et al. 2012, Warton et al. 2015, Ovaskainen et al. 2016). To account for the influence of missing environmental covariates in the estimation of species co-occurrence, I included multiple random effects at the level of a sample, assuming that the heterogeneity driving variation in residual correlation at each

sampling site was environmental. This ensured that environmental heterogeneity did not influence latent variables and the estimation of residual correlations (Haak et al. 2020). Due to a relatively small sample size ($n = 16$) and the relatively high incidence of zeros in species counts data, it was not possible to successfully estimate model parameters with all five covariates included in a single model. For this reason, I built two separate models: one model was fitted with two categorical covariates (season and habitat type), and the other was fitted with three numerical physicochemical water parameters (water depth, dissolved oxygen and temperature) in order to assess their contributions to variation in species abundances and co-occurrence.

Inference of species responses to environmental variables

The two JSDMs were fitted to species abundance assuming Poisson responses with a log link function in order to control for positively skewed variation among samples (Hui 2016). I estimated parameters assuming non-informative priors (Hui 2016). I fitted the models by running three chains of 40,000 iterations with the first 10,000 discarded as burn-in. The remaining iterations were thinned by a factor of 30, resulting in 1000 samples per chain for inference. Model convergence was inspected using Dunn–Smyth residuals and residual QQ plots. Species response to each explanatory variable was assessed by inspecting the magnitude and direction of posterior median coefficients for each species and their 95% credible intervals.

Inference of interspecific interactions

Interspecific interactions were inferred by assessing posterior residual correlation coefficients among species pairs and their 95% credible intervals. I categorized potential

prerequisites for positive and negative species interactions according to Stachowicz (2001) and Kneitel and Chase (2004) (Table 2). I assigned species to trophic guilds (Table 3) following Taylor et al. (2017), and types of biotic interactions were inferred by assessing intra and inter-guild pairs (Kohli et al. 2018). All analyses were carried out in R (R Core Team 2019), using the boral package (Hui, 2016).

Table 2. Types of interactions, direction, and the inferred assembly mechanisms. Inferences were based on Stachowicz (2001) and Kneitel and Chase (2004).

Type of Interaction	Direction of interaction	Inferred assembly mechanism
Intra-guild	Positive	Species congregating in suitable habitat
Inter-guild (involving non-predatory species)	Positive	Species seeking refuge from competition
Predator-prey	Positive	Increased prey abundance
Intra-guild	Negative	Competition
Inter-guild (involving non-predatory species)	Negative	Differential tolerance to abiotic conditions
Predator-prey	Negative	Predation or predator avoidance

Table 3. Habitat preference and feeding guilds of species that were analyzed in this study. Biological and ecological descriptions were obtained from Skelton (2001). Feeding guilds were categorized according to Taylor et al. (2017).

Species	Preferred habitat	Feeding guild
<i>Enteromius radiatus</i>	Marshes and marginal vegetation of streams, rivers and lakes	Invertivore Preys on insects and other small organisms.
<i>Enteromius poechi</i>	Riverine and floodplain habitats. Co-occurs with <i>Brycinus lateralis</i>	Invertivore Preys on insects and other small organisms.
<i>Enteromius paludinosus</i>	Hardy, preferring quiet, well-vegetated areas in lakes, marshes and marginal areas of rivers and slow flowing streams.	Invertivore Feeds on a wide variety of small organisms including insects, small snails, crustaceans, diatoms and detritus.
<i>Mormyrus lacerda</i>	Quiet stretches of river channels, deep pools and floodplain lagoons with aquatic vegetation	Invertivore Feeds on insect larvae, shrimps, small snails, and small fish.
<i>Marcusenius altisambesi</i>	Well vegetated, muddy-bottomed marginal habitats of rivers and floodplains. Moves inshore after dark.	Invertivore Feeds on a wide range of invertebrates, especially midge and mayfly larvae and pupae taken from the bottom and off plant stems. A major prey for clariid catfishes
<i>Petrocephalus okovangoensis</i>	Quiet reaches of rivers and floodplains	Invertivore Feeds on insect larvae and other small invertebrates
<i>Brycinus lateralis</i>	Clear, slow-flowing or quiet, well-vegetated habitats. Co-occurs with <i>E. poechi</i>	Invertivore Feeds on small aquatic and terrestrial organisms
<i>Hepsetus cuvieri</i>	Quiet deep water in channels and lagoons of large floodplains. Juveniles inhabit well-vegetated marginal habitats	Predator Juveniles feed on small invertebrates and fish and adults feed on fish
<i>Clarias gariepinus</i>	A hardy species that can endure harsh conditions (e.g., extreme turbidity, high temperature, hypoxia); frequently the last inhabitant of drying pools.	Predator/ omnivore Feeds on fish, birds, frogs, small mammals, reptiles, snails, crabs, shrimps, insects, zooplankton, other invertebrates and plant material, such as fruit and seeds.
<i>Clarias ngamensis</i>	Vegetated habitats in swamps and riverine floodplains. Tolerant of hypoxia and often co-occurs with <i>C. gariepinus</i>	Predator/omnivore Feeds on molluscs, terrestrial and aquatic insects, shrimps, crabs and fish

Table 3. continued

Species	Preferred habitat	Feeding guild
<i>Schilbe intermedius</i>	Slow-flowing habitats in rivers and floodplains, usually with vegetation. Usually active at night	Predator/omnivore Feeds on fish, insects, shrimps, snails, plant seeds, and fruit
<i>Synodontis spp</i>	Slow-flowing, vegetated habitats in rivers and floodplains	Invertivore Feeds on molluscs, crustaceans, aquatic insects, small fishes, detritus, algae and plant material
<i>Sargochromis carlottae</i>	Permanent floodplain channels and lagoons with sandy bottom and vegetation	Invertivore Feeds on aquatic insects, crustaceans and snails
<i>Sargochromis codringtonii</i>	Slow-flowing channels and floodplain lagoons	Invertivore Feeds on seeds, snails, bivalves and aquatic insects
<i>Serranochromis altus</i>	Slow-flowing, vegetated areas along channel margins.	Predator Feeds on fish, insects and crustaceans
<i>Serranochromis angusticeps</i>	Lagoons and quiet backwaters with dense vegetation; impoundments	Predator Feeds on small fishes such as robbers and barbs
<i>Serranochromis macrocephalus</i>	Common in a broad range of habitats from margins of large rivers to floodplain channels and lagoons	Predator Feeds on insects and small fish, including mormyrids and barbs, which are taken near the bottom.
<i>Serranochromis thumbergi</i>	Floodplain channels and lagoons. Favors open water.	Predator Feeds on insects, crustaceans and fish
<i>Coptodon rendalli</i>	Slow flowing, well-vegetated areas along river margins, backwaters, floodplains. Tolerant of a wide range of temperatures and salinity	Herbivore Feeds on water-plants and algae and also aquatic insects

Table 3. continued

Species	Preferred habitat	Feeding guild
<i>Tilapia sparmanii</i>	Quiet or standing waters with submerged or emergent vegetation in a wide range of habitats.	Herbivore Feeds on available foods including algae, soft plants, small invertebrates such as insects and even small fish
<i>Oreochromis andersonii</i>	Tolerates fresh and brackish water. Found in slow-flowing water or standing water in pools, backwaters and floodplain lagoons. Adults occupy deeper habitats than juveniles.	Detritivore Feeds on detritus, diatoms and zooplankton
<i>Oreochromis macrochir</i>	Quiet waters along river margins and backwaters in floodplain habitats and impoundments.	Detritivore Feeds on microscopic foods such as algae, diatoms and detritus taken from the bottom.
<i>Pseudocrenilabrus philander</i>	Wide range of habitats from flowing waters to lakes and isolated sink holes. Favors vegetated areas.	Invertivore Feeds on insects, shrimps and small fish

Results

Determining important environmental variables

Depth, DO, and temperature were the most important environmental variables showing high loadings on the PCoA axes (correlation coefficients > 0.6). Variation in environmental variables was largely associated with hydrology ($F = 7.87$; $DF = 1$; $P = 0.001$) and habitat type ($F = 4.06$; $DF = 1$; $P = 0.02$). Permanent habitats during the high-water period were separate from ephemeral habitats during the low-water period along the first RDA axis. DO and depth were positively associated with high water and permanent habitat, and temperature was positively associated with ephemeral habitat and low water (Figure 9).

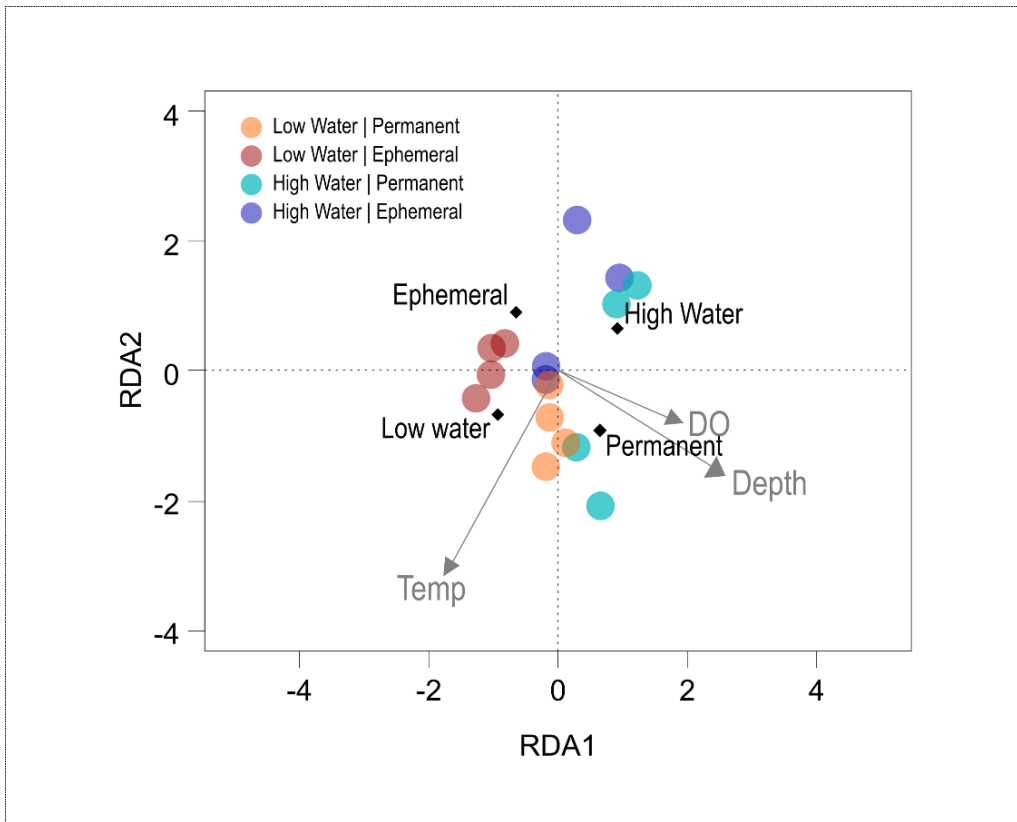


Figure 9. Redundancy analysis showing the relationship between environmental variables, habitat type, and seasonal variation in hydrology.

Species responses to abiotic environmental factors

I collected a total of 8,289 fish specimens comprising 30 species during the duration of the study. Seven species (*Hippopotamyrus ansorgii* (3 individuals), *Pharyngochromis acuticeps* (2 individuals), *Parauchenoglanis ngamensis* (2 individuals), *Enteromius bifrenatus* (2 individuals), *Enteromius spp* (2 individuals), *Clarias theodora* (1 individual) and *Enteromius barnardi* (1 individual)) had sample

sizes < 5 and therefore were removed from the analysis. This resulted in 8,276 specimens comprising 23 species included in the dataset for analysis.

Local densities of all species tended to be greater during low-water periods, as expected. The positive association of sample abundance with low water was strong for *Mormyrus lacerda*, *Enteromius radiatus*, *Enteromius poechi*, *Hepsetus odoe*, *Clarias gariepinus*, *Sargochromis carlottae*, *Sargochromis codringtonii*, *Serranochromis altus*, *Serranochromis angusticeps*, and *Coptodon rendalli* (Figure 10, A). Abundance of *H. cuvieri*, *C. gariepinus*, and *S. altus* was positively associated with ephemeral habitat (Figure 10, B). Only *Tilapia sparmanii* was strongly associated with permanent habitat.

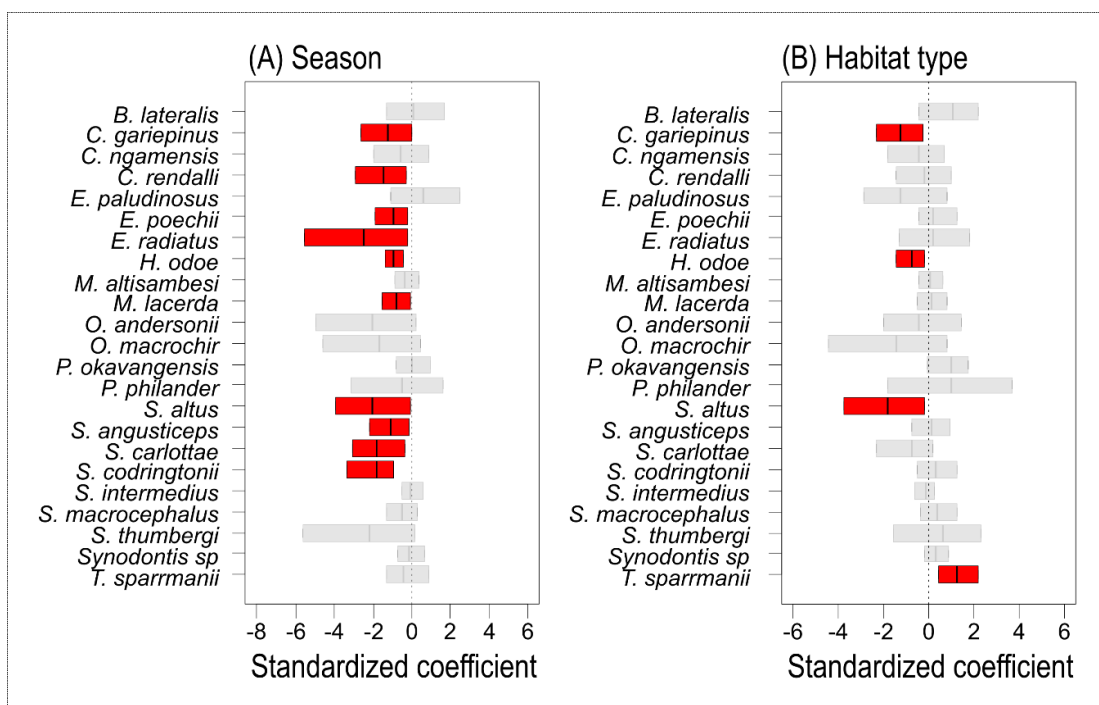


Figure 10. Estimated posterior median coefficients for each species correlation with seasonal change in hydrology and habitat type with 95% credible intervals. Significant species correlations are shown in red. Negative values of the standardized correlation coefficient represent responses to increasing drought (dry season) and positive values indicate responses to increasing wet conditions (wet season).

Two small cyprinids, *E. poechi* and *E. paludinosus*, were positively associated with shallow habitats (Figure 11, A) that were oxygen-rich (Figure 11, C). *E. paludinosus* was negatively associated with temperature, whereas abundance of *Petrocephalus okovangoensis*, *E. poechi*, *Serranochromis macrocephalus*, and *T. sparrmanii* was positively associated with temperature (Figure 11, B). The sharptooth catfish (*C. gariepinus*) and humpback bream (*S. altus*) were more common in habitats with lower dissolved oxygen.

Inference of interspecific interactions

For the model including depth and water quality, twenty-seven significant residual interspecific associations were obtained, of which fifteen were positive and twelve were negative (Figure 12). Intra-guild associations, inter-guild associations involving non-predatory species, and pairs of predatory and potential prey species all had similar proportions of positive correlations (Figure 13). Most negative correlations (58%) were intra-guild pairings. Three quarters (75%) of these intra-guild segregations involved non-predatory species, with the other 25% occurring among predators.

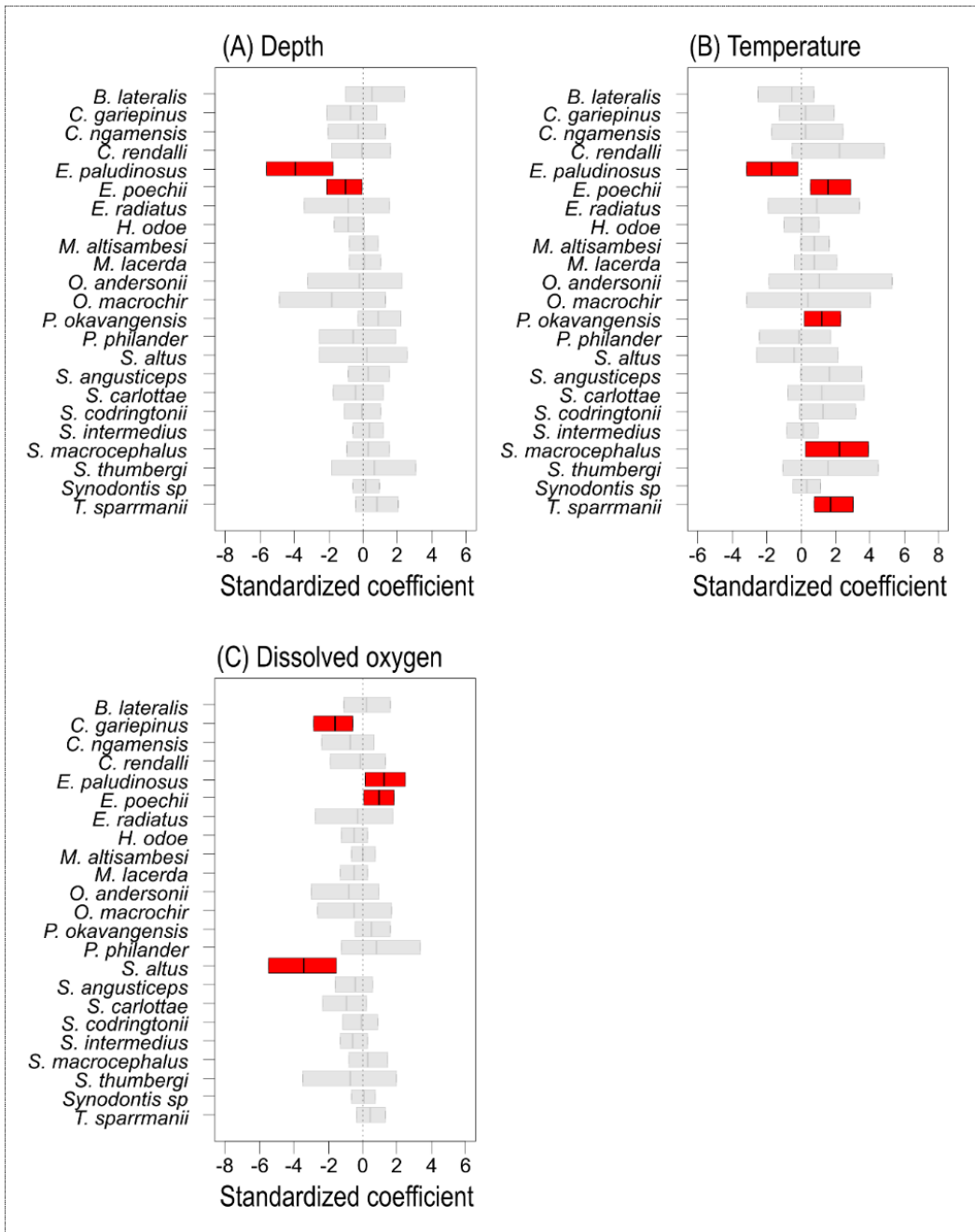


Figure 11. Estimated posterior median coefficients for each species correlation with depth (A), temperature (B), and dissolved oxygen (C) with 95% credible intervals. Significant species correlations are shown in red. Negative values of the standardized correlation coefficient represent decreasing magnitudes of the environmental variables and positive values represent increase in environmental variables.

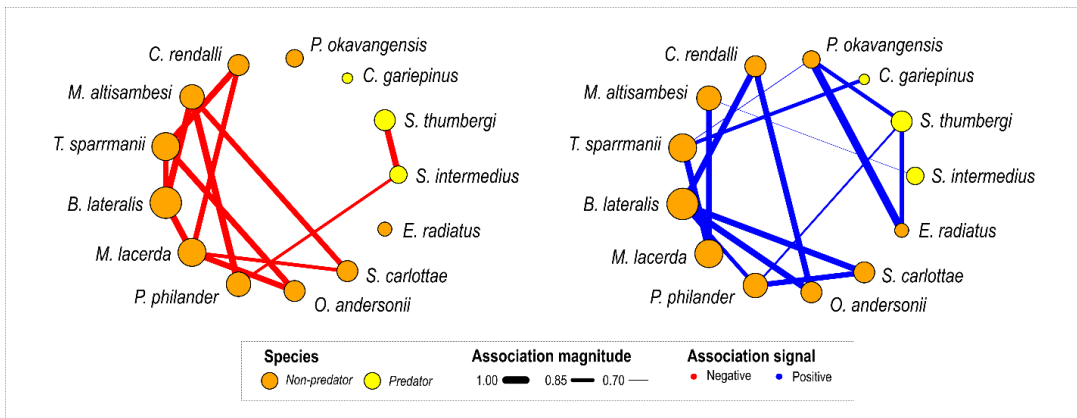


Figure 12. Estimated interspecific residual posterior correlation coefficients after controlling for depth, DO, and temperature. Only significant correlations based on 95% credible intervals are shown. There was a total of twenty-seven non-random species pairs. Fifteen were positively correlated (shown in red) and twelve were negatively correlated (shown in blue).

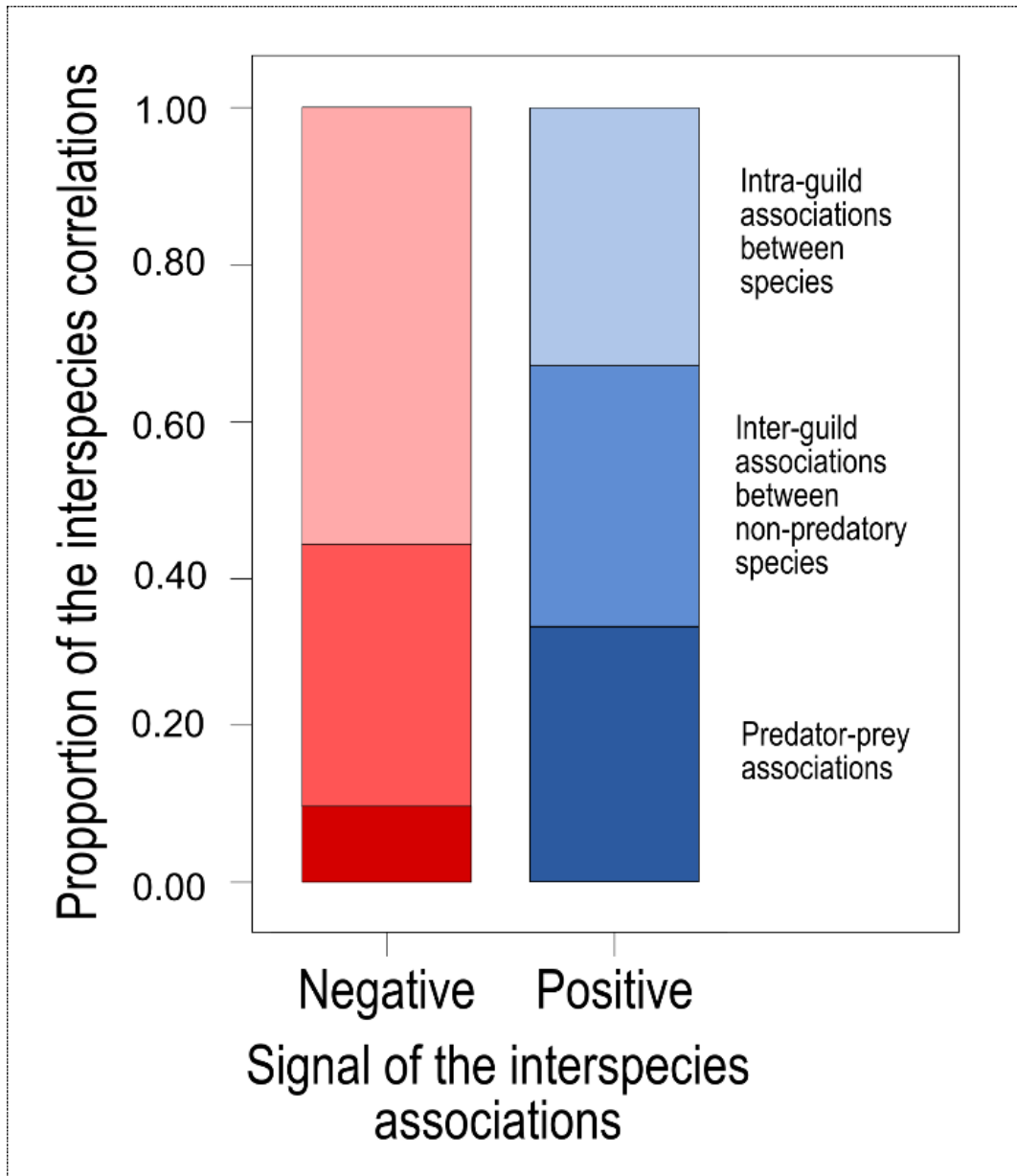


Figure 13. The proportion of negative and positive intra and inter-guild species pairs after controlling for the influence of depth and water quality. There were equal proportions of Positive correlations for Intra-guild correlations, inter-guild correlations involving non-predatory species, and predator-prey interactions. The majority of negative correlations (58%) were intra-guild species associations. Thirty-three percent of negative correlations were inter-guild associations involving non-predatory species, and (9%) were predator-prey interactions.

For the model including seasonal variation in hydrology and habitat type, half (nineteen) of the thirty-eight significant residual interspecific associations were positive and half were negative (Figure 14). Most of the significant positive correlations (42%) were intra-guild species associations (Figure 15). A substantial number of positive correlations (32%) were predator-prey associations. Only 26% of positive correlations were between non-predatory species belonging to different guilds. Many of the significant negative correlations (42%) involved predators and potential prey, and a relatively large proportion (32%) of negative correlations were intra-guild associations. Only (26%) of negative correlations involved non-predatory species from different guilds.

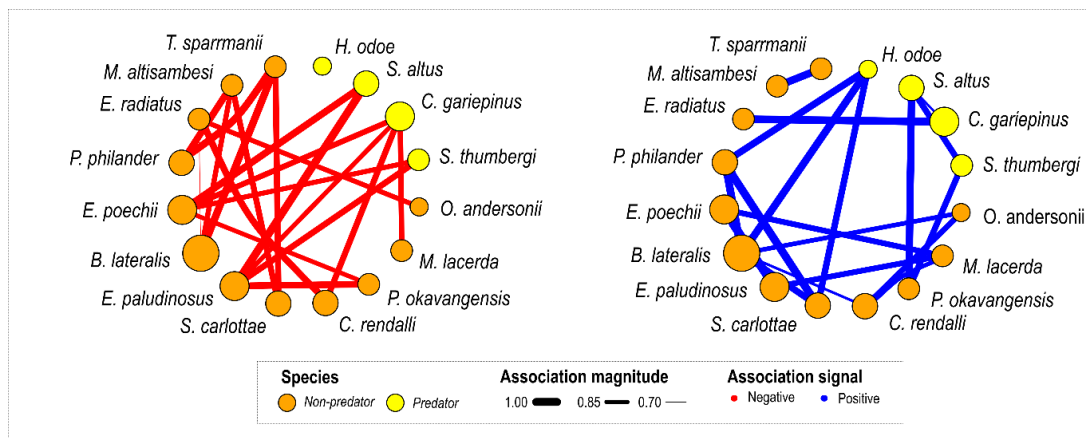


Figure 14. Estimated interspecific residual posterior correlation coefficients after controlling for seasonal change in hydrology and habitat type. Only significant correlations based on 95% credible intervals are shown. There was a total of thirty-eight non-random species pairs. Nineteen were positively correlated (shown in red) and nineteen were negatively correlated (shown in blue).

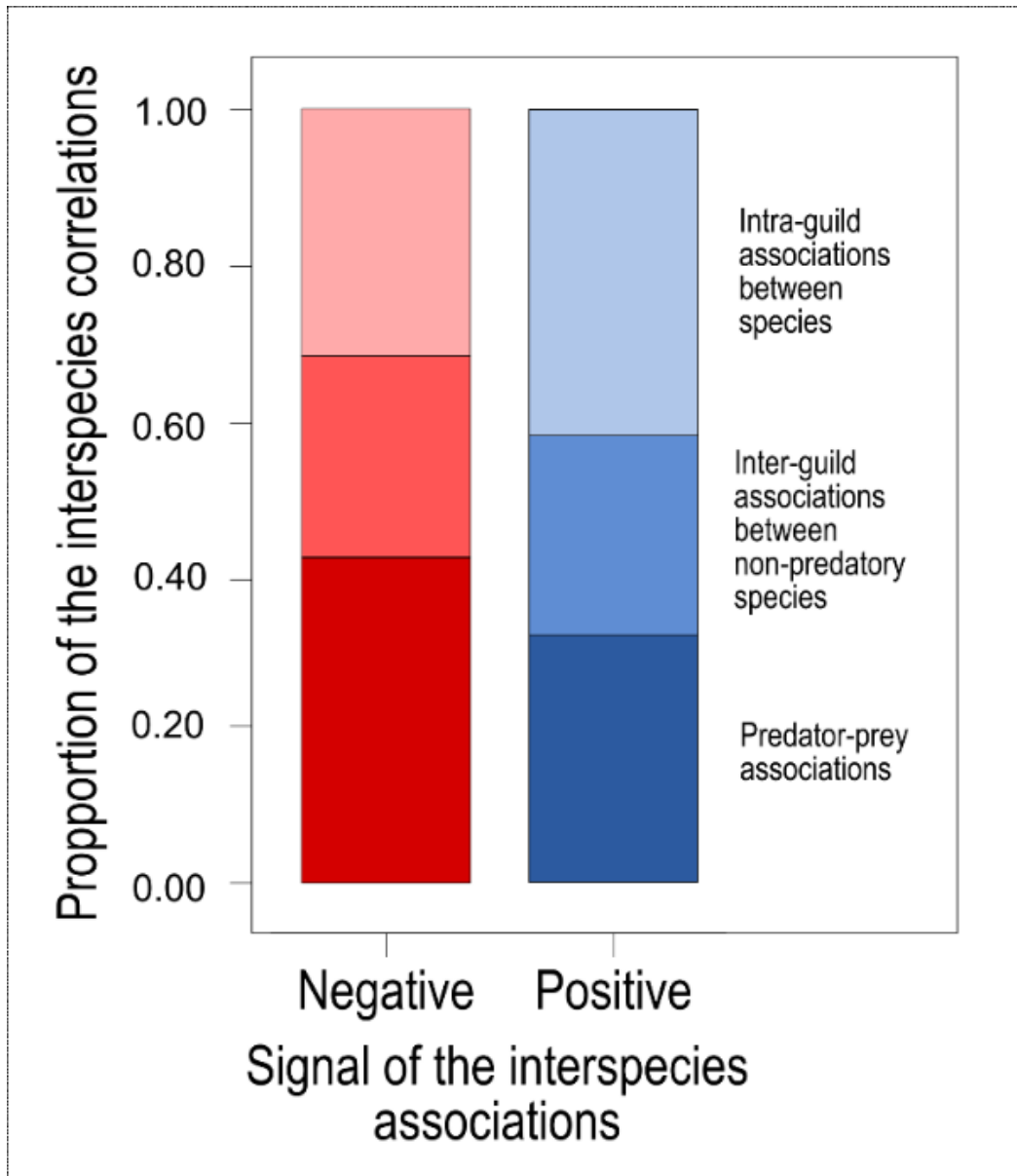


Figure 15. The proportion of negative and positive intra and inter-guild species pairs after controlling for seasonal change in hydrology and habitat type. The majority of positive co-occurrences (42%) were intra-guild species associations. Twenty-six percent (26%) were inter-guild associations involving non-predatory species and (32%) were predator-prey interactions. Most negative co-occurrences (42%) reflected predator-prey interactions. Thirty-two percent of negative co-occurrences were intra-guild species associations, and (26%) were inter-guild associations involving non-predatory species.

Discussion

The analyses of species co-occurrence patterns based on JSDBMs provide insights into how abiotic environmental conditions and biotic interactions affect fish community assembly in intermittent rivers of the lower Okavango Delta. Modeling species responses to seasonal variation in hydrology and habitat type resulted in more significant correlation coefficients for species co-occurrence than did modeling species responses to water depth, temperature and dissolved oxygen. Analysis of residual species correlations from the model including hydrology and habitat type showed that removing the influence of hydrology and habitat type on species abundance resulted in many positive co-occurrence values among species in the same trophic guild, suggesting that many fishes selected and remained within areas with suitable conditions and resources. Most negative associations from this model were between predatory species and potential prey species, suggesting that prey avoided areas with predators or predators depleted prey. When I modeled species responses to water depth, temperature and dissolved oxygen, most species had higher abundance in habitats with higher temperatures. Analysis of residual species correlations from the model including water depth and water quality parameters showed that when the direct influence of water depth and quality on fish abundance was removed, many potential prey species had positive species co-occurrence that suggested similar responses to suitable habitat conditions. Negatively correlated species belonging to the same trophic guild were inferred to be driven by competition for limited habitat or food resources within shrinking and increasingly isolated habitats during the dry season.

Of the twenty-three species captured during the surveys, ten were most common in dry season samples, suggesting that these species return to the river channel as water drains from the floodplain (Merron and Bruton 1995, Winemiller and Jepson 1998). Four of these species (*H. odoe*, *C. gariepinus*, *S. altus*, and *S. angusticeps*) were predators, and the others (*M. lacerda*, *E. radiatus*, *E. poechi*, *S. carlottae*, *S. codringtonii*, and *C. rendalli*) were potential prey. Three of the predators (*H. odoe*, *C. gariepinus*, and *S. altus*) were also associated with ephemeral sites, suggesting that their distributions were, at least partially, affected by habitat preferences and/or availability of prey (Jackson et al. 2001, Inoue et al. 2017). Because ephemeral habitats shrink considerably during the low-water period, per-unit-volume densities tend to increase for fish species unable to disperse into larger and more permanent water bodies. Predators that remain in these shrinking habitats benefit from high encounter rates with potential prey. Offsetting this advantage is the risk of being stranded in isolated water bodies with deteriorating water quality. *Tilapia sparrmanii*, one of the most abundant fishes in the Okavango, is found in slow-moving or standing water with dense vegetation (Skelton 2001), but the species apparently does poorly in ephemeral habitats in my study area during the low-water period. The paucity of significant positive species associations during the wet season may be attributed to low species densities within the main river channel due to fish dispersal into newly inundated floodplains.

Two small cyprinids (*E. poechi* and *E. paludinosus*) were significantly associated with shallow water depth and high DO. However, *E. paludinosus* was associated with cooler water, and *E. poechi* was associated with warmer water. This suggests that

temperature and/or dissolved oxygen levels determined the distribution of these species within shallow habitats. At least one predator (*S. macrocephalus*) and two potential prey (*T. sparrmanii* and *P. okavangoensis*) also were associated with warmer temperature. Temperature affects fish metabolism and swimming performance (Zeng et al. 2009, Lorig et al. 2013), but it is unclear why warmer conditions might favor prey more than their predators. The significant association of *C. gariepinus* with hypoxic conditions could be related to its ability to endure harsh conditions (Skelton 2001). *Serranochromis altus* also was more abundant in habitats with lower dissolved oxygen; however, it is not known if this species is tolerant of hypoxia. In the Upper Zambezi River, *S. altus* is common underneath dense mats of floating grasses along channel margins where it feeds heavily on nocturnal mormyrids (Winemiller 1991). In my analysis, *S. altus* often co-occurred with the mormyrid *P. okavangoensis*, a species also found in slow-flowing, vegetated areas along channel margins (Winemiller 1991).

It is reasonable to assume that biotic interactions and abiotic environmental factors jointly influenced patterns of species co-occurrence. When I modeled species responses to water depth and quality, most of the residual positive species associations were strongly influenced by samples obtained during the low-water period. Stream drying may result in a simultaneous increase in the importance of both abiotic and biotic environmental factors in structuring aquatic biota (Gasith and Resh 1999). In river-floodplain systems, drying reduces aquatic habitat, which leads to higher fish densities, more frequent encounters between potential competitors, predators and prey, and potential depletion of resources (Fitzgerald et al. 2017). Modeling species responses to

hydrology and habitat type resulted in stronger residual positive correlations among species belonging to the same trophic guild. A large proportion of these positive associations involved non-predatory species that prefer areas with abundant aquatic vegetation (Skelton 2001), suggesting aggregation within habitats that provided suitable conditions for survival (Cordero and Jackson 2019). Flow reduction in intermittent rivers creates isolated pools where declining environmental conditions, such as low dissolved oxygen and high temperature, force many fishes to seek locations with the greatest water depth (Gómez et al. 2017). Other studies have inferred that abiotic environmental factors played a major role in structuring fish assemblages. Species-habitat relationships appeared to be more important than biotic interactions in structuring fish communities in the Macau River, Brazil (Peres-Neto 2004), and functional redundancy increased as the number of co-occurring species increased at all spatial scales in Patos Lagoon, Brazil (Mouchet et al. 2013).

When I modeled species responses to depth and water quality and then analyzed species co-occurrence based on species residual correlations, most negative species correlations involved fishes within the same trophic guild, and most of these involved non-predatory species during the low-water period. This finding suggests competition may have influenced spatial segregation of these species during low-water conditions of the dry season. It appears that during the initial stages of drying, many species colonized and remained in the same habitats, but following a prolonged period of drying and reduction in habitat and resources, species in the same trophic guild became increasingly segregated in space.

Modeling species responses to hydrological stage and habitat type followed by the analysis of species residual correlations resulted in many negative correlations between predatory and potential prey species, which is consistent with the idea that predation can influence species spatial segregation (Englund et al. 2009, Cordero and Jackson 2019). A few of the positive species associations were between predatory species, possibly because predators responded similarly to prey availability (Sih 1984, Englund et al. 2009). At the same time, predators may have depleted prey populations within isolated habitats during the low-water period. In tropical rivers, one or a few species of predatory fishes can exert a disproportionately large top-down effect on prey populations (Winemiller 2004), allowing piscivory to affect fish community dynamics both directly and indirectly (Power et al. 1985, 1989, Jackson et al. 2001). When flows diminish, habitat conditions in intermittent rivers of the lower Okavango Delta become dominated by shallow marginal areas supporting growth of aquatic macrophytes that provide refuge from large predators. This can drive species segregation. Two small cyprinids (*E. poechi* and *E. paludinosus*) occupied such areas and were involved in many of the negative correlations with predatory fishes. My results suggest that predation could drive segregation (negative patterns of co-occurrence) either by locally depleting prey or by prey avoiding predators (Power et al. 1985, 1989, Gilliam and Fraser 2001). This decoupling of predator-prey interactions may be facilitated by habitat complexity, allowing coexistence and increasing ecosystem stability (Kovalenko et al. 2012).

Rivers in the Okavango Delta experience flooding and drying that produce temporal shifts among lentic, lotic, and terrestrial conditions to which aquatic organisms

must respond. By relating residual species correlations from JSDMs to fish trophic guilds, I was able to infer mechanisms influencing community assembly. However, it is important to note that I derived species correlations from latent variables, and these correlations could have been influenced by abiotic factors that I did not consider in this study. For example, nutrient concentrations and ecosystem productivity may vary over relatively small spatial scales in intermittent rivers (Dent et al. 2001, Gómez et al. 2009), with a potential impact on species distribution and co-occurrence (Inoue et al. 2017). Nonetheless, my results demonstrate that analysis of residual species correlations from JSDMs, in conjunction with fish trophic guilds, may help ecologists to disentangle residual correlations and tease apart putative biotic interactions from the interactions driven by unmeasured environmental factors in local fish assemblages of intermittent rivers.

The rapid pace of climate change (Williams and Jackson 2007, Terry and Rowe 2015) is likely to increase hydrological extremes in the Okavango Delta and other semiarid regions, with adverse ecological impacts (Acuña et al. 2014, Ruhí et al. 2016). Changes to the flow regime, when coupled with other environmental impacts, will likely alter interspecific interactions (Gilman et al. 2010). Consequently, environmental management should emphasize the maintenance of a relatively natural environmental flow regime to sustain suitable habitat that can support the persistence of ecological mechanisms that structure fish communities in the lower Okavango Delta. Moreover, investigation of food web ecology using field surveys, dietary analysis, field experiments, and ecological modeling is necessary to provide more insights into how

biotic and abiotic factors influence species distributions and co-occurrence in this system.

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CHAPTER IV
SEASONAL HYDROLOGY AND ENERGY CHANNELS IN FOOD WEBS OF
RIVERS IN THE LOWER OKAVANGO DELTA

Introduction

Food webs in river-floodplain systems are complex with thousands of food chains connected in a complex network (Winemiller 2004, Layman et al. 2012). Network structure and stability are affected by the ability of consumers to switch their feeding according to changes in food availability (Liem 1980, Winemiller 1989, Winemiller and Jepsen 1998). Consumers in dynamic systems may cross habitat boundaries to exploit resource pulses and areas with high productivity (Polis and Strong 1996, Vander Zanden and Vadeboncoeur 2002, McCann et al. 2005). Adaptive foraging, and the ability to exploit alternative food resources based on availability can increase the probability of species persistence in fluctuating environments (Kondoh 2003). Therefore, a better understanding of food web structure in dynamic systems requires characterization of pathways of energy and matter transfer among food web compartments and their variation through time and across space.

Aquatic food webs are supported by both algal-grazer and detrital-microbial energy pathways (Winemiller 1990,1996, Vadeboncoeur et al. 2003, Moline et al. 2004, McIntosh et al. 2017). These pathways are sometimes referred to as green versus brown food webs (Wolkovich et al. 2014, Zou et al. 2016). Numerous studies of aquatic ecosystems have emphasized the importance of the green food web (Rooney and

McCann 2012, Roach and Winemiller 2015, McIntosh et al. 2017), presumably because, for most metazoan consumers, plant tissue is more easily digested and provides higher nutritional value than detritus and associated microbial decomposers (Thorp and Delong 1994, Lewis et al. 2001). Whereas macrophytes may be abundant within streams and riparian areas, they usually do not contribute much material to the biomass of aquatic organisms at positions higher in food webs (Bunn et al. 2003). This appears to be due to the inability of most aquatic macroinvertebrates and vertebrates to digest and absorb nutrients from macrophyte tissues (Renaud et al. 1999, Cotner and Biddanda 2002). Nonetheless, a few studies suggest that heterotrophy and the brown food web may predominate in ecosystems with a high abundance and diversity of consumers but low primary productivity (Legendre and Rassoulzadegan 1995, Cotner and Biddanda 2002).

Hydroperiod stage and the dynamics of basal resources are major determinants of spatial and temporal shifts in predominant energy pathways and interactions in river food webs (McCann et al. 1998, Kondoh 2003). Using stable isotope analysis, several studies inferred that carbon and nitrogen originating from macrophytes supported fish biomass in rivers during high flow pulses (Jardine et al. 2012, Zeug and Winemiller 2008, Roach and Winemiller 2015, Ou and Winemiller 2016). A few fish species in the Amazon River in Brazil and the Apure River in Venezuela were reported to assimilate material derived primarily from terrestrial C₄ grasses, a basal source that tends to have higher ¹³C/¹²C ratios than other sources (Forsberg et al. 1993, Jepson and Winemiller 2007). In many fluvial systems, both materials originating from outside the aquatic ecosystem and production from within the aquatic ecosystem appear to support biomass

of fish and other metazoan consumers, especially during low-flow periods (Bunn et al. 2003, Thorp and Delong 1994, Zeug and Winemiller 2008, Roach and Winemiller 2015, Ou and Winemiller 2016, Venarsky et al. 2020).

Perhaps the most comprehensive model seeking to predict general patterns of material and energy flow in river food webs is the river wave concept (RWC) (Humphries et al. 2014). The RWC equates river flow to waves traversing the landscape in both longitudinal and lateral dimensions. It posits that at the trough of the river wave (low flow), energy from in-stream primary production and local terrestrial inputs should predominate. During the ascending and descending limbs of the wave, upstream allochthonous inputs and downstream export of basal sources and consumers are important. However, at the crest of the wave (high flow), energy from terrestrial inputs and primary production in the floodplain assume greater importance (Humphries et al. 2014).

Our understanding of energy sources that support food webs of river-floodplain ecosystems and wetlands has increased in recent years, with a noticeable rise in investigations of river food webs in Africa (Hill et al. 2015, Taylor et al. 2017, Peel et al. 2019, Masese et al. 2020). Even so, the influence of wet-dry seasonality and flow pulses on aquatic food web dynamics is poorly understood even at the global scale (McMeans et al. 2015, McIntosh et al. 2017). In this study, I sampled reaches in the Boro and Boteti tributaries in the lower Okavango Delta, a large wetland complex located within a semiarid region of southern Africa, during high and low flow periods within one hydrological cycle. I investigated changes in carbon sources supporting aquatic food

webs across a gradient of water residence time. During the study period, the study reach in the Boro River was ephemeral and experienced habitat fragmentation and eventual desiccation during the dry season. In contrast, the study reach in the Boteti River retained water throughout the duration of the study without loss of longitudinal habitat connectivity. I inferred seasonal changes in predominant energy pathways and trophic structure using stable isotope ratios of carbon and nitrogen. Carbon and nitrogen stable isotopes are useful tracers in food web research because nitrogen ratios estimate organisms' vertical trophic positions, and carbon ratios often are useful for estimating the energy sources supporting consumer biomass (Minagawa and Wada 1984, Vander Zanden and Rasmussen 1999).

I hypothesized that food webs in both rivers would follow predictions of the RWC. First, I expected energy from autochthonous production within the river channel and local allochthonous inputs to support fish biomass during periods with low flows. During high flows, production sources from the floodplain should provide the most important inputs to aquatic food webs, as predicted by the RWC. Second, I predicted that in both rivers, many fish species would be trophic generalists, linked to many food chains and diverse basal production sources. Other species were predicted to be trophic specialists linked to fewer food chains originating from only a few sources. Third, I postulated that species integrating multiple basal sources and food chains will be positioned higher in the food web, and those deriving large proportions of their tissues from one source will be positioned lower in the food web. This is because fish

positioned higher in the food web have more opportunity to integrate inputs from multiple food chains that originate from different basal sources.

Methods

Study area

The Okavango Delta is the largest water body in Botswana, and it is supported by the annual flood pulse that originates in Angolan highlands. About 16 km³ of water enters the Delta every year around December/January at Mohembo, the majority of which (96%) is lost to evapotranspiration, 2% is lost through seepage, and only 2% leaves the wetland as surface flow around May/June, mainly through the Boro River channel (Ellery and McCarthy 1998). The Boro River forms a confluence with the Thamalakane River at Matlapaneng and flows in the south-west direction until it branches at Dikgathong to form Boteti River and Nhabe River. Generally, the lower Delta experiences wetting, and increased flow conditions between May and October, while reduced flows and dry season conditions extend from November to April (Akoko et al. 2013).

I analyzed food webs by sampling Boro and Boteti Rivers during wet and dry seasons within one annual flood cycle. I sampled four sites in Boro River along a *c.* 20 km reach from the buffalo fence to the Boro-Thamalakane junction at Matlapaneng (Figure 16). The substrate in this reach is fine sand within the main river channel, along channel margins and in floodplains. Waterlily, submerged aquatic macrophytes and hippo grass were observed. Deciduous trees and acacia species comprised the majority

of riparian trees. I sampled two sites in Boteti River in a *c.* 30-km reach from the Thamalakane-Boteti River junction to Chanoga Lagoon. The substrate in Boteti River is mainly solid bed rock, boulders and clay within the main river channel. Channel margins and floodplains consist of silty sand, and pebbles in some parts. Aquatic macrophytes and riparian vegetation were similar to those in Boro River. Hippopotamus (*Hippopotamus amphibious*) were frequently sighted throughout the study period in Boteti River reach. When the river flow was bankful, channel width was relatively similar for most parts of the two reaches, except in Chanoga Lagoon where the channel widened ~ two-fold.

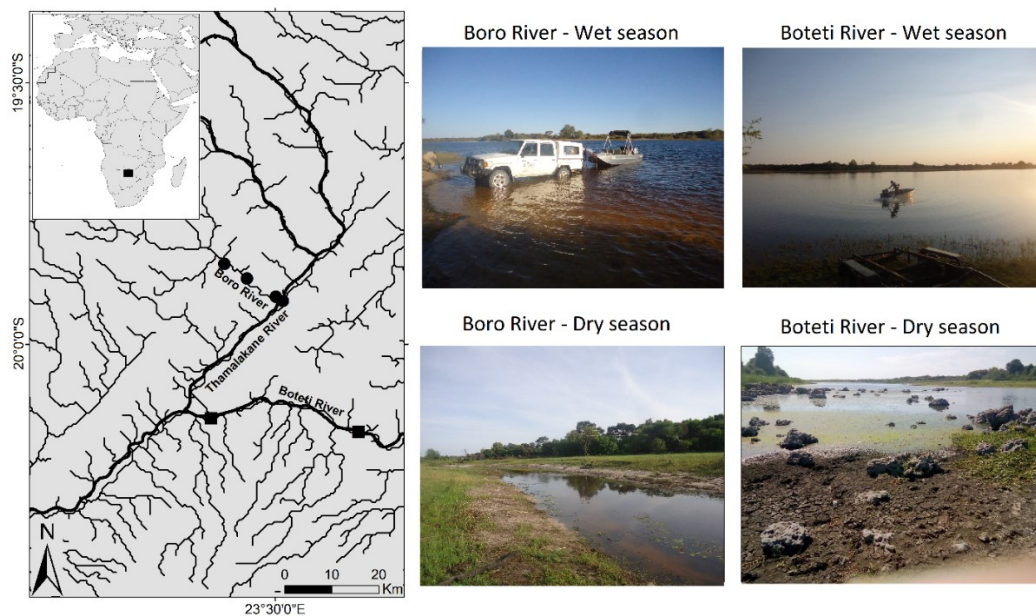


Figure 16. Sampling sites in the Boro and Boteti Rivers during the wet and dry seasons. During the wet season, water volume was high and a motorised boat was used to access sampling sites.

Fish sampling

I sampled fishes using a nylon multifilament gillnet that had 11 panels of different mesh sizes (12 mm, 16 mm, 22 mm, 28 mm, 35 mm, 45 mm, 57 mm, 73 mm, 93 mm, 108 mm, 150 mm; stretched mesh) each with a length of 10 m and approximately 2.5 m deep, a seine net and two double-ended fyke nets with 1.2 m D-openings and 25 mm mesh size to capture different species of varying sizes. I set the gill net in the main channel, and fyke nets were set perpendicular to the main channel stretching from the riverbank into the floodplain. The gill net and fyke nets were set overnight from *c.* 1800 hr in the evening and retrieved the following morning at *c.* 0600 hr. I seined opportunistically during the daytime when conditions were deemed safe from crocodiles. I quickly euthanized specimens (TAMU AUP IACUC 2017-0069), obtained samples of muscle tissue from the right flank below the base of the dorsal fin of select specimens, fixed voucher specimens in formalin, and preserved them in ethanol for archiving at the Biodiversity Research and Teaching Collection at Texas A&M University, College Station. I identified specimens to species level based on keys and illustrations in Skelton (2001).

Collection and preparation of isotopic samples

In each river and during each season, I collected samples from six basal resources (seston, riparian C3 plants, terrestrial C4 grasses, periphyton, waterlily) and fish muscle tissues. I collected periphyton by scraping submerged tree branches. I obtained seston (which may consist of either allochthonous or autochthonous materials depending on the hydroperiod stage) from surface water that I filtered through pre-

combusted Whatman GF/F filters with a pore size of 0.7 μm (methods follow those reported in Ou and Winemiller 2016). I collected leaves of riparian trees, shrubs, and grasses (allochthonous sources) that were prevalent along channel margins and in the floodplain. I also collected leaves and stems of dominant floating and submerged aquatic macrophytes from the main river channel. I considered waterlily to be a separate source from other aquatic macrophytes because of its distinct isotope signature. I also collected muscle tissue from snails (*Radix* spp.) to serve as the isotopic baseline (aquatic primary consumer) for estimation of fish trophic positions (see below). To account for individual variability in the isotope values of fish and basal resources, three to five samples of each species of fish and basal resources were collected at each site.

I sampled basal sources and fish tissues during the peak flood (August 10 – 14, 2017, and October 12 – 20, 2017) and during the period of lowest flows (December 2– 8, 2017 and February 16 – 25, 2018). Thus, samples were obtained 3 – 5 months after the beginning of the wet season and 1 – 3 months after the start of the dry season. The isotopic half-life of fish muscle tissue ranges from 10 – 60 days with a mean of 25 days (Boecklen et al. 2011). Therefore, I assumed that isotope ratios of consumers reflected feeding history during the season when the samples were collected (Hobson and Clark 1992, Bearhop et al. 2004, Ou and Winemiller 2016). I packaged basal source and fish muscle tissue samples in plastic bags and preserved them in salt for later analysis in the laboratory.

Following the protocol described by Arrington and Winemiller (2002), I first soaked the salt-preserved material in distilled water and then rinsed them to remove salt.

I then dried the material in an oven at 60°C for 48 hours and ground the dried material into a fine powder using mortar and pestle. I weighed powdered subsamples to the nearest 0.02 mg and packaged them into Ultrapure® tin capsules. Analysis of carbon and nitrogen isotope ratios were carried out at the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, USA. Stable isotopes of carbon and nitrogen were analyzed following standard procedures. Isotope ratios were reported in parts per thousand (‰) relative to the Pee Dee Belemnite (C) and atmospheric nitrogen (N) such that; $\delta X(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 10^3$, where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

Data analysis

I used Bayesian stable isotope mixing models to infer the proportion of basal sources assimilated by fish. I adjusted for trophic fractionation (TF) of $\delta^{15}\text{N}$ in the models using values for Southern African fishes obtained from Taylor et al. (2017) and $\delta^{13}\text{C}$ TF was obtained by averaging values from the literature (Bastos et al. 2017) (TF of $\delta^{13}\text{C} = 0.54 \pm 0.53$, TF of $\delta^{15}\text{N} = 3.37 \pm 1.30$ [mean \pm SD]). The resulting plot was assessed to ensure that consumer isotopic values fell within the isospace defined by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of potential food sources (Phillips et al. 2014, Arantes et al. 2019). Lipid correction was not considered to be necessary because the C:N ratio of fish muscles was fairly small (Post et al. 2007). Following the approach reported by Ou and Winemiller (2016), I ran isotopic source mixing models for individual fish species in each river and season within a Bayesian framework using the R package, *simmr* (Parnell 2020). Chains of all mixing models converged (Gelman-Rubin Statistic < 1.1), and I recorded the

median contribution of each source to fish biomass with 95% credible intervals. I determined the ability of the models to adequately separate food sources assimilated by fish through the assessment of correlations between sources in the isospace. Except for a few relatively high correlations between sources, which is a common problem for stable isotope mixing models (Phillips et al. 2014), isotopic discrimination among sources was sufficient to allow models to estimate proportional assimilation among alternative sources.

I estimated trophic position based on the Bayesian model proposed by Quezada-Romegialli et al. (2018). I used the mean $\delta^{15}\text{N}$ value of snails (aquatic consumer at trophic level 2) as my baseline (Arantes et al. 2019), and both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic determination factors (TDFs) for muscle tissues to estimate fish trophic position (McCutchan et al. 2003). I used linear regression to estimate the relationship between the degree of dependence on one major source and the modal trophic position for fish species in both rivers during each season. The response variable was the modal trophic position obtained from the probability distribution of estimated trophic positions for each species during a particular period/season, and the explanatory variable was the highest value for estimated mean percent contribution among basal sources for that species for the same period/season.

All analyses were conducted in R (R Core Team 2020). Mixing models were run in the *simmr* package (Parnell 2020). Trophic position was calculated using the package *tRophicPosition* (Quezada-Romegialli et al. 2018).

Results

Stable isotope signatures of basal production sources, and fishes

A total of 220 samples encompassing the six basal sources were collected during the study period (Table 4). A greater number of samples was obtained during the dry season (Boteti = 70; Boro = 66) than wet season (Boteti = 25; Boro = 59). Consistent with most prior studies, terrestrial C4 grass had highest $\delta^{13}\text{C}$ values among plants (Figures 17 and 18).

Tissue samples were collected from 486 fish specimens representing 25 species (Table 5). In both rivers, more species were collected during the dry season (Boteti = 19 species; Boro = 21 species) than wet season (Boteti = 15 species; Boro = 17 species). Detritivorous fishes tended to have low values for $\delta^{15}\text{N}$, and, as expected, piscivorous fishes had highest $\delta^{15}\text{N}$ values.

Table 4. Sample size (n), mean carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), and their standard deviations (SD) for basal production sources from the intermittent reaches of the lower Okavango Delta.

Source	Species	n	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$
Aquatic macrophyte	<i>Aquatic plant</i>	19	-26.90	1.63	3.39	2.92
	<i>Hippo grass</i>	5	-27.30	1.24	2.78	1.21
C3 plant	<i>Riparian tree</i>	80	-28.19	1.65	3.27	2.32
	<i>Shrub</i>	8	-29.30	0.49	4.60	1.36
C4 grass		17	-12.47	0.72	3.55	3.09
Periphyton		18	-29.17	2.90	2.76	2.56
Seston		40	-25.79	1.24	4.67	1.58
Water lily		33	-25.55	1.33	1.58	3.85

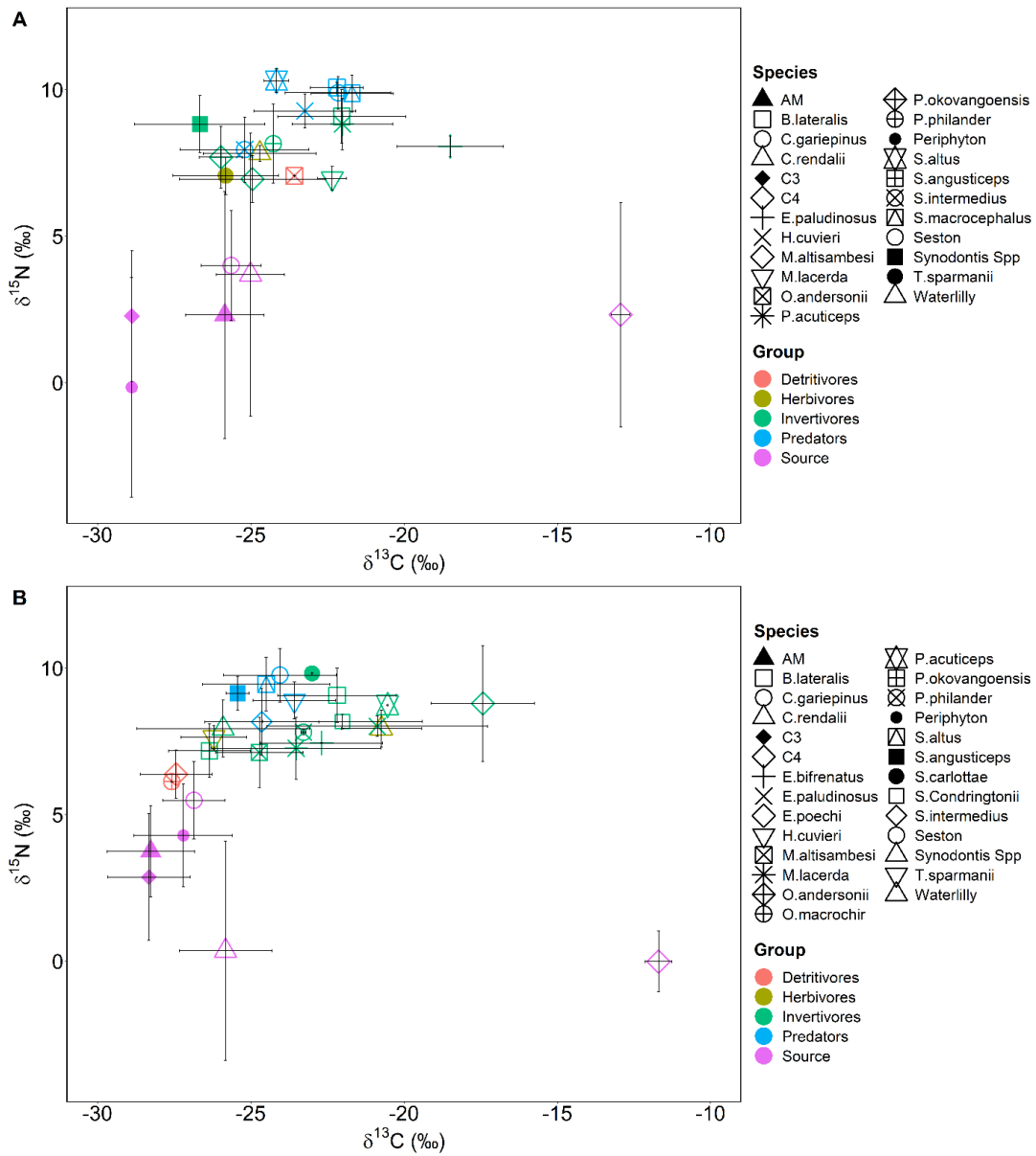


Figure 17. Biplots of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (\pm standard deviation) for basal production sources and fishes from Boro River during wet (A) and dry (B) seasons.

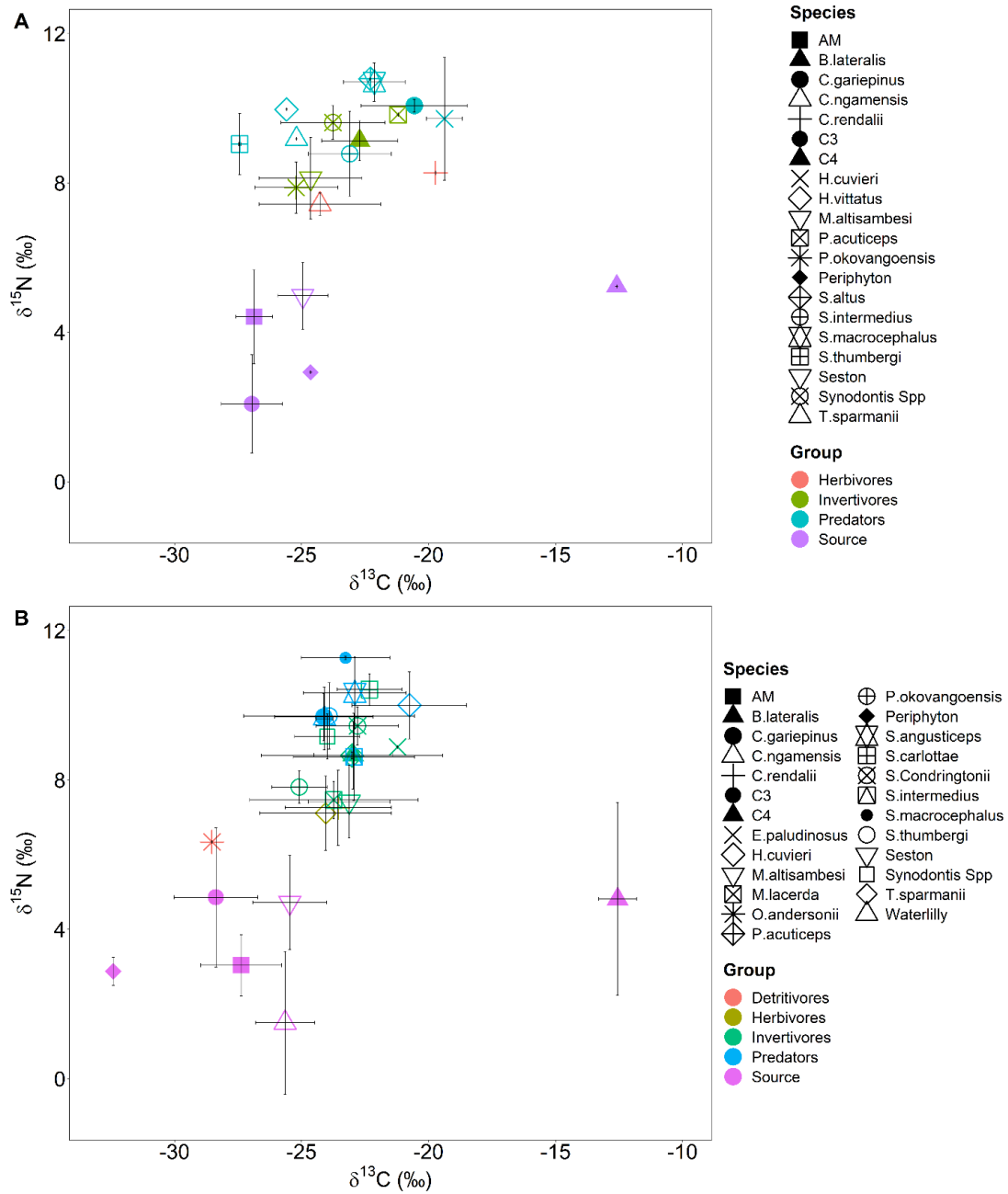


Figure 18. Biplots of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (\pm standard deviation) for basal production sources and fishes from Boteti River during wet (A) and dry (B) seasons.

Table 5. Sample size (n), mean carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), and their standard deviations (SD) for fish species that were analyzed in this study.

Species	n	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$
<i>Oreochromis andersonii</i>	7	-27.04	1.85	6.47	0.72
<i>Oreochromis macrochir</i>	1	-27.58	-	6.13	-
<i>Coptodon rendalli</i>	11	-22.39	2.36	7.70	0.76
<i>Tilapia sparmanii</i>	34	-25.15	2.16	7.25	0.74
<i>Enteromius bifrenatus</i>	2	-22.69	1.99	7.45	0.01
<i>Brycinus lateralis</i>	54	-22.44	1.81	8.99	0.84
<i>Enteromius paludinosus</i>	16	-19.85	2.97	8.09	0.39
<i>Enteromius poechi</i>	2	-17.43	1.68	8.80	1.97
<i>Mormyrus lacerda</i>	11	-23.28	2.45	7.26	0.70
<i>Marcusenius altisambesi</i>	70	-24.57	2.09	7.30	1.05
<i>Pharyngochromis acuticeps</i>	9	-21.98	1.88	8.89	0.71
<i>Petrocephalus okovangoensis</i>	34	-25.61	1.36	7.66	0.81
<i>Pseudocrenilabrus philander</i>	4	-23.77	3.37	7.99	0.81
<i>Sargochromis carlottae</i>	3	-22.55	0.98	10.22	0.46
<i>Sargochromis condringtonii</i>	9	-22.45	2.00	8.88	0.77
<i>Synodontis spp.</i>	37	-25.41	2.50	8.72	1.03
<i>Clarias gariepinus</i>	25	-23.25	2.08	9.81	0.73
<i>Clarias ngamensis</i>	3	-24.47	0.68	9.49	0.65
<i>Hepsetus cuvieri</i>	47	-22.61	2.12	9.32	0.82
<i>Hydrocynus vittatus</i>	1	-25.59	-	9.97	-
<i>Serranochromis altus</i>	7	-24.09	1.68	9.89	0.88
<i>Serranochromis angusticeps</i>	11	-23.69	1.93	9.85	0.89
<i>Schilbe intermedius</i>	75	-24.23	2.22	8.29	1.16
<i>Serranochromis macrocephalus</i>	7	-22.27	1.36	10.51	0.76
<i>Serranochromis thumbergi</i>	6	-25.09	3.18	9.49	0.86

Source contributions to consumers

Across rivers and seasons, the biomass of virtually all fish species likely was supported by multiple energy pathways originating from various basal sources (Table 6).

Nonetheless, various source contributions to fish biomass varied depending on location and season for several species.

Table 6. Median, lower and upper 95% credible intervals of estimated contributions of basal production sources to the biomass of fish species in the Boro and Boteti River systems during the wet and dry seasons. The most important source for each species is highlighted in bold and marked with an asterisk. Species with > than one source contributing > 20% of their tissues are highlighted in bold.

Species	Source	Median	LCI	UCI
BORO WET SEASON				
<i>Brycinus lateralis</i>	Aquatic macrophyte	0.06	0.01	0.30
	Riparian C3 plant	0.05	0.01	0.22
	Terrestrial C4 grass	0.24	0.14	0.33
	Periphyton	0.04	0.01	0.14
	*Seston	0.27	0.02	0.66
	Waterlily	0.24	0.02	0.63
<i>Enteromius paludinosus</i>	Aquatic macrophyte	0.07	0.01	0.28
	Riparian C3 plant	0.07	0.01	0.23
	Terrestrial C4 grass	0.52	0.26	0.64
	Periphyton	0.05	0.01	0.19
	Seston	0.10	0.01	0.38
	Waterlily	0.10	0.01	0.34
<i>Clarias gariepinus</i>	Aquatic macrophyte	0.10	0.01	0.46
	Riparian C3 plant	0.09	0.01	0.34
	Terrestrial C4 grass	0.25	0.07	0.39
	Periphyton	0.07	0.01	0.27
	Seston	0.15	0.02	0.58
	Waterlily	0.17	0.02	0.62
<i>Hepsetus cuvieri</i>	Aquatic macrophyte	0.07	0.01	0.34
	Riparian C3 plant	0.06	0.01	0.25
	Terrestrial C4 grass	0.15	0.06	0.24
	Periphyton	0.04	0.01	0.15
	Seston	0.30	0.02	0.76
	Waterlily	0.26	0.02	0.70
<i>Mormyrus lacerda</i>	Aquatic macrophyte	0.12	0.02	0.44
	Riparian C3 plant	0.11	0.02	0.39
	Terrestrial C4 grass	0.25	0.05	0.38
	Periphyton	0.09	0.01	0.32
	Seston	0.17	0.02	0.57
	Waterlily	0.13	0.02	0.48
<i>Marcusenius altisambesi</i>	Aquatic macrophyte	0.06	0.01	0.19
	Riparian C3 plant	0.10	0.02	0.26
	Terrestrial C4 grass	0.05	0.01	0.11
	Periphyton	0.04	0.01	0.11
	Seston	0.63	0.44	0.80
	Waterlily	0.08	0.01	0.20

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Oreochromis andersonii</i>	Aquatic macrophyte	0.13	0.02	0.54
	Riparian C3 plant	0.11	0.01	0.44
	Terrestrial C4 grass	0.16	0.04	0.28
	Periphyton	0.10	0.01	0.40
	Seston	0.16	0.02	0.63
	Waterlily	0.16	0.02	0.58
<i>Pharyngochromis acuticeps</i>	Aquatic macrophyte	0.11	0.01	0.47
	Riparian C3 plant	0.09	0.01	0.36
	Terrestrial C4 grass	0.25	0.05	0.41
	Periphyton	0.07	0.01	0.31
	Seston	0.15	0.02	0.59
	Waterlily	0.16	0.02	0.61
<i>Petrocephalus okavangoensis</i>	Aquatic macrophyte	0.11	0.01	0.49
	Riparian C3 plant	0.22	0.02	0.51
	Terrestrial C4 grass	0.03	0.01	0.10
	Periphyton	0.09	0.01	0.34
	*Seston	0.26	0.02	0.75
	Waterlily	0.13	0.01	0.47
<i>Pseudocrenilabrus philander</i>	Aquatic macrophyte	0.13	0.02	0.56
	Riparian C3 plant	0.12	0.02	0.55
	Terrestrial C4 grass	0.12	0.02	0.49
	Periphyton	0.10	0.01	0.50
	Seston	0.14	0.02	0.61
	Waterlily	0.13	0.02	0.57
<i>Serranochromis altus</i>	Aquatic macrophyte	0.14	0.02	0.57
	Riparian C3 plant	0.12	0.02	0.48
	Terrestrial C4 grass	0.12	0.02	0.36
	Periphyton	0.11	0.01	0.46
	Seston	0.14	0.02	0.62
	Waterlily	0.15	0.02	0.63
<i>Serranochromis angusticeps</i>	Aquatic macrophyte	0.12	0.02	0.55
	Riparian C3 plant	0.11	0.02	0.44
	Terrestrial C4 grass	0.20	0.02	0.45
	Periphyton	0.10	0.01	0.44
	Seston	0.13	0.01	0.55
	Waterlily	0.14	0.02	0.60

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Schilbe intermedius</i>	Aquatic macrophyte	0.03	0.00	0.13
	Riparian C3 plant	0.03	0.00	0.14
	Terrestrial C4 grass	0.02	0.00	0.06
	Periphyton	0.02	0.00	0.07
	Seston	0.82	0.52	0.93
	Waterlily	0.05	0.01	0.29
<i>Serranochromis macrocephalus</i>	Aquatic macrophyte	0.12	0.01	0.49
	Riparian C3 plant	0.10	0.01	0.41
	Terrestrial C4 grass	0.25	0.03	0.47
	Periphyton	0.09	0.01	0.36
	Seston	0.13	0.02	0.56
	Waterlily	0.14	0.02	0.57
<i>Synodontis spp.</i>	Aquatic macrophyte	0.08	0.01	0.48
	Riparian C3 plant	0.19	0.01	0.68
	Terrestrial C4 grass	0.04	0.01	0.11
	Periphyton	0.07	0.01	0.36
	Seston	0.25	0.02	0.86
	Waterlily	0.13	0.01	0.58
<i>Coptodon rendalli</i>	Aquatic macrophyte	0.13	0.02	0.58
	Riparian C3 plant	0.13	0.02	0.53
	Terrestrial C4 grass	0.11	0.01	0.40
	Periphyton	0.11	0.01	0.49
	Seston	0.15	0.02	0.63
	Waterlily	0.14	0.02	0.60
<i>Tilapia sparrmanii</i>	Aquatic macrophyte	0.08	0.01	0.33
	Riparian C3 plant	0.15	0.02	0.48
	Terrestrial C4 grass	0.04	0.01	0.11
	Periphyton	0.06	0.01	0.22
	Seston	0.52	0.08	0.80
	Waterlily	0.09	0.01	0.33
BORO DRY SEASON				
<i>Enteromius bifrenatus</i>	Aquatic macrophyte	0.13	0.02	0.54
	Riparian C3 Plants	0.12	0.02	0.50
	Terrestrial C4 grass	0.14	0.02	0.41
	Periphyton	0.13	0.02	0.58
	Seston	0.16	0.02	0.60
	Waterlily	0.10	0.01	0.45

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Brycinus lateralis</i>	Aquatic macrophyte	0.09	0.01	0.38
	Riparian C3 Plants	0.07	0.01	0.34
	Terrestrial C4 grass	0.24	0.03	0.35
	Periphyton	0.12	0.01	0.52
	*Seston	0.27	0.02	0.79
	Waterlily	0.06	0.01	0.30
<i>Enteromius paludinosus</i>	Aquatic macrophyte	0.07	0.01	0.34
	Riparian C3 Plants	0.06	0.01	0.24
	Terrestrial C4 grass	0.07	0.01	0.27
	Periphyton	0.10	0.01	0.50
	Seston	0.59	0.09	0.80
	Waterlily	0.04	0.01	0.16
<i>Enteromius poechii</i>	Aquatic macrophyte	0.11	0.01	0.54
	Riparian C3 Plants	0.11	0.01	0.53
	Terrestrial C4 grass	0.16	0.02	0.63
	Periphyton	0.12	0.01	0.57
	Seston	0.12	0.02	0.58
	Waterlily	0.10	0.01	0.50
<i>Clarias gariepinus</i>	Aquatic macrophyte	0.06	0.01	0.36
	Riparian C3 Plants	0.05	0.01	0.27
	Terrestrial C4 grass	0.12	0.02	0.21
	Periphyton	0.08	0.01	0.54
	Seston	0.57	0.05	0.87
	Waterlily	0.04	0.01	0.19
<i>Hepsetus cuvieri</i>	Aquatic macrophyte	0.03	0.01	0.16
	Riparian C3 Plants	0.03	0.00	0.13
	Terrestrial C4 grass	0.15	0.03	0.21
	Periphyton	0.04	0.01	0.27
	Seston	0.70	0.31	0.86
	Waterlily	0.02	0.00	0.10
<i>Mormyrus lacerda</i>	Aquatic macrophyte	0.12	0.01	0.54
	Riparian C3 Plants	0.11	0.02	0.47
	Terrestrial C4 grass	0.11	0.02	0.29
	Periphyton	0.14	0.02	0.59
	Seston	0.23	0.02	0.66
	Waterlily	0.08	0.01	0.38

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Marcusenius altisambesi</i>	Aquatic macrophyte	0.09	0.01	0.40
	Riparian C3 Plants	0.07	0.01	0.29
	Terrestrial C4 grass	0.11	0.05	0.17
	Periphyton	0.15	0.02	0.65
	Seston	0.42	0.04	0.69
	Waterlily	0.06	0.01	0.21
<i>Oreochromis andersonii</i>	Aquatic macrophyte	0.25	0.02	0.74
	Riparian C3 Plants	0.19	0.02	0.65
	Terrestrial C4 grass	0.04	0.01	0.14
	Periphyton	0.14	0.01	0.57
	Seston	0.12	0.01	0.45
	Waterlily	0.08	0.01	0.29
<i>Oreochromis macrochir</i>	Aquatic macrophyte	0.21	0.02	0.72
	Riparian C3 Plants	0.19	0.02	0.70
	Terrestrial C4 grass	0.03	0.01	0.10
	Periphyton	0.13	0.01	0.66
	Seston	0.10	0.01	0.51
	Waterlily	0.08	0.01	0.40
<i>Pharyngochromis acuticeps</i>	Aquatic macrophyte	0.05	0.01	0.20
	Riparian C3 Plants	0.05	0.01	0.31
	Terrestrial C4 grass	0.32	0.14	0.42
	Periphyton	0.06	0.01	0.57
	Seston	0.07	0.01	0.53
	*Waterlily	0.36	0.01	0.66
<i>Petrocephalus okavangoensis</i>	Aquatic macrophyte	0.16	0.02	0.63
	Riparian C3 Plants	0.11	0.01	0.42
	Terrestrial C4 grass	0.04	0.01	0.10
	Periphyton	0.18	0.02	0.68
	Seston	0.29	0.03	0.67
	Waterlily	0.06	0.01	0.21
<i>Pseudocrenilabrus philander</i>	Aquatic macrophyte	0.12	0.02	0.52
	Riparian C3 Plants	0.11	0.02	0.48
	Terrestrial C4 grass	0.17	0.02	0.35
	Periphyton	0.14	0.02	0.56
	Seston	0.16	0.02	0.61
	Waterlily	0.11	0.01	0.49

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Serranochromis altus</i>	Aquatic macrophyte	0.12	0.01	0.55
	Riparian C3 Plants	0.10	0.01	0.50
	Terrestrial C4 grass	0.10	0.01	0.26
	Periphyton	0.14	0.02	0.64
	Seston	0.19	0.02	0.74
	Waterlily	0.09	0.01	0.50
<i>Serranochromis angusticeps</i>	Aquatic macrophyte	0.12	0.01	0.47
	Riparian C3 Plants	0.11	0.01	0.45
	Terrestrial C4 grass	0.08	0.02	0.15
	Periphyton	0.13	0.02	0.56
	Seston	0.28	0.03	0.78
	Waterlily	0.09	0.01	0.43
<i>Sargochromis carlottae</i>	Aquatic macrophyte	0.05	0.01	0.24
	Riparian C3 Plants	0.05	0.01	0.30
	Terrestrial C4 grass	0.13	0.02	0.25
	Periphyton	0.08	0.01	0.78
	Seston	0.08	0.01	0.73
	Waterlily	0.46	0.01	0.79
<i>Sargochromis codringtoni</i>	Aquatic macrophyte	0.10	0.01	0.47
	Riparian C3 Plants	0.09	0.01	0.42
	Terrestrial C4 grass	0.11	0.01	0.37
	Periphyton	0.13	0.01	0.61
	Seston	0.28	0.02	0.76
	Waterlily	0.07	0.01	0.37
<i>Schilbe intermedius</i>	Aquatic macrophyte	0.04	0.01	0.18
	Riparian C3 Plants	0.03	0.01	0.14
	Terrestrial C4 grass	0.08	0.02	0.14
	Periphyton	0.05	0.01	0.31
	Seston	0.73	0.40	0.86
	Waterlily	0.03	0.01	0.11
<i>Synodontis spp.</i>	Aquatic macrophyte	0.07	0.01	0.32
	Riparian C3 Plants	0.06	0.01	0.22
	Terrestrial C4 grass	0.04	0.01	0.10
	Periphyton	0.09	0.01	0.52
	Seston	0.64	0.18	0.84
	Waterlily	0.04	0.01	0.13

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Coptodon rendalli</i>	Aquatic macrophyte	0.10	0.01	0.43
	Riparian C3 Plants	0.09	0.01	0.38
	Terrestrial C4 grass	0.29	0.02	0.46
	Periphyton	0.12	0.02	0.55
	Seston	0.18	0.02	0.66
	Waterlily	0.08	0.01	0.35
<i>Tilapia sparrmanii</i>	Aquatic macrophyte	0.12	0.02	0.46
	Riparian C3 Plants	0.08	0.01	0.29
	Terrestrial C4 grass	0.04	0.01	0.08
	Periphyton	0.14	0.02	0.55
	Seston	0.48	0.10	0.76
	Waterlily	0.05	0.01	0.16
BOTETI WET SEASON				
<i>Brycinus lateralis</i>	Aquatic macrophyte	0.11	0.01	0.55
	Riparian C3 plant	0.05	0.01	0.20
	Terrestrial C4 grass	0.17	0.08	0.27
	Periphyton	0.06	0.01	0.25
	Seston	0.59	0.07	0.82
<i>Clarias gariepinus</i>	Aquatic macrophyte	0.14	0.02	0.56
	Riparian C3 plant	0.13	0.02	0.53
	Terrestrial C4 grass	0.24	0.03	0.59
	Periphyton	0.13	0.02	0.57
	Seston	0.16	0.02	0.65
<i>Clarias ngamensis</i>	Aquatic macrophyte	0.61	0.02	0.85
	Riparian C3 plant	0.06	0.01	0.29
	Terrestrial C4 grass	0.05	0.01	0.13
	Periphyton	0.06	0.01	0.22
	Seston	0.15	0.01	0.86
<i>Hepsetus cuvieri</i>	Aquatic macrophyte	0.13	0.02	0.54
	Riparian C3 plant	0.12	0.02	0.48
	Terrestrial C4 grass	0.34	0.03	0.62
	Periphyton	0.13	0.02	0.52
	Seston	0.15	0.02	0.57
<i>Hydrocynus vittatus</i>	Aquatic macrophyte	0.74	0.02	0.91
	Riparian C3 plant	0.05	0.01	0.19
	Terrestrial C4 grass	0.04	0.01	0.11
	Periphyton	0.04	0.01	0.17
	Seston	0.07	0.01	0.87

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Marcusenius altisambesi</i>	Aquatic macrophyte	0.15	0.01	0.76
	Riparian C3 plant	0.05	0.01	0.20
	Terrestrial C4 grass	0.05	0.01	0.15
	Periphyton	0.05	0.01	0.23
	Seston	0.65	0.05	0.91
<i>Pharyngochromis acuticeps</i>	Aquatic macrophyte	0.10	0.01	0.61
	Riparian C3 plant	0.04	0.01	0.12
	Terrestrial C4 grass	0.27	0.07	0.38
	Periphyton	0.04	0.01	0.13
	*Seston	0.54	0.01	0.83
<i>Petrocephalus okavangoensis</i>	Aquatic macrophyte	0.31	0.02	0.77
	Riparian C3 plant	0.05	0.01	0.18
	Terrestrial C4 grass	0.04	0.01	0.12
	Periphyton	0.06	0.01	0.21
	*Seston	0.51	0.04	0.85
<i>Serranochromis altus</i>	Aquatic macrophyte	0.05	0.01	0.72
	Riparian C3 plant	0.03	0.00	0.10
	Terrestrial C4 grass	0.12	0.01	0.29
	Periphyton	0.03	0.01	0.11
	Seston	0.76	0.01	0.93
<i>Schilbe intermedius</i>	Aquatic macrophyte	0.11	0.01	0.58
	Riparian C3 plant	0.05	0.01	0.20
	Terrestrial C4 grass	0.14	0.05	0.23
	Periphyton	0.06	0.01	0.26
	Seston	0.61	0.08	0.86
<i>Serranochromis macrocephalus</i>	Aquatic macrophyte	0.15	0.02	0.60
	Riparian C3 plant	0.14	0.02	0.54
	Terrestrial C4 grass	0.19	0.03	0.49
	Periphyton	0.16	0.02	0.62
	Seston	0.18	0.02	0.66
<i>Serranochromis thumbergi</i>	Aquatic macrophyte	0.18	0.02	0.72
	Riparian C3 plant	0.14	0.02	0.64
	Terrestrial C4 grass	0.11	0.01	0.55
	Periphyton	0.13	0.01	0.59
	Seston	0.17	0.02	0.68

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Synodontis spp.</i>	Aquatic macrophyte	0.18	0.02	0.64
	Riparian C3 plant	0.08	0.01	0.40
	Terrestrial C4 grass	0.11	0.02	0.26
	Periphyton	0.10	0.01	0.49
	Seston	0.37	0.03	0.84
<i>Coptodon rendalli</i>	Aquatic macrophyte	0.16	0.02	0.41
	Riparian C3 plant	0.07	0.01	0.28
	*Terrestrial C4 grass	0.42	0.32	0.49
	Periphyton	0.07	0.01	0.22
	Seston	0.23	0.03	0.51
<i>Tilapia sparrmanii</i>	Aquatic macrophyte	0.20	0.02	0.63
	Riparian C3 plant	0.12	0.02	0.46
	Terrestrial C4 grass	0.13	0.02	0.48
	Periphyton	0.14	0.02	0.49
	*Seston	0.26	0.03	0.68
	BOTETI DRY SESON			
<i>Brycinus lateralis</i>	Aquatic macrophyte	0.05	0.01	0.25
	Riparian C3 plant	0.24	0.02	0.58
	*Terrestrial C4 grass	0.26	0.14	0.36
	Periphyton	0.05	0.01	0.21
	Seston	0.25	0.02	0.74
	Waterlily	0.04	0.01	0.16
<i>Enteromius paludinosus</i>	Aquatic macrophyte	0.09	0.01	0.33
	Riparian C3 plant	0.11	0.01	0.38
	Terrestrial C4 grass	0.39	0.26	0.49
	Periphyton	0.08	0.01	0.26
	Seston	0.13	0.02	0.49
	Waterlily	0.08	0.01	0.33
<i>Clarias gariepinus</i>	Aquatic macrophyte	0.12	0.01	0.54
	Riparian C3 plant	0.14	0.02	0.59
	Terrestrial C4 grass	0.15	0.02	0.41
	Periphyton	0.10	0.01	0.40
	Seston	0.15	0.02	0.68
	Waterlily	0.11	0.01	0.51

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Clarias ngamensis</i>	Aquatic macrophyte	0.12	0.02	0.49
	Riparian C3 plant	0.13	0.02	0.53
	Terrestrial C4 grass	0.16	0.02	0.41
	Periphyton	0.11	0.01	0.41
	Seston	0.15	0.02	0.62
	Waterlily	0.12	0.02	0.55
<i>Hepsetus cuvieri</i>	Aquatic macrophyte	0.08	0.01	0.29
	Riparian C3 plant	0.13	0.02	0.41
	Terrestrial C4 grass	0.41	0.28	0.53
	Periphyton	0.07	0.01	0.24
	Seston	0.15	0.02	0.50
	Waterlily	0.06	0.01	0.25
<i>Mormyrus lacerda</i>	Aquatic macrophyte	0.12	0.02	0.47
	Riparian C3 plant	0.15	0.02	0.51
	Terrestrial C4 grass	0.17	0.03	0.41
	Periphyton	0.10	0.01	0.37
	Seston	0.21	0.02	0.66
	Waterlily	0.08	0.01	0.35
<i>Marcusenius altisambesi</i>	Aquatic macrophyte	0.09	0.01	0.35
	Riparian C3 plant	0.16	0.02	0.45
	*Terrestrial C4 grass	0.25	0.12	0.37
	Periphyton	0.08	0.01	0.30
	Seston	0.22	0.03	0.64
	Waterlily	0.07	0.01	0.23
<i>Oreochromis andersonii</i>	Aquatic macrophyte	0.11	0.01	0.59
	Riparian C3 plant	0.11	0.01	0.57
	Terrestrial C4 grass	0.05	0.01	0.12
	Periphyton	0.45	0.05	0.70
	Seston	0.08	0.01	0.33
	Waterlily	0.08	0.01	0.29
<i>Pharyngochromis acuticeps</i>	Aquatic macrophyte	0.12	0.01	0.52
	Riparian C3 plant	0.14	0.01	0.58
	Terrestrial C4 grass	0.16	0.02	0.51
	Periphyton	0.10	0.01	0.45
	Seston	0.14	0.02	0.63
	Waterlily	0.10	0.01	0.50

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Petrocephalus okavangoensis</i>	Aquatic macrophyte	0.09	0.01	0.36
	Riparian C3 plant	0.21	0.02	0.56
	Terrestrial C4 grass	0.11	0.02	0.23
	Periphyton	0.08	0.01	0.28
	*Seston	0.38	0.04	0.76
	Waterlily	0.06	0.01	0.22
<i>Serranochromis angusticeps</i>	Aquatic macrophyte	0.11	0.02	0.44
	Riparian C3 plant	0.13	0.02	0.49
	Terrestrial C4 grass	0.24	0.04	0.43
	Periphyton	0.09	0.01	0.32
	Seston	0.16	0.02	0.64
	Waterlily	0.09	0.01	0.43
<i>Sargochromis carlottae</i>	Aquatic macrophyte	0.11	0.01	0.50
	Riparian C3 plant	0.12	0.02	0.50
	Terrestrial C4 grass	0.22	0.02	0.51
	Periphyton	0.10	0.01	0.43
	Seston	0.13	0.02	0.58
	Waterlily	0.12	0.01	0.51
<i>Sargochromis codringtoni</i>	Aquatic macrophyte	0.10	0.01	0.41
	Riparian C3 plant	0.14	0.02	0.52
	Terrestrial C4 grass	0.26	0.06	0.42
	Periphyton	0.08	0.01	0.32
	Seston	0.17	0.02	0.63
	Waterlily	0.08	0.01	0.39
<i>Schilbe intermedius</i>	Aquatic macrophyte	0.06	0.01	0.25
	Riparian C3 plant	0.24	0.02	0.59
	*Terrestrial C4 grass	0.26	0.10	0.38
	Periphyton	0.05	0.01	0.22
	Seston	0.24	0.02	0.75
	Waterlily	0.04	0.01	0.17
<i>Serranochromis macrocephalus</i>	Aquatic macrophyte	0.12	0.02	0.51
	Riparian C3 plant	0.12	0.01	0.54
	Terrestrial C4 grass	0.17	0.02	0.48
	Periphyton	0.10	0.01	0.43
	Seston	0.14	0.02	0.60
	Waterlily	0.12	0.01	0.56

Table 6. continued

Species	Source	Median	LCI	UCI
<i>Serranochromis thumbergi</i>	Aquatic macrophyte	0.11	0.01	0.49
	Riparian C3 plant	0.15	0.02	0.59
	Terrestrial C4 grass	0.16	0.02	0.45
	Periphyton	0.10	0.01	0.41
	Seston	0.17	0.02	0.69
	Waterlily	0.10	0.01	0.45
<i>Synodontis spp.</i>	Aquatic macrophyte	0.09	0.01	0.42
	Riparian C3 plant	0.17	0.02	0.59
	Terrestrial C4 grass	0.19	0.05	0.31
	Periphyton	0.08	0.01	0.32
	Seston	0.22	0.02	0.75
	Waterlily	0.07	0.01	0.35
<i>Coptodon rendalli</i>	Aquatic macrophyte	0.11	0.02	0.46
	Riparian C3 plant	0.15	0.02	0.50
	Terrestrial C4 grass	0.19	0.03	0.39
	Periphyton	0.10	0.01	0.35
	Seston	0.18	0.02	0.62
	Waterlily	0.10	0.01	0.39
<i>Tilapia sparrmanii</i>	Aquatic macrophyte	0.12	0.02	0.41
	Riparian C3 plant	0.17	0.02	0.47
	Terrestrial C4 grass	0.19	0.05	0.32
	Periphyton	0.10	0.02	0.33
	Seston	0.23	0.03	0.65
	Waterlily	0.09	0.01	0.28

During the wet season, three basal resources (seston, riparian C3 plants, and terrestrial C4 grass) were each estimated to contribute more than 20 percent to the biomass of several fish species in the Boro River (Figure 19). This inference is based on the mean value from the probability distribution of mixing model estimates of source contributions for each species. Five out of seventeen (29%) species likely derived more than 30 percent of their muscle tissue mainly from one source. Seston was estimated to be a major production source supporting the biomass of four out of the five species (80%)

that derived more than 30 percent of their muscle tissue from a single source, i.e. predators *H. cuvieri* and *S. intermedius*, the invertivorous mormyrid *M. altisambesi*, and the herbivorous cichlid *T. sparmanii*. Terrestrial C4 grass was at the base of food chains supporting the biomass of the invertivorous straight-fin barb, *E. paludinosus*.

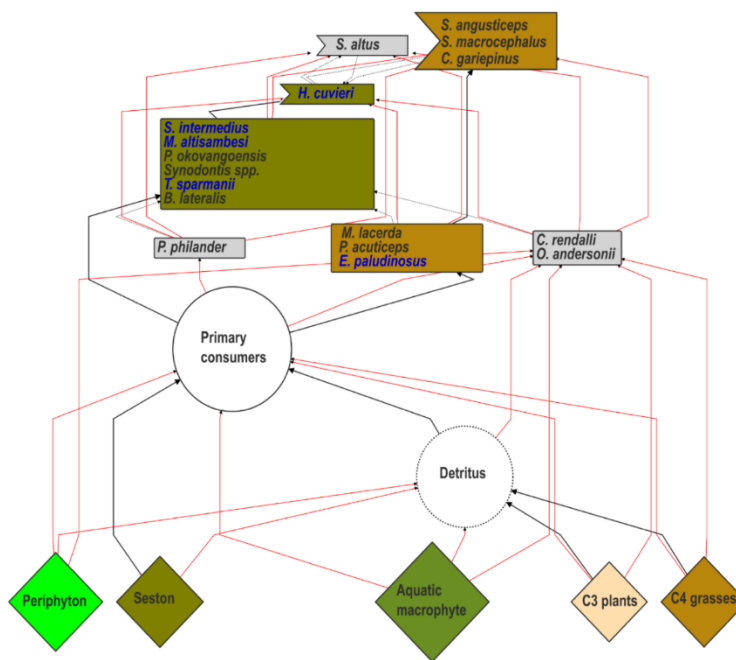


Figure 19. Energy flow and fish trophic interactions in Boro River during the wet season. Modal trophic position ranged from 3.15 - 4.32 (Table 7). Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by modal trophic position: Basal sources (◇), detritus (dotted circle), primary consumers (●), species with modal trophic position < 3.94 (□), and species with modal trophic position ≥ 3.94 (▣). Solid black arrows represent major energy pathways (contributing ≥20% to fish biomass), and red arrows represent pathways contributing <20% of basal sources to fish biomass. Dotted arrows show feeding interactions within the same trophic group. If a population derived ≥20% of its tissues from more than one source, it was assigned to the compartment with the greatest contribution. Within a compartment, populations that assimilated >30% of the resource are shown in blue. Consumer-resource interactions were inferred from literature reporting diets of these species in the Upper Zambezi river-floodplain system (Winemiller 1991, Winemiller and Kelso-Winemiller 1994, 1996, 2003). Autochthonous sources are shown in green and allochthonous sources in brown.

Table 7. The lower and upper credible intervals of the median posterior trophic position, and the modal posterior trophic position of fish populations in the Boro River during the wet season.

<i>Species</i>	<i>Lower</i>	<i>Upper</i>	<i>Median</i>	<i>Mode</i>
<i>O. andersonii</i>	2.00	9.32	4.79	3.20
<i>T. sparmanii</i>	2.87	3.63	3.22	3.19
<i>C. rendalli</i>	2.00	7.31	3.57	3.46
<i>Synodontis spp.</i>	3.34	4.44	3.83	3.79
<i>M. altisambesi</i>	2.88	3.56	3.18	3.15
<i>P. philander</i>	2.00	8.09	3.84	3.55
<i>P. okavangoensis</i>	2.94	4.09	3.44	3.41
<i>B. lateralis</i>	3.45	4.53	3.92	3.87
<i>P. acuticeps</i>	3.19	4.62	3.84	3.79
<i>M. lacerda</i>	2.25	4.28	3.20	3.16
<i>E. paludinosus</i>	3.17	4.08	3.57	3.54
<i>S. intermedius</i>	3.14	4.04	3.54	3.50
<i>H. cuvieri</i>	3.51	4.63	3.99	3.94
<i>C. gariepinus</i>	3.65	4.91	4.22	4.15
<i>S. altus</i>	2.01	7.80	4.45	4.32
<i>S. macrocephalus</i>	2.97	5.87	4.22	4.14
<i>S. angusticeps</i>	2.01	7.53	4.32	4.20

During the dry season, aquatic macrophytes replaced riparian C3 plants among the three basal resources that were estimated to contribute more than 20 percent to the biomass of one or more fish species in the Boro River (Fig 20). Nine out of twenty-one (43%) species derived more than 30 percent of their muscle tissue mainly from one source. Seston was an important basal source in food chains supporting the biomass of seven out of nine species (78%), including predators (*C. gariepinus*, *H. cuvieri*, and *S. intermedius*), invertivores (*E. paludinosus*, *M. altisambesi*, and *Synodontis spp.*) and the herbivorous cichlid *T. sparmanii*. Waterlily was at the base of food chains supporting the biomass of two species (22%) of invertivorous cichlids, *P. acuticeps* and *S. carlottae*.

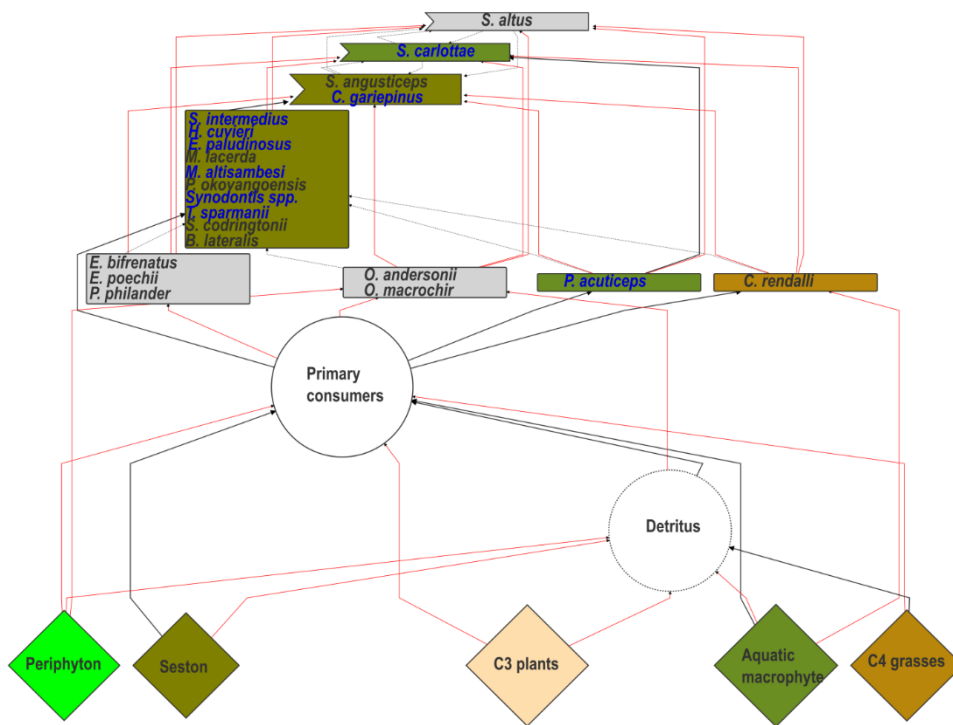


Figure 20. Energy flow and fish trophic interactions in Boro River during the dry season. Modal trophic position ranged from 2.42 – 3.61 (Table 8). Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by modal trophic position: Basal sources (◊), detritus (dotted circle), primary consumers (○), species with modal trophic position < 3.49 (□), and species with modal trophic position ≥ 3.49 (▒). Solid black arrows represent major energy pathways (contributing ≥20% to fish biomass), and red arrows represent pathways contributing <20% of basal sources to fish biomass. Dotted arrows show feeding interactions within the same trophic group. If a population derived ≥20% of its tissues from more than one source, it was assigned to the compartment with the greatest contribution. Within a compartment, populations that assimilated >30% of the resource are shown in blue. Consumer-resource interactions were inferred from literature reporting diets of these species in the Upper Zambezi river-floodplain system (Winemiller 1991, Winemiller and Kelso-Winemiller 1994, 1996, 2003). Autochthonous sources are shown in green and allochthonous sources in brown.

Table 8. The lower and upper credible intervals of the median posterior trophic position, and the modal posterior trophic position of fish populations in the Boro River during the dry season.

<i>Species</i>	<i>Lower</i>	<i>Upper</i>	<i>Median</i>	<i>Mode</i>
<i>O. andersonii</i>	2.00	3.04	2.51	2.49
<i>O. macrochir</i>	2.00	9.31	4.73	2.42
<i>T. sparmanii</i>	2.51	3.50	2.95	2.93
<i>C. rendalli</i>	2.42	3.86	3.05	3.02
<i>Synodontis Spp</i>	2.55	3.62	3.04	3.01
<i>P. okavangoensis</i>	2.27	3.36	2.78	2.74
<i>M. altisambesi</i>	2.26	3.28	2.76	2.73
<i>M. lacerda</i>	2.00	3.63	2.83	2.84
<i>E. paludinosus</i>	2.62	3.63	3.07	3.05
<i>B. lateralis</i>	2.86	4.13	3.44	3.42
<i>S. codringtonii</i>	2.61	3.73	3.13	3.08
<i>E. bifrenatus</i>	2.00	6.11	2.93	2.85
<i>P. philander</i>	2.00	6.47	3.08	2.96
<i>S. carlotta</i>	2.01	9.40	4.91	3.60
<i>P. acuticeps</i>	2.00	9.32	4.78	3.30
<i>E. poechi</i>	2.00	8.27	3.77	3.30
<i>S. intermedius</i>	2.61	3.72	3.12	3.10
<i>H. cuvieri</i>	2.85	3.99	3.38	3.36
<i>C. gariepinus</i>	3.10	4.32	3.68	3.61
<i>S. altus</i>	2.70	4.59	3.57	3.52
<i>S. angusticeps</i>	2.77	4.30	3.48	3.49

During the wet season, the same three basal resources (seston, aquatic macrophytes, and terrestrial C4 grass) were each estimated to contribute more than 20 percent to the biomass of fishes in Boteti River (Figure 21). Eleven out of fifteen (73%) species derived more than 30 percent of their muscle tissue mainly from one source. Seston was estimated to be a major production source supporting the biomass of seven out of eleven species (64%), including predators (*S. intermedius* and *S. altus*) and invertivores (*P. okavangoensis*, *P. acuticeps*, *M. altisambesi*, *Synodontis spp.*, and *B. lateralis*). Aquatic macrophytes were the most important basal source in food chains

supporting the biomass of two predatory species, *H. vittatus* and *C. ngamensis*. The predatory African pike, *H. cuvieri*, and the herbivorous cichlid *C. rendalli* were primarily supported by terrestrial C4 grass.

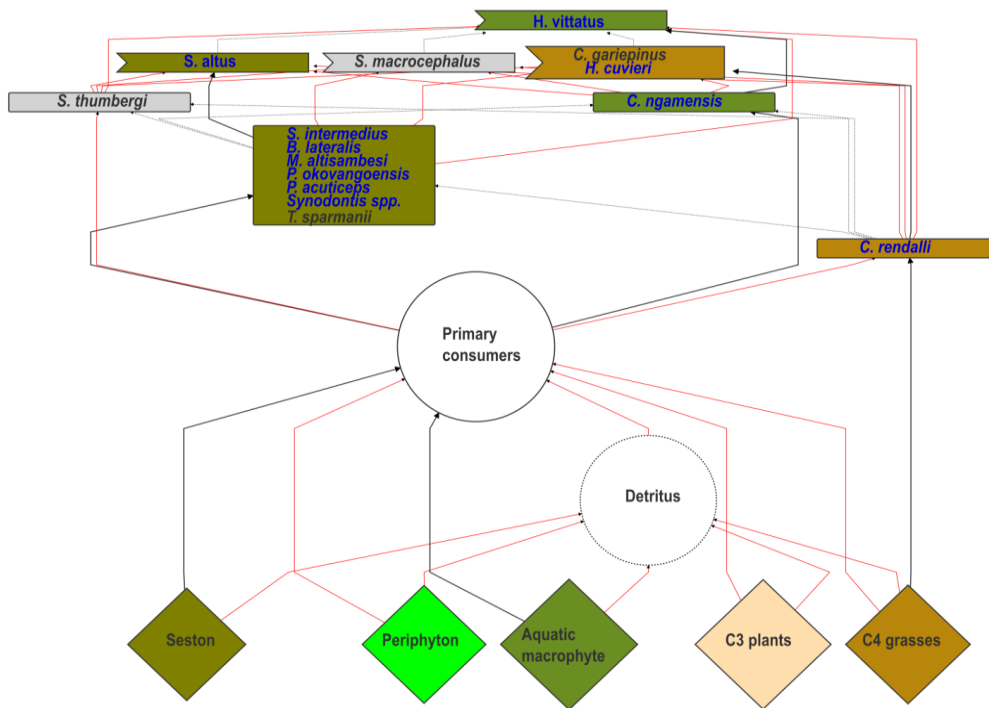


Figure 21. Energy flow and fish trophic interactions in Boteti River during the wet season. Modal trophic position ranged from 2.84 – 4.06 (Table 9). Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by modal trophic position: Basal sources (\diamond), detritus (dotted circle), primary consumers (\odot), fish with modal trophic position < 3.71 (\square), and fish with modal trophic position ≥ 3.71 (\blacksquare). Solid black arrows represent major energy pathways (contributing $\geq 20\%$ to fish biomass), and red arrows represent pathways contributing $< 20\%$ of basal sources to fish biomass. Dotted arrows show feeding interactions within the same trophic group. If a population derived $\geq 20\%$ of its tissues from more than one source, it was assigned to the compartment with the greatest contribution. Within a compartment, populations that assimilated $> 30\%$ of the resource are shown in blue. Consumer-resource interactions were inferred from literature reporting diets of these species in the Upper Zambezi river-floodplain system (Winemiller 1991, Winemiller and Kelso-Winemiller 1994, 1996, 2003). Autochthonous sources are shown in green and allochthonous sources in brown.

Table 9. The lower and upper credible intervals of the median posterior trophic position, and the modal posterior trophic position of fish populations in Boteti River during the wet season.

<i>Species</i>	<i>Lower</i>	<i>Upper</i>	<i>Median</i>	<i>Mode</i>
<i>T. sparmanii</i>	2.00	6.56	2.98	2.84
<i>C. rendalli</i>	2.00	9.41	5.07	3.27
<i>P. okavangoensis</i>	2.00	5.72	3.08	3.01
<i>M. altisambesi</i>	2.00	6.95	3.21	3.08
<i>B. lateralis</i>	2.00	7.50	3.55	3.42
<i>Synodontis Spp</i>	2.00	7.61	3.72	3.60
<i>P. acuticeps</i>	2.00	9.42	5.09	3.68
<i>S. thumbergi</i>	2.00	8.61	3.87	3.41
<i>S. intermedius</i>	2.00	7.43	3.45	3.31
<i>H. vittatus</i>	2.06	9.49	5.21	3.71
<i>C. ngamensis</i>	2.00	9.38	5.14	3.26
<i>S. macrocephalus</i>	2.00	8.68	4.28	3.97
<i>S. altus</i>	2.02	9.41	5.35	4.06
<i>C. gariepinus</i>	2.00	8.39	4.01	3.73
<i>H. cuvieri</i>	2.01	8.82	4.28	3.71

During the dry season, four basal sources (seston, periphyton, riparian C3 plants, and terrestrial C4 grass) were each estimated to contribute more than 20 percent to the biomass of fishes in the Boteti River (Figure 22). Four out of nine-teen (21%) species derived more than 30 percent of their muscle tissue mainly from a single source. Out of the four populations, terrestrial C4 grass was at the base of food chains leading to the biomass of two species, the invertivorous straight-fin barb, *E. paludinosus*, and predatory *H. cuvieri*. Periphyton was estimated to be the major basal source contributing to the biomass of the detritivorous cichlid *O. andersonii*, and seston was estimated to be the basal source in food chains supporting biomass of the invertivorous mormyrid *P. okavangoensis*.

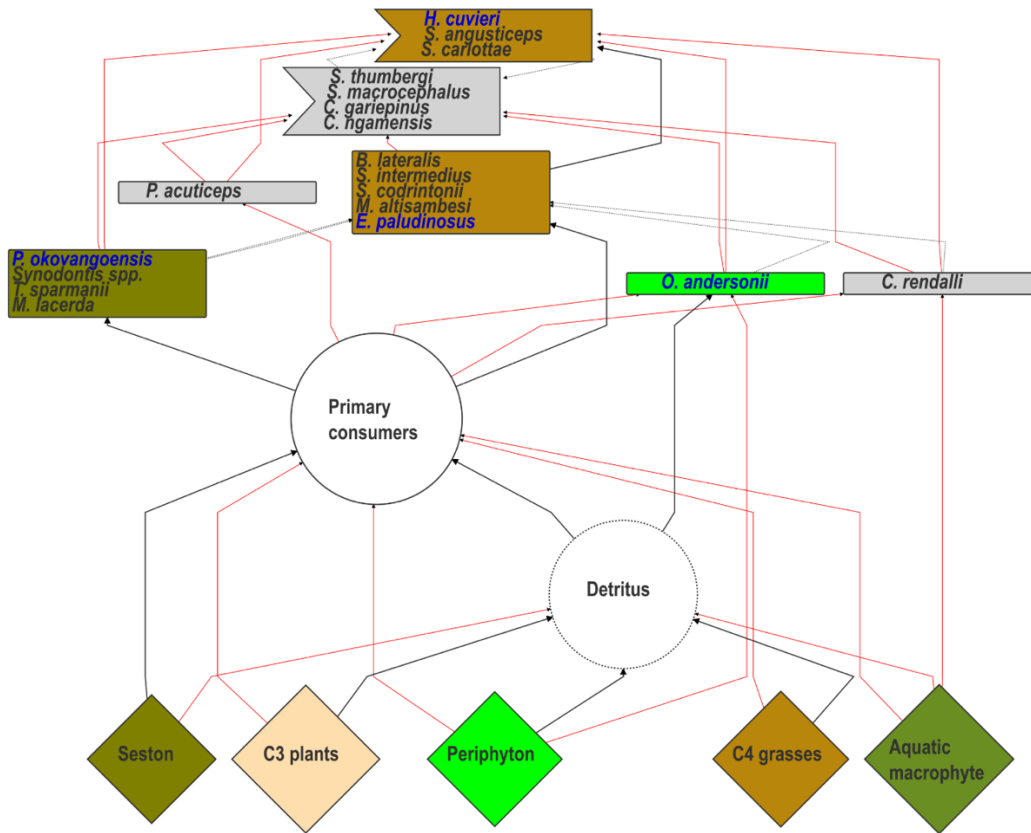


Figure 22. Energy flow and fish trophic interactions in Boteti River during the dry season. Modal trophic position ranged from 2.62 – 4.34 (Table 10). Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by modal trophic position: Basal sources (◇), detritus (dotted circle) primary consumers (○), fish with modal trophic position < 3.78 (□), and fish with modal trophic position ≥3.78 (▢). Solid black arrows represent major energy pathways (contributing ≥20% to fish biomass), and red arrows represent pathways contributing <20% of basal sources to fish biomass. Dotted arrows show feeding interactions within the same trophic group. If a population derived ≥20% of its tissues from more than one source, it was assigned to the compartment with the greatest contribution. Within a compartment, populations that assimilated >30% of the resource are shown in blue. Consumer-resource interactions were inferred from literature reporting diets of these species in the Upper Zambezi river-floodplain system (Winemiller 1991, Winemiller and Kelso-Winemiller 1994, 1996, 2003). Autochthonous sources are shown in green and allochthonous sources in brown.

Table 10. The lower and upper credible intervals of the median posterior trophic position, and the modal posterior trophic position of fish populations in Boteti River during the dry season.

Species	Lower	Upper	Median	Mode
<i>O. andersonii</i>	2.01	9.34	4.72	2.62
<i>T. sparmanii</i>	2.18	3.83	2.94	2.92
<i>C. rendalli</i>	2.01	4.11	3.00	2.94
<i>M. lacerda</i>	2.13	4.01	3.05	3.01
<i>P. okavangoensis</i>	2.33	4.09	3.16	3.13
<i>P. acuticeps</i>	2.00	6.87	3.56	3.42
<i>B. lateralis</i>	2.52	4.57	3.47	3.41
<i>Synodontis spp.</i>	2.64	4.82	3.66	3.62
<i>S. codringtoni</i>	2.64	4.92	3.74	3.70
<i>M. altisambesi</i>	2.05	4.04	3.05	3.00
<i>S. carlottae</i>	2.04	7.87	4.18	4.02
<i>E. paludinosus</i>	2.00	9.35	4.83	3.60
<i>S. thumbergi</i>	2.58	5.21	3.83	3.78
<i>S. intermedius</i>	2.50	4.54	3.45	3.38
<i>C. gariepinus</i>	2.24	5.56	3.84	3.78
<i>S. angusticeps</i>	2.85	5.37	4.05	3.98
<i>S. macrocephalus</i>	2.07	7.25	4.42	4.34
<i>C. ngamensis</i>	2.01	8.17	4.01	3.78
<i>H. cuvieri</i>	2.90	5.16	3.93	3.89

Relationship between the degree of dependence on one basal source and modal fish trophic position

During the wet season in the Boro River, the relationship between trophic position and the degree of dependence on single basal source was negative ($y = 3.9 - 0.78x$, $R^2 = 0.15$). Trophic position did not vary with the degree of dependence on a single basal source ($y = 3.5 + 0.04x$, $R^2 = 0.00$), during the wet season in the Boteti River. During the dry season, the relationship between trophic position and the degree of dependence on a single basal source was positive in the Boro River ($y = 2.9 + 0.45x$, $R^2 = 0.06$) and negative in Boteti River ($y = 3.9 - 1.6x$, $R^2 = 0.11$).

Discussion

Fishes in the Lower Okavango Delta have diverse trophic niches, and most species appeared to be supported by multiple basal production sources. Seston was estimated to be the most important basal source supporting most fishes in the Boro River during both wet and dry seasons. In the Boteti River, seston was at the base of food chains supporting the biomass of most fish species during the wet season. The composition of seston samples was not determined, but visual inspection of the samples indicated fine particulate organic matter (detritus) that probably originated from some combination of algae, cyanobacteria, and macrophyte tissues (Peel et al. 2019). Although not a dominant input, C4 grasses apparently assumed greater importance in the Boteti food web during the dry season, suggesting that at least some fish and/or macroinvertebrates that are consumed by carnivorous fishes changed their foraging strategies seasonally in response to shifts in resource availability. Although the dynamics of seston production are undocumented in this system, my results are consistent with the idea that both autochthonous and allochthonous resources should be major inputs to aquatic food webs in river-floodplain ecosystems (Humphries et al. 2014). Seston production may vary seasonally with higher proportions of seston deriving from autochthonous sources during the dry season, whereas the contribution of allochthonous sources may be greater during the wet season (Ellis et al. 2012). Interestingly, C4 grasses were a more important input to the aquatic food web during the dry season when flows were minimal and access to the floodplain was restricted. One explanation for this could be a time lag between the senescence and death of grasses while submersed during the

flood and the conditioning of grass tissue by microbial decomposers that increase its nutritional value for metazoan consumers.

Although most fishes could have consumed variable fractions of all five of the basal production sources obtained for isotopic analysis, the biomass of several species was estimated to have been largely supported by just one or two sources. In the Boro River, several species positioned higher in the food web may have assimilated a large fraction of organic matter from a single basal source during the dry season. Assimilation of larger fractions of material from a single source during low-flow conditions of the dry season is consistent with the idea that habitat reduction and isolation results in stronger trophic interactions (McCann et al. 2005). During the study period, the Boro River study reach underwent habitat fragmentation when flows declined. At the peak of the dry season, the channel contained a series of isolated pools of water that gradually shrank, with some of them eventually drying. Isolation within shrinking aquatic habitats resulted in greater reliance of fishes on local sources of production, a pattern observed in other tropical rivers (Taylor et al. 2006, Jardine et al. 2012). Generalist predators may exhibit specialized foraging habits in isolated pools during the dry season and switch to a diverse diet during the wet season (Balcombe et al. 2015). This could explain why species higher in the food web apparently had assimilated material disproportionately from one source during the dry season. However, during the wet-season flood pulse, both longitudinal and lateral connectivity increased the amount of aquatic habitat and the potential for fish dispersal. Consequently, fish movement would have linked local food webs that had been spatially subdivided, with generalist predators expanding their niche

breadth, especially in adjacent floodplains where primary and secondary production is high (Winemiller and Jepsen 1998, Høberg et al. 2002, Lindholm et al. 2007). These patterns support Liem's paradox, which posits that fish with obvious adaptations for trophic specialization should nonetheless retain the ability to feed on diverse food items to enable exploitation of profitable resources when they become abundant (Liem 1980).

In the Boteti River, species positioned higher in the food web appeared to assimilate organic matter from multiple sources during the dry season, a pattern similar to that observed in the Boro River during the wet season. This pattern could result from contrasting seasonal patterns of habitat size and connectivity in the two rivers. Variation in flow conditions and habitat connectivity in fluvial systems are significant determinants of resource availability for aquatic consumers (Junk et al. 1989, Jardine et al. 2012, Humphries et al. 2014, Garcia et al. 2017, Venarsky et al. 2020). Streams with different degrees of habitat connectivity and water residence time likely have different microbial communities affecting ecosystem heterotrophy. For example, carbon turnover from microbial respiration was higher in permanent streams by up to eight orders of magnitude compared to ephemeral streams in Chicken Creek, Germany (Gerull et al. 2011). Similarly, Febria et al. (2015) found that the abundance of carbon fixers was higher in perennial habitats, and nitrogen fixers dominated in ephemeral habitats in North American headwater streams.

The Boteti River reach in my study remained longitudinally connected throughout the duration of the study period. However, connectivity in the lateral dimension was reduced when flows declined during the dry season. Predator-prey

interactions intensify during the dry season when fishes move from the floodplain into more restricted habitat within the river channel (Bogan and Lytle 2007, McHugh et al. 2010). Higher predator densities in the river channel could yield competition that drives dispersal in the longitudinal dimension and encounters with a greater diversity of food resources. This could explain why species higher in the food web assimilated multiple basal sources during the dry season in the Boteti River. In fluctuating environments, consumers should forage preferentially on the most abundant and nutritious resources (Kondoh 2003, Forest et al. 2008). This opportunity presents itself to fishes at all trophic levels during the wet season in Boteti River, when aquatic habitat volume and connectivity increase.

My results suggest that in the Boro River, most fishes switched from feeding mostly from food chains originating from seston during the dry season to those supported by terrestrial C4 grass during the wet season. Whereas C4 grasses generally have low nutritional value when compared to other production sources (Minson 1971) and generally are reported to be minor contributors to fish biomass (Arantes et al. 2019), there is some evidence that C4 grasses may be the foundation of food chains that support the biomass of at least some fishes in tropical river-floodplain systems. As water levels fall in floodplains, biomass from decomposing C4 grasses is deposited in sediments; this material can enter aquatic food chains during the flood pulse when detritivores feed on this material and the tissues of decomposing microorganisms (Høberg et al. 2002, Cole et al. 2011). For example, C4 grasses were inferred to be important basal sources in food chains supporting the biomass of air-breathing fishes that are common in floodplains of

the Lower Mekong Basin (Ou and Winemiller 2016). Similarly, C4 grasses were important basal sources supporting food chains of air-breathing catfishes in the genus *Clarias* that were collected from the floodplains of the Oueme River in Benin (Jackson et al. 2013). In the Boro River, the catfish *Clarias gariepinus* switched from being supported mostly by food chains originating from seston during the dry season to those supported by terrestrial C4 grass when the floodplain was inundated during the wet season.

Most fishes in Boteti River were supported by food chains originating from seston during the wet season. During the dry season, their support shifted to energy and material pathways with terrestrial C4 grass as the production source. Organic material derived from the floodplain was found to support more than half of the fish biomass during the dry season in Cooper Creek, a dryland river in south-western Queensland, Australia (Burford et al. 2008). Okavango fishes were unable to forage in floodplains during the dry season; however, hippopotamus were frequently sighted in Boteti River throughout the duration of the study, and these megaherbivores could have transferred material from C4 grasses between terrestrial and aquatic habitats. Hippos were estimated to deposit ~36,000 kg of dung per day in the Mara River in Kenya (Subalusky et al. 2015), and this dung is reported to contain large proportions of terrestrial C4 grasses that support aquatic food webs (Masese et al. 2015). Therefore, terrestrial C4 grass could have entered aquatic food chains during the dry season in Boteti River as undigested material in hippopotamus dung or through the microbial-loop energy pathway within the main river channel. Microbes colonize organic matter, and microbial metabolism has

been shown to increase under low-flow conditions, leading to rapid mobilization of nutrients to primary producers that are subsequently consumed by aquatic invertebrates (Closs and Lake 1994, Finlay and Kendall 2007). My results suggest that two invertivores (*Brycinus lateralis* and *Marcusenius altisambesi*) and an omnivore (*Schilbe intermedius*) were supported largely by seston during the wet season and C4 grass during the dry season, with grass and possibly even seston likely associated with microbial processing. The detritivorous cichlid *Oreochromis andersonii* was captured in the Boteti River only during the dry season. The isotopic analysis estimated that periphyton was the most important basal source supporting biomass of this detritivore, which may have fed on algae and other material in biofilms either directly or indirectly in the form of detritus and associated microbes (Bunn et al. 2003, Winemiller and Kelso-Winemiller 2003, Reid et al. 2008, Peel et al. 2019).

My findings indicate that seasonal changes in connectivity and aquatic habitat size likely drove changes in basal resource availability and the predominant energy pathways supporting fish biomass in the Lower Okavango Delta. Notable is the major role of seston and terrestrial C4 grass in supporting food chains that support fishes in Boteti River, which agrees with a prediction from the river wave concept that under low-flow conditions during the dry season, aquatic food webs are supported by both in-channel primary production and allochthonous material from riparian plants (Humphries et al. 2014). Adaptive foraging is one mechanism that could enhance food web resilience to fluctuations caused by extreme seasonal hydrology in the lower Okavango Delta. My findings support previous claims that maintenance of a relatively natural flow regime is

critical for maintenance of biodiversity and productivity of river-floodplain ecosystems (Junk et al. 1989, Winemiller and Jepson 1998, Poff et al. 1997, Winemiller 2004, Zeug and Winemiller 2008, Jardine et al. 2012, Roach 2013, Humphries et al. 2014, Arantes et al. 2019). The annual flood pulse expands the aquatic habitat of the lower Okavango Delta and provides fish and other aquatic organisms with access to abundant autochthonous and allochthonous resources, including basal sources with high nutritional value. In theory, the extensive multichannel foraging that results from these temporal and spatial dynamics enhances the stability of these complex systems (Kondoh 2003, Wolkovich et al. 2014).

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CHAPTER V

CONCLUSIONS

Ecosystem disturbances and climate change are on the rise, and the need to understand community organization in complex and dynamic ecosystems cannot be overstated (Datry et al. 2017). Rivers in the lower Okavango Delta experience flooding and drying that produce temporal shifts among lentic, lotic, and terrestrial conditions to which aquatic organisms must respond. Analysis of fish diversity patterns in chapter II supported the idea that hydrology plays a crucial role in structuring aquatic communities in river-floodplain systems. Within habitat types, α diversity was lowest during the high-water period, and α diversity was highest during low flows. This pattern suggests that greater connectivity of aquatic habitats during the wet season enhanced fish dispersal within the greatly expanded volume of water, whereas aquatic habitat reduction during the dry season resulted in higher per-unit-area densities of fishes within disconnected water bodies. Similarly, β diversity was generally higher during the dry season compared to the wet season, suggesting greater potential for demographic and environmental stochasticity to influence local assemblage structures within and among habitat types during this period. Chapter III tested whether analysis of residual species correlations from JSDMs, in conjunction with fish trophic guilds, may facilitate inferences about interspecific interactions structuring local fish assemblages in the highly heterogeneous environment of the lower Okavango Delta. Although environmental data were limited and much variation in fish assemblage structure remained unexplained by the models, patterns of species co-occurrence, when interpreted from the standpoint of trophic

guilds, suggested periods when fish responses to abiotic environmental conditions and interspecific interactions may have influenced local community assemblage.

Results from chapter IV indicate that seasonal changes in connectivity and aquatic habitat volume likely drove changes in basal resource availability and the predominant energy pathways supporting fish biomass in the Lower Okavango Delta. It appears that any disruptive effects from extreme seasonal fluctuations in hydrology are more than compensated by the ability of fishes to disperse into the floodplain and exploit abundant food resources. The annual flood pulse in the lower Okavango Delta provides fishes and other aquatic organisms with access to abundant autochthonous and allochthonous resources, including basal sources with high nutritional value. With regards to the ecological complexity-stability debate (May 2001, McCann et al. 1998), the annual flood pulse probably enhances fish community and aquatic food web resilience to what appears, on the surface, to be a major disturbance. In theory, extensive multichannel foraging by fishes enhances the stability of these complex trophic networks (Kondoh 2003, Wolkovich et al. 2014).

Findings from the three studies in this dissertation suggest that maintenance of a relatively natural flow regime is critical for sustaining fish diversity and fisheries production of the lower Okavango Delta. The Okavango Delta faces environmental threats from large-scale water diversion for irrigation, pollution and water diversion for mining, hydropower generation, and other local human activities, including infrastructure development and farming on floodplains. These activities clearly would impact the region's subsistence and commercial fisheries and result in reduced food

security as well as negative consequences for the ecotourism industry and economic security of local communities. Moreover, climate change is predicted to increase hydrological extremes in the Okavango Delta and other semiarid regions, with adverse ecological impacts (Acuña et al. 2014, Ruhí et al. 2016). Changes to the flow regime likely would alter interspecific interactions within aquatic and riparian habitats, with unknown long-term effects on taxonomic and functional diversity as well as primary and secondary production (Arthington et al. 2010, Gilman et al. 2010, Arantes et al. 2019).

This dissertation provides new empirical data on fish ecology and also expands our understanding of the ecology of river-floodplain ecosystems in a semi-arid region. By analyzing multiple components of fish diversity, community assembly and food web ecology, this dissertation provides comprehensive baseline information for future ecological studies in this system and others in the ecoregion. The information contained herein should be immediately useful for conservation planning and fisheries management in the lower Okavango Delta. In the face of increasing numbers of streams and rivers that are drying due to climate change and demand for water by humans, there is an urgent need to expand research efforts on rivers in semi-arid regions, not only in southern Africa but throughout the continent and world.

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