# Seasonal hydrology influences energy channels in food webs of rivers in the lower Okavango Delta

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**Abstract** Floodplain aquatic ecosystems experience temporal changes in basal production sources and inputs from allochthonous sources that influence energy flow. We analyzed stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from 449 fish muscles representing 18 species to characterize energy pathways in two rivers of the lower Okavango Delta, Botswana. We sampled fish during wet and dry seasons and used mixing models to estimate proportions of major basal production sources assimilated by fishes. We estimated trophic position (TP) for each fish population and assessed the association between TP and the degree that fish biomass was supported by a single production source. During the wet season, fishes in the Boteti River assimilated material through food chains originating mainly from aquatic macrophytes. During the dry season, terrestrial $C_3$ plants and terrestrial $C_4$ grasses assumed greater importance. In the Boro River, terrestrial $C_3$ plants were inferred to be an important production source supporting fishes during the wet season, with aquatic macrophytes becoming more important during the dry season. In both rivers and seasons, the degree of dependence on a single source was negatively related to TP, supporting the hypothesis that organisms positioned higher in the food web tend to be supported by multiple food chains and basal sources, whereas organisms lower in the food web may be supported by many or few food chains. We showed that consumers in river food webs shift foraging habits in response to seasonal patterns of connectivity and habitat availability, thus promoting long-term population and community stability.

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## Introduction

Aquatic food webs in river-floodplain systems are complex with multiple spatial compartments linked via movements of water and organisms (Winemiller 2004; Layman et al. 2012). Network structure and stability are affected by the ability of consumers to switch their feeding according to spatial and temporal

variation in food availability (Liem 1980; Winemiller 1989; Winemiller and Jepsen 1998). Consumers in dynamic systems may cross habitat boundaries to exploit resource pulses or 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 ecology requires the characterization of variation in pathways of energy and matter transfer through time and across space.

Aquatic food webs may contain algal-grazer, macrophyte-grazer, and detrital-microbial energy pathways (Winemiller 1990; Winemiller 1996; Vadeboncoeur et al. 2003; Moline et al. 2004; McIntosh et al. 2017). These pathways are sometimes referred to as green (plant-based) versus brown (detritus-based) 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 the biomass of 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 directly contribute much material to the biomass of aquatic organisms at positions higher in food webs (Bunn et al. 2003; but see Correa and Winemiller 2014, 2018). This appears to be due to the limited ability of most aquatic macroinvertebrates and vertebrates to digest and absorb nutrients directly 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 aquatic 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 organic material originating from macrophytes supported, directly or indirectly, 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 $C_4$ grasses, a basal source that tends to have higher $^{13}C/^{12}C$ stable isotope ratios than other sources (Forsberg et al. 1993; Jepsen 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 recent rise in investigations of river food webs in Africa (e.g., 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 in most regions of the world (McMeans et al. 2015; McIntosh et al. 2017). In this study, we sampled reaches in the Boro and Boteti Rivers in the lower Okavango Delta, a large wetland complex located within a semiarid region of southern Africa. Field studies were conducted during high- and low-flow periods within one hydrological

cycle to investigate changes in basal production sources supporting fish biomass 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 study without loss of longitudinal habitat connectivity. We inferred seasonal changes in predominant energy pathways and trophic structure using stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Carbon and nitrogen stable isotopes are useful tracers in food web research because $\delta^{13}C$ often can be used to estimate the energy sources supporting consumer biomass, and $\delta^{15}N$ can serve as an indicator of organisms' vertical trophic positions (Minagawa and Wada 1984; Vander Zanden and Rasmussen 1999).

We hypothesized that food webs in both rivers would follow predictions of the RWC. First, we 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, we predicted that in both rivers, many fish species would be trophic generalists, linked to many food chains and diverse basal production sources. However, we predicted that a few species (e.g., herbivorous cichlids) would be trophic specialists linked to fewer food chains originating from only a few basal production categories. Third, we postulated that species integrating multiple food chains and production sources would be positioned higher in the food web, and those deriving large proportions of their tissues from one source would be positioned lower in the food web. This is because (1) predators are often larger than their prey and may feed on diverse prey to sustain their higher energetic demand (Arim et al. 2010), (2) the maximum size of food items ingested by fish tends to be limited by mouth gape size, such that large fish at higher TPs may ingest larger items than smaller fish at lower TPs while still retaining the ability to ingest small items (Montaña et al. 2011), and (3) predators are often more mobile than their prey and might encounter and feed on a greater diversity of food items (Costa 2009).

## 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 the Angolan highlands. About 16 $km^3$ 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 increased flows and flooding between May and October and dry conditions with reduced flows from November to April (Akoko et al. 2013).

We analyzed food webs by sampling basal resources and fish in the Boro and Boteti Rivers during wet and dry seasons within one annual flood cycle. We sampled four sites in the Boro River along a *c.* 20-km reach from the buffalo fence to the Boro-Thamalakane junction (Fig. 1). The substrate in this reach is fine sand within the main river channel, along channel margins, and in floodplains. Submerged aquatic macrophytes (water lily) and hippo grass were common in this reach. Deciduous trees, including *Acacia* species, were common in riparian areas. Two sites were sampled in the 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 bedrock, boulders, and clay within the main river channel. Channel margins and floodplains consist of silt and sand with pebbles in some parts. Aquatic macrophytes and riparian vegetation were similar those in the Boro River. Hippopotamus (*Hippopotamus amphibious*) were frequently sighted throughout the study period in the Boteti River reach. At this location, channel width varied little with flow level; the only exception was Chanoga Lagoon where the channel widened ~ two-fold between low flow and bankful conditions.
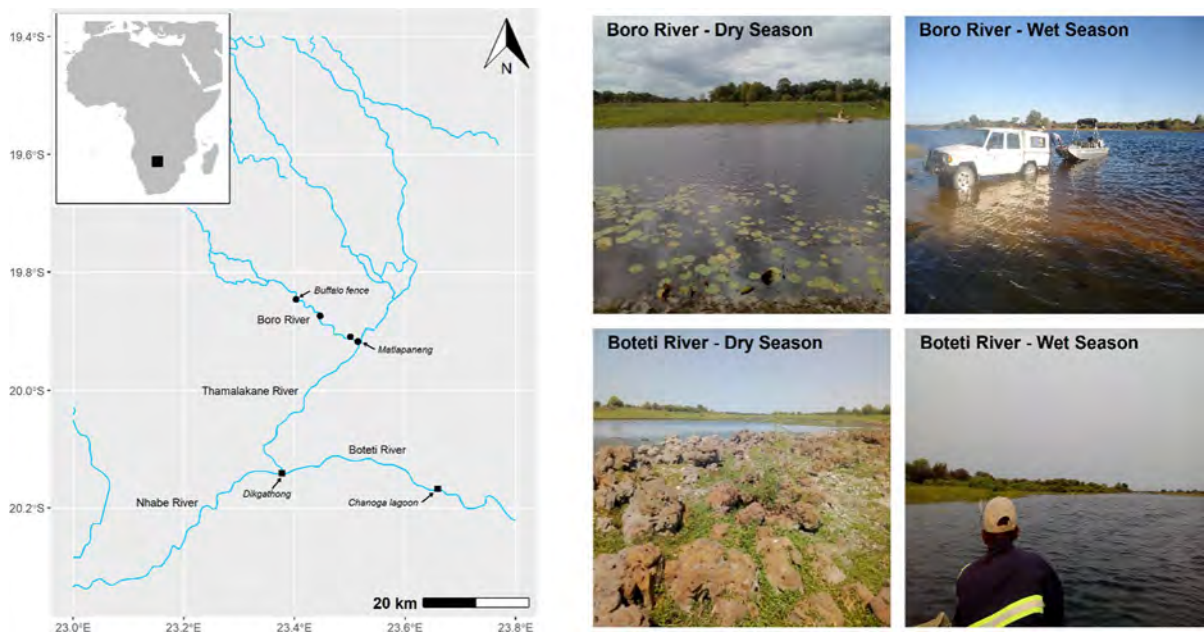
**Fig. 1** Sampling sites in the Boro and Boteti rivers in the lower Okavango Delta, Botswana, during wet (high water) and dry (low water) seasons

Fish sampling

Fishes were sampled using a nylon multifilament gill-net that had 11 panels of different mesh sizes (12-, 16-, 22-, 28-, 35-, 45-, 57-, 73-, 93-, 108- and 150-mm stretched mesh), each with a length of 10-m and 2.5-m depth. Fish also were collected using a seine net (length = 7.6 m, depth = 1.8 m, mesh = 3.2 mm) and two double-ended fyke nets with 1.2-m D-openings and 25-mm mesh. The gillnet was set in the main channel, and fyke nets were set perpendicular to the main channel stretching from the riverbank into the floodplain. The gillnet and fyke nets were set overnight from *c.* 1800 h in the evening and retrieved the following morning at *c.* 0600 h. Seining was conducted opportunistically during the daytime when conditions were deemed safe from crocodiles. Fish specimens were quickly euthanized (TAMU AUP IACUC 2017–0069), and samples of muscle tissue were obtained from the right flank below the base of the dorsal fin of select specimens. Voucher specimens were fixed in formalin and preserved in ethanol for archiving at the Biodiversity Research and Teaching Collection at Texas A&M University, College Station. Specimens were identified to species level based on keys and illustrations in Skelton (2001).

Collection and preparation of tissue samples for isotopic analysis

In each river and during each season, tissue samples were obtained from six basal production sources (seston, terrestrial $C_3$ plants, terrestrial $C_4$ grasses, periphyton, and waterlily) and fishes. Periphyton was scarce in both rivers and biofilm samples were obtained by gently scraping submerged tree branches. Seston (which likely consisted mostly of allochthonous and/or autochthonous detritus, given the clarity of the water and extremely low water-column primary production reported for the Okavango Delta; Mazebedi (2019) was obtained from surface water that was 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). We collected leaves from riparian trees, shrubs, and grasses (allochthonous sources) that were prevalent along channel margins and in the floodplain. We also collected leaves and stems of dominant floating (hippo grass (*Vossia cuspidata*); *Cyperus articulatus*) and submerged aquatic macrophytes (*Nesaea crassicaulis*; *Rotala myriophylloides; Ceratophyllum demersum*) from river channels. Because of its distinct isotope signature, water lily was treated as a

basal source separate from other aquatic macrophytes. We 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 variability in the isotope values of fish species and basal source categories, our goal was to obtain 3–5 samples of each species and basal source category at each site during each survey period.

Basal sources and fish tissues were sampled during the flood period (August 10–14, 2017, and October 12–20, 2017) and low-flow period (December 2–8, 2017, and February 16–25, 2018). Thus, flood period samples were obtained 3–5 months after the beginning of the wet season, and low-flow samples were obtained 1–3 months after the start of the dry season. The carbon isotopic half-life of fish muscle tissue ranges from 10 to 60 days with a mean of 25 days (Boecklen et al. 2011). Therefore, we 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). Basal source and fish muscle tissue samples were packaged in plastic bags and preserved in salt for later analysis in the laboratory.

Following the protocol described by Arrington and Winemiller (2002), salt-preserved material was soaked in distilled water and then rinsed to remove the salt. Rinsed material was dried in an oven at 60 °C for 48 h and then ground into a fine powder using mortar and pestle. Powdered subsamples were weighed to the nearest 0.02 mg and packaged into Ultrapure® tin capsules. Analyses of carbon and nitrogen isotope ratios were carried out following standard procedures at the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, USA (https://siel.uga.edu/mass-spectrometry-overview). Samples were dry combusted (microDumas technique) using a Carlo Erba CHN elemental analyzer, and the purified gases released from the process were introduced into a Finnigan Delta C mass spectrometer. Stable isotope ratios were quantified in parts per mil (‰) as deviations relative to standard materials (atmospheric nitrogen for $\delta^{15}$N and Pee Dee Belemnite for $\delta^{13}$C) such that; $\delta X(‰) = [(R_{sample}/R_{standard})-1] \times 10^3$, where $X = {}^{13}$C or ${}^{15}$N, and $R = {}^{13}$C/${}^{12}$C or ${}^{15}$N/${}^{14}$N. Isotopic ratios had a precision of $\leq 0.4\%$ for $\delta^{15}$N and $\leq 1.1\%$ for $\delta^{13}$C, measured as the maximum deviation to the mean of bovine (Standard Reference Material [SRM]

1577c). Reference samples were measured after every 12 fish tissue samples.

Data analysis

We used Bayesian stable isotope mixing models to infer the proportion of basal sources assimilated by fish. We adjusted for trophic fractionation in the models using separate trophic discrimination factors (TDF) for $\delta^{15}$N and $\delta^{13}$C. The combined use of $\delta^{13}$C and $\delta^{15}$N stable isotope ratios increases the ability to detect relationships between food sources and consumers, especially when there are more than two important basal sources (Post 2002). For $\delta^{15}$N, we used the TDF for Southern African freshwater fishes ($\Delta\delta^{15}$N $= 3.37 \pm 1.30‰$ (mean $\pm$ SD)) that was reported by Taylor et al. (2017), and TDF for $\delta^{13}$C ($\Delta\delta^{13}$C $= 0.54 \pm 0.53‰$) was obtained by averaging values reported for tropical freshwater fish in the literature (Bastos et al. 2017; Arantes et al. 2019). We evaluated isospace plots to ensure that consumer isotopic values fell within the space defined by $\delta^{13}$C and $\delta^{15}$N values of potential sources (Phillips et al. 2014; Arantes et al. 2019). The C:N ratio of fish muscle tissue across sites and seasons was $3.8 \pm 0.7\%$ (mean $\pm$ SD). Therefore, $\delta^{13}$C for fish muscle tissue was corrected for lipids using the equation in Post et al. (2007). Following the approach reported by Ou and Winemiller (2016), we 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; R Core Team 2020). In each river and season, only fish with overall sample sizes $\geq 10$ were included in the mixing model (Peel et al. 2019). Chains of all mixing models were checked for convergence to ensure that Gelman-Rubin Statistics were close to 1. Convergence was further ascertained through visual inspection of posterior plots and posterior predictive checks.

We recorded the median contribution of each source to fish biomass with 95% credible intervals. The ability of the models to adequately separate food sources assimilated by fish was determined through the assessment of correlations between sources within the isospace and visual inspection of posterior probability distributions. Where two sources were plotting close together in the isospace, combining sources was done a posteriori to preserve the covariation structure among source proportions (Phillips et al. 2014).

Grouping sources was based on functional categories to ensure biological relevance. For example, in the Boro River, aquatic macrophytes and waterlily were not significantly different in the isospace during the wet season (Fig S1), and they were combined to form a general group of aquatic macrophytes. A similar combination was done in the dry season to allow for comparison of source contributions among seasons. In the Boteti River, water lily was not collected during the wet season, and to allow for comparison of source contributions among seasons, water lily was excluded from the dry season analysis.

Samples of seston and periphyton were collected, but they were excluded from the mixing model analyses because they revealed high variation that suggests they may represent detritus from a mixture of origins. More importantly, recent measurements of water column and benthic primary production in the Okavango Delta and rivers of the basin reveal extremely low rates in this oligotrophic system (Taylor et al. 2017; Mazebedi 2019). Consequently, these two sources were considered to be relatively unimportant basal production sources supporting fishes in this system. Therefore, seston and periphyton were excluded from the mixing model to improve resolution among autochthonous and allochthonous macrophytes that dominate habitats of the Boro and Boteti rivers. Taylor et al. (2017) suggested that two benthic-feeding cyprinids (*Labeo cylindricus, L. lunatus*) feed on periphyton; they reported collecting only a few samples of periphyton and did not report isotopic ratios.

We estimated trophic positions of fishes using the R package *tRophicPosition* which is based on the Bayesian model proposed by Quezada-Romegialli et al. (2018). We used the mean $\delta^{15}N$ value of snails (aquatic consumer at trophic level 2) as our baseline (Arantes et al. 2019), and $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ TDF values described above to estimate fish trophic position (McCutchan et al. 2003). The sample sizes of snails used in the model per river and season are shown in Table S1. Only fish species with sample sizes $\geq 3$ were included in the analysis of trophic position. To ensure that the models were fitted properly, were ran posterior predictive checks and visually inspected posterior plots of trophic position. We used Pearson correlation tests to estimate the relationship between the estimated dependence on a single major basal source and the median trophic position for fish species in both rivers during each season. The variables that were included in the analysis were the median trophic position obtained from the probability distribution of estimated trophic positions for each species during a particular period/season, and the highest value for the estimated mean percent contribution among basal sources for that species during the same period.

## Results

### Stable isotope signatures of basal production sources and fishes

A total of 109 samples from three basal sources was analyzed in this study (Table 1). More samples came from the dry season (Boteti = 29; Boro = 42)

**Table 1** Sample size (*n*), mean carbon and nitrogen isotope ratios ($\delta^{13}C$, $\delta^{15}N$) and their standard deviations (SD) for basal production sources from the intermittent reaches of the lower Okavango delta

| Site | Season | Source | n | Mean $\delta^{13}C$ | SD $\delta^{13}C$ | Mean $\delta^{15}N$ | SD $\delta^{15}N$ |
|------|--------|--------|---|------|------|------|------|
| Boro | Wet | Aquatic macrophyte | 4 | −23.8 | 1.4 | −1.9 | 0.9 |
| | | C$_3$ plant | 13 | −28.9 | 1.6 | 1.4 | 2.2 |
| | | C$_4$ grass | 2 | −13.0 | 0.4 | 0.4 | 2.7 |
| | Dry | Aquatic macrophyte | 3 | −29.0 | 0.9 | 4.7 | 0.5 |
| | | C$_3$ plant | 23 | −28.5 | 1.2 | 2.8 | 2.2 |
| | | C$_4$ grass | 3 | −11.7 | 0.4 | −0.01 | 1.0 |
| Boteti | Wet | Aquatic macrophyte | 3 | −27.7 | 0.2 | 3.8 | 1.3 |
| | | C$_3$ plant | 11 | −27.0 | 1.2 | 2.1 | 1.3 |
| | | C$_4$ grass | 2 | −19.2 | 9.3 | 4.5 | 1.0 |
| | Dry | Aquatic macrophyte | 10 | −25.9 | 4.3 | 2.6 | 1.8 |
| | | C$_3$ plant | 13 | −28.8 | 1.6 | 3.1 | 1.4 |
| | | C$_4$ grass | 6 | −12.9 | 0.2 | 3.0 | 1.3 |

compared to the wet season (Boteti = 16; Boro = 22). Terrestrial $C_4$ grass had the highest $\delta^{13}C$ values among plants (Figs. 2 and 3) with average values of − 14.2 (sd = 3.4). Terrestrial $C_3$ plants and aquatic macrophytes had similar $\delta^{13}C$ values ranging from − 29.0 to − 23.8. We found high variation and overlap in $\delta^{15}N$ values among the different basal resource categories (Table 1).

A total of 449 fish specimens was analyzed in this study (Table S1). In both rivers, more species were obtained during the dry season (Boteti = 14 species; Boro = 15 species) compared to the wet season (Boteti = 6 species; Boro = 12 species). Herbivorous and detritivorous fishes tended to have lower values for $\delta^{15}N$ than carnivorous fishes. $\delta^{13}C$ values were low for most species (approximately − 26 to − 18) with relatively high variation associated with seasonal and spatial patterns (Table S2, Figs. 2 and 3).



**Fig. 2** Biplots of corrected mean $\delta^{13}C$ and $\delta^{15}N$ (± standard deviation) for basal production sources and fishes from Boro River during wet (top) and dry (bottom) seasons

**Fig. 3** Biplots of corrected mean δ¹³C and δ¹⁵N (± standard deviation) for basal production sources and fishes from Boteti River during wet (top) and dry (bottom) seasons
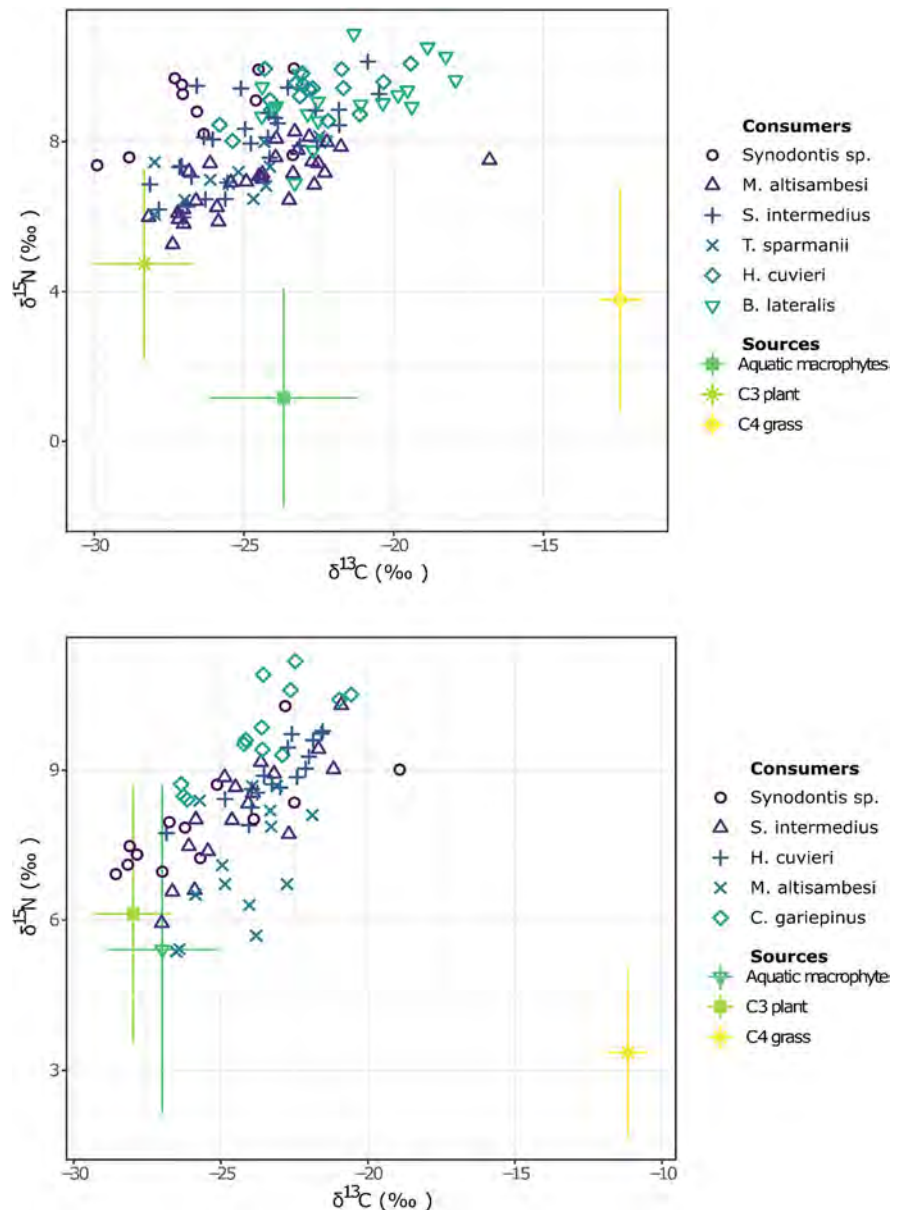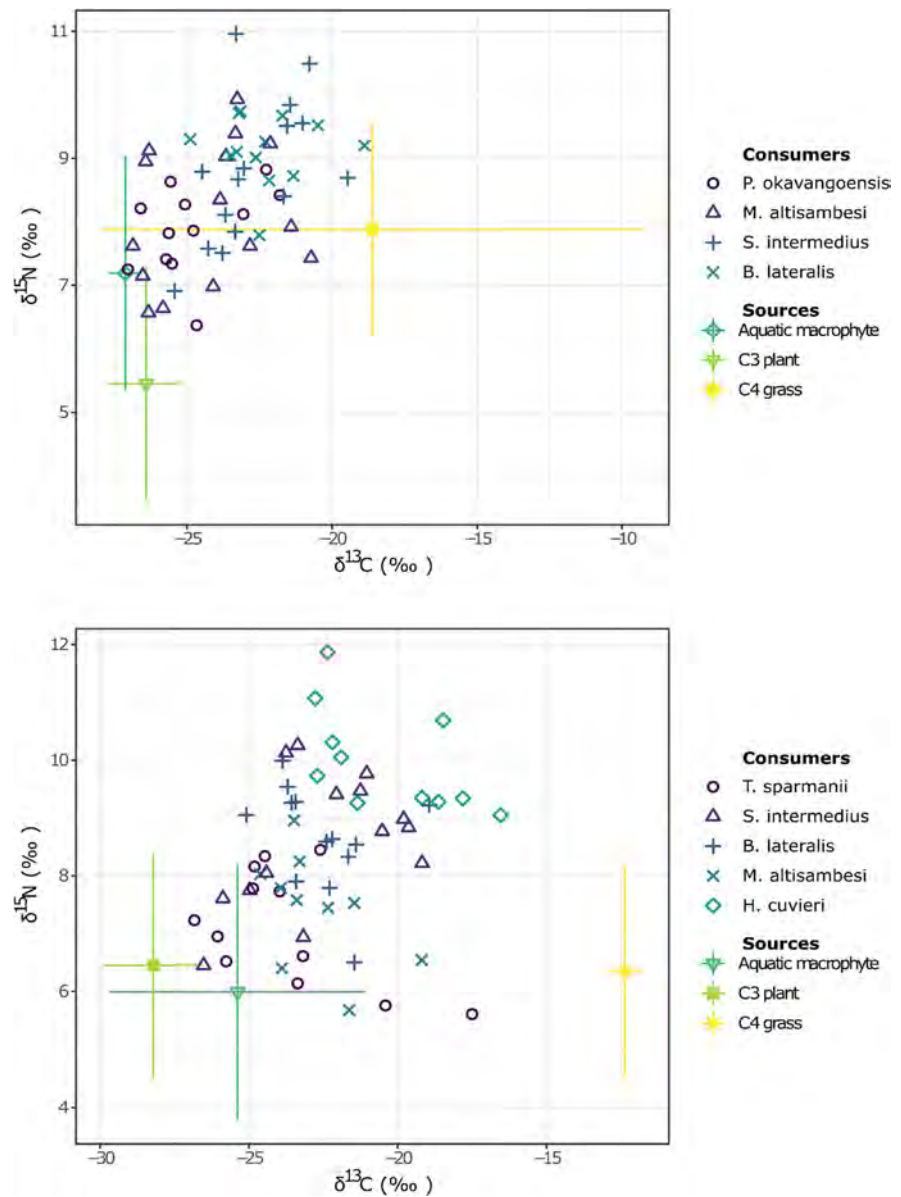


Source contributions to consumers

All models converged with Gelman statistics lower than 1.1. The fitted mixing models showed large negative correlations between aquatic macrophytes and terrestrial C$_3$ plants (−0.95), and between aquatic macrophytes and terrestrial C$_4$ grass (−0.81) during the wet season in the Boro River, indicating that the model struggled to separate these sources in the isospace (Fig S2). Similarly, aquatic macrophytes vs C$_3$ plants had large negative correlations in the Boro

River during the dry season (−0.97), the Boteti River during the wet season (−0.81), and the Boteti River during the dry season (−0.96). Visual inspection of the posterior distributions for all the sources showed that the distributions were not flat across seasons and rivers. Posterior distributions for terrestrial C$_4$ grass were the most constrained across seasons and rivers. Whereas posterior distributions for terrestrial C$_3$ plants and aquatic macrophytes were relatively diffuse, which is a common problem for stable isotope mixing models (Phillips et al. 2014), they all had

distinct unimodal peaks across seasons and rivers, indicating that model results were informed by data. Moreover, credible intervals of contributions of these sources to the biomass of most species had relatively high minima and low maxima (Table S1), suggesting that they were sufficiently robust for use in the interpretation of food web dynamics (Phillips et al. 2014).

Across rivers and seasons, the biomass of nearly all fish species likely was supported by multiple basal sources (Table S2). Nonetheless, various source contributions to fish biomass varied substantially depending on location and season for several species.

In the Boro River, three basal resources (aquatic macrophytes, terrestrial $C_3$ plants, and terrestrial $C_4$

grass) were each estimated to contribute more than 20% to the biomass of six fish species that were included in the mixing model during the wet season (Fig. 4). This inference is based on the median value from the probability distribution of mixing model estimates of source contributions for each species. All six species were estimated to derive more than 30% of their muscle mass through the energy channel originating from terrestrial $C_3$ plants suggesting that these plants could be the major production source supporting the biomass of fishes during the wet season. Terrestrial $C_4$ grasses were at the base of food chains important for three species (invertivorous *Marcusenius altisambesi*
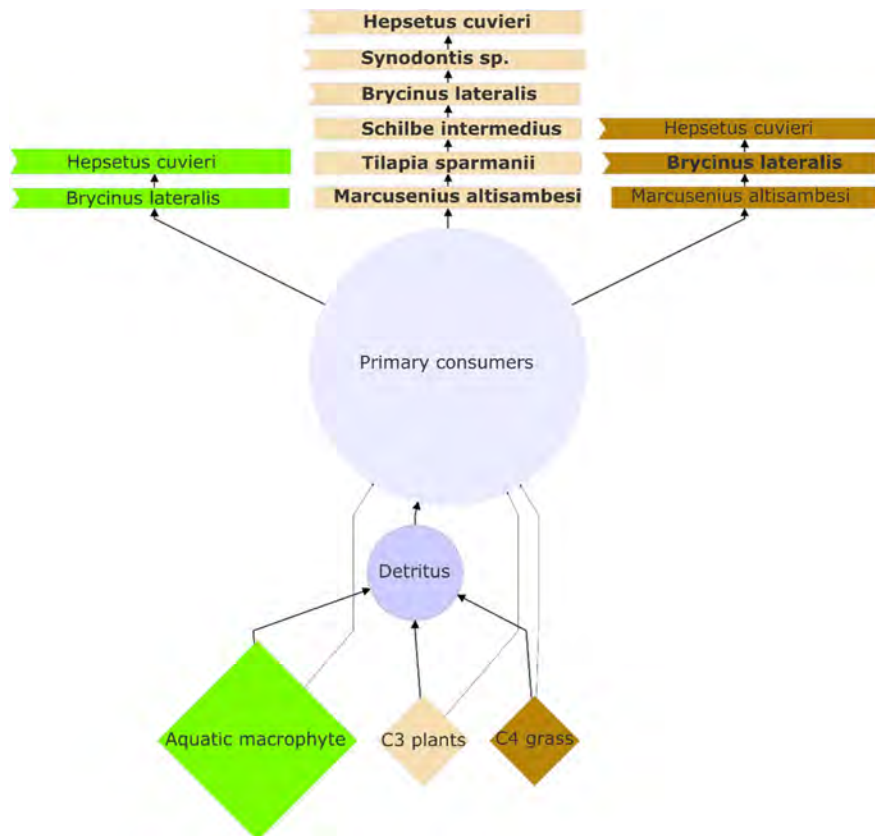


**Fig. 4** Energy flow and fish trophic interactions in Boro River during the wet season. Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by median trophic position: basal sources (◇), detritus (dotted circle), primary consumers (◯), species with modal trophic position ≤ 3.5 (▭), and species with modal trophic position > 3.5 (▭). Only the major energy pathways contributing ≥ 20%

to the biomass of fish species that had sample sizes ≥ 10 are shown. Within a compartment, populations that assimilated ≥ 30% of the resource are shown in bold. 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

and *Brycinus lateralis*, and the piscivore *Hepsetus cuvieri*). Only one fish species (*B. lateralis*) derived more than 30% of its biomass through food chains originating from terrestrial $C_4$ grasses. In addition, aquatic macrophytes were at the base of food chains supporting two of these species (*B. lateralis* and *H. cuvieri*).

During the dry season, aquatic macrophytes and terrestrial $C_4$ grass were estimated to contribute more than 20% to the biomass of two invertivorous fishes (*M. altisambesi* and *Synodontis* sp.), one omnivore (*Schilbe intermedius*) and two predators (*H. cuvieri* and *Clarias gariepinus*) in the Boro River (Fig. 5). All analyzed species were estimated to derive more than 30% of their muscle tissue mainly through energy channels originating from aquatic macrophytes during the dry season. $C_4$ grasses were at the base of food chains supporting the biomass of four of these species (*M. altisambesi*, *S. intermedius*, *H. cuvieri*, and *Clarias gariepinus*), but none of them derived more than 30% of their tissues from material originating from this source.

In the Boteti River during the wet season, aquatic macrophytes were each estimated to contribute at least 30% to the biomass of *M. altisambesi, S. intermedius, B. lateralis*, and *Petrocephalus okavangoensis* (Fig. 6). *Brycinus lateralis* and *S. intermedius* were estimated to derive at least 20% of their biomass through energy channels originating from terrestrial $C_4$ grass and *M. altisambesi* and *P. okavangoensis* may have derived at least 20% from $C_4$ grass.

During the dry season in the Boteti River, all three basal sources (aquatic macrophytes, terrestrial C3 plants, and terrestrial $C_4$ grass) were estimated to contribute at least 20% to the biomass of five species ( herbivore *Tilapia sparrmanii,* invertivores *M. altisambesi, B. lateralis*, omnivore *S. intermedius*, and predator *H. cuvieri*; Fig. 7). *Tilapia sparrmanii, M. altisambesi, B. lateralis, and S. intermedius* may have derived more than 30% of their muscle tissue from terrestrial $C_3$ plants; *M. altisambesi, B. lateralis, S. intermedius*, and *H. cuvieri* may have derived more than 30% from terrestrial $C_4$ grass. Only two species (*S. intermedius* and *H. cuvieri*) were likely to have obtained more than 30% of their muscle tissue through energy pathways originating from aquatic macrophytes.
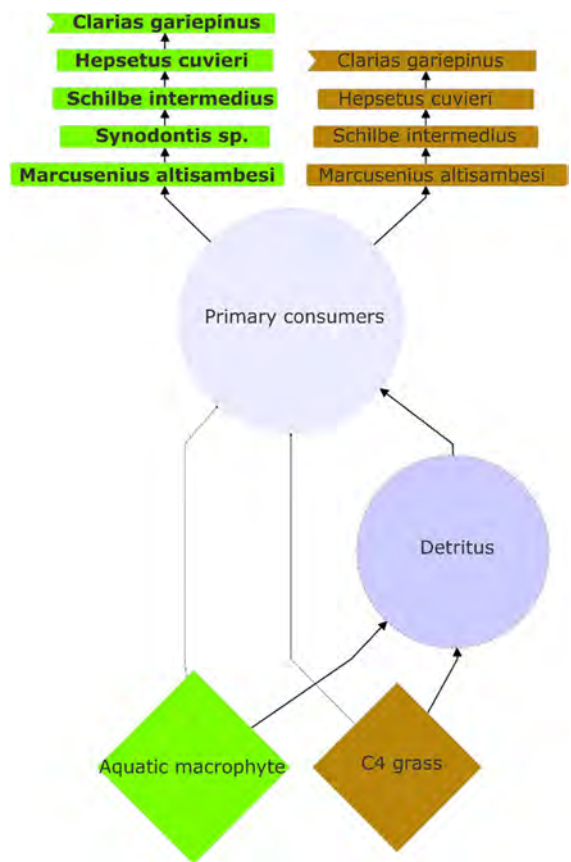


**Fig. 5** Energy flow and fish trophic interactions in Boro River during the dry season. Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by median trophic position: basal sources (◇), detritus (dotted circle), primary consumers (○), species with modal trophic position ≤ 3.5 (▭), and species with modal trophic position > 3.5 (▭). Only the major energy pathways contributing ≥ 20% to the biomass of fish species that had sample sizes ≥ 10 are shown. Within a compartment, populations that assimilated ≥ 30% of the resource are shown in bold. 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

Fish trophic positions and food web length

Visual inspection of the fitted trophic position model showed that the median posterior trophic position was adequately estimated by the model for most of the fishes from the Boro River, with narrow 95% credible intervals during both wet and dry seasons (Fig
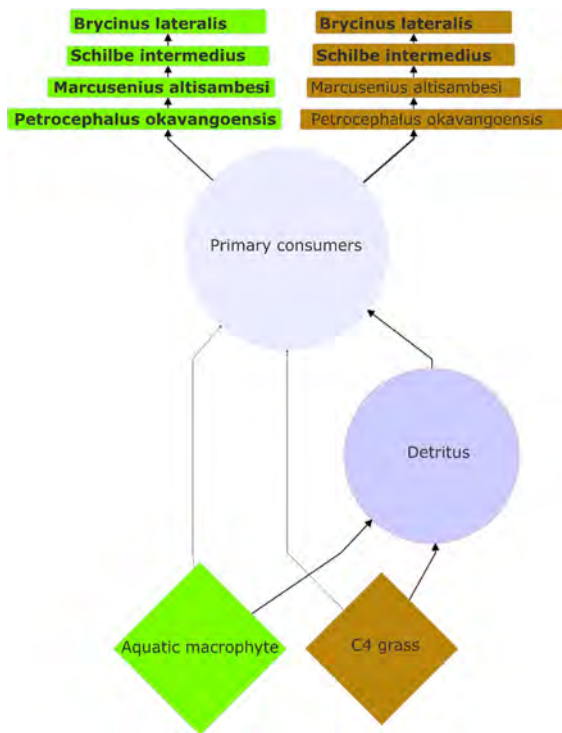
**Fig. 6** Energy flow and fish trophic interactions in Boteti River during the wet season. Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by median trophic position. Basal sources (◇), detritus (dotted circle), primary consumers (○), species with modal trophic position ≤ 3.5 (▭), and species with modal trophic position > 3.5 (▭). Only the major energy pathways contributing ≥ 20% to the biomass of fish species that had sample sizes ≥ 10 are shown. Within a compartment, populations that assimilated ≥ 30% of the resource are shown in bold. 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

S3a). For the Boteti River, estimates of trophic position were fairly precise for most species during the dry season (Fig S3b). During the wet season, trophic position estimates exhibited wide credible intervals, perhaps because of a small sample size for snails during this season.

Median trophic position values obtained from our Bayesian models indicated that food web length was less than 4.5 in both rivers (Table S3-S4). In the Boro River, *Serranochromis macrocephalus* had the highest TP during the wet season, and *Clarias gariepinus*

had the highest TP during the dry season. In the Boteti River, *Synodontis* sp. had the highest TP during the wet season, and *Serranochromis angusticeps* had the highest TP during the dry season. Although some species have been classified as herbivores and detritivores in previous studies, median TP was > 2.5 for all fishes from both rivers during both seasons.

**The association between the degree of dependence on major basal sources and median fish trophic position**

For the Boro River, the correlation between trophic position and the degree of dependence on a single major basal source was negative and not significant during both wet (t = − 1.87, df = 4, P = 0.13, cor = − 0.68) and dry seasons (t = − 1.31, df = 3, p = 0.28, cor = − 0.60) (Fig S4). In the Boteti River, the correlation between trophic position and the degree of dependence on a single major basal source was negative and significant during the wet season (t = − 8.14, df = 2, p = 0.01, cor = − 0.98), and the relationship was negative and not significant during the dry season (t = − 0.66, df = 3, p = 0.56, cor = − 0.35).

**Discussion**

Fishes in the Lower Okavango Delta have diverse trophic niches, and the biomass of most species appeared to be supported by multiple basal production sources. Aquatic macrophytes were estimated to be the most important basal source supporting most fishes in the Boro River during the wet season, and terrestrial $C_3$ plants were more important during the dry season. During the wet season in the Boteti River, food chains originating from aquatic macrophytes likely supported much of the biomass of most species, and terrestrial $C_4$ grasses assumed greater importance during the dry season. One mechanism for these shifts in food web dynamics would be if prey consumed by carnivorous fishes change their foraging strategies in response to seasonal shifts in resource availability. Our results are consistent with the idea that both autochthonous and allochthonous resources should be major inputs to aquatic food webs in river-floodplain ecosystems, but their relative importance depends on hydrology and aquatic habitat dynamics (Humphries et al. 2014). Interestingly, terrestrial $C_4$ grasses were a
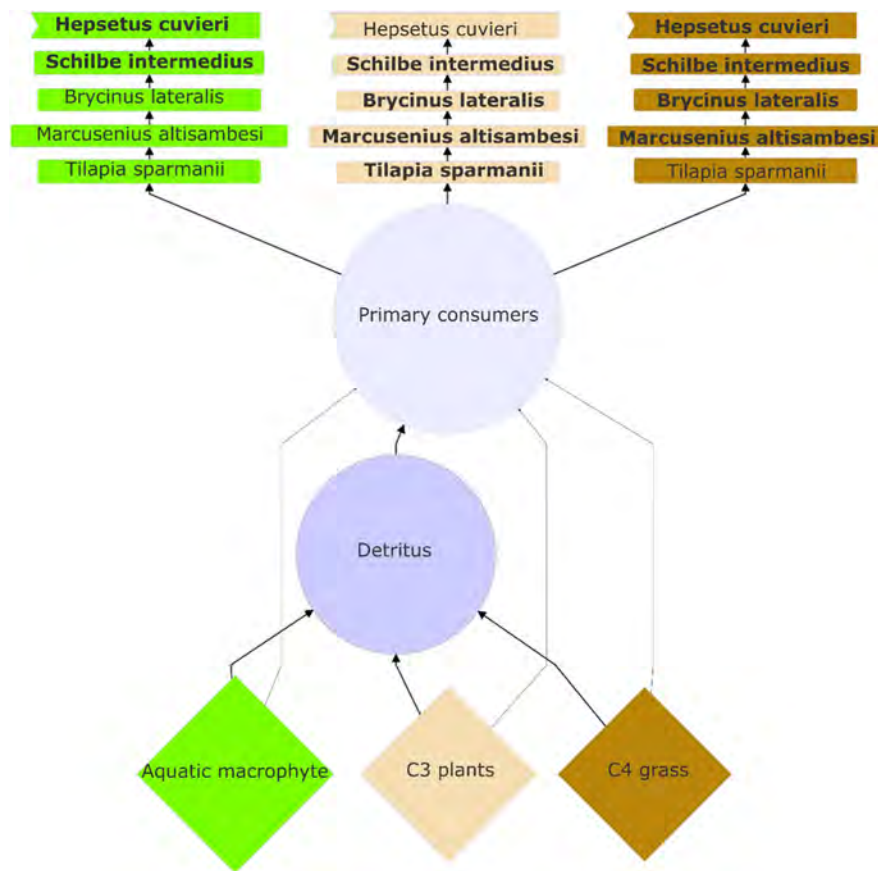
**Fig. 7** Energy flow and fish trophic interactions in the Boteti River during the dry season. Different node shapes and connecting arrows represent energy pathways and the species they support (food web compartments) categorized vertically by median trophic position. Basal sources (◇), detritus (dotted circle), primary consumers (◯), species with modal trophic position ≤ 3.5 (▭), and species with modal trophic position > 3.5 (▬). Only the major energy pathways contributing ≥ 20% to the biomass of fish species that had sample sizes ≥ 10 are shown. Within a compartment, populations that assimilated ≥ 30% of the resource are shown in bold. 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

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 increases its nutritional value for metazoan consumers.

Although most fishes could have consumed variable fractions of all three 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 all rivers and seasons, the relationship between trophic position and the contribution of a single major basal source to fish biomass was negative, supporting the hypothesis that species integrating multiple basal sources and food chains should be positioned higher in the food web, while those positioned lower in the food web may derive a large proportion of their biomass from fewer basal sources.

In both rivers, 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 (Winemiller 1990; Bogan and Lytle 2007; McHugh et al. 2010; McMeans et al. 2019).

Higher predator densities in the river channel could result in competition that causes fish to disperse along the river corridor and thereby encounter a greater diversity of food resources before habitat fragmentation occurs. This could explain why species higher in the food web assimilated material derived from multiple basal sources during the dry season, supporting the idea that large, highly mobile predators at high trophic positions may exploit a greater number of energy pathways (Arim et al. 2010). However, prolonged drought could result in the opposite pattern if habitat reduction and dispersal limitation results in strong trophic interactions with greater reliance on a few local sources of production in isolated pools (Winemiller 1990; McCann et al. 2005; Taylor et al. 2006; Jardine et al. 2012; Balcombe et al. 2015).

During the wet season flood pulse, both longitudinal and lateral connectivities increased the amount of aquatic habitat and the potential for fish to disperse. 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).

Our results suggest that in the Boro River, four out of six species switched from being supported mostly by food chains originating from terrestrial $C_3$ plants during the wet season to those supported by aquatic macrophytes during the dry season. As water levels fall in the main river channel and the floodplain, biomass from decomposing aquatic macrophytes and terrestrial $C_3$ plants is deposited in sediments. During the flood pulse, terrestrial plant detritus enters aquatic food chains when detritivores feed on this material and associated microorganisms (Høberg et al. 2002; Cole et al. 2011). During low flows, material from aquatic macrophytes within the main river channel may become more important. This supports the idea that fish biomass that accrues during the wet season sometimes is dependent upon energy derived from aquatic refuges during the dry season (Vernasky et al. 2020).

The five fish species analyzed from the Boteti River during the wet season apparently had derived most of their biomass from food chains originating from aquatic macrophytes. During the dry season, their support shifted to energy and material pathways with terrestrial $C_4$ grass and $C_3$ plants as production sources. By comparison, 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). Whereas $C_4$ grasses generally have low direct nutritional value when compared to other production sources (Minson 1971) and generally are reported to be minor contributors to fish biomass (e.g., Jepsen & Winemiller 2007; Arantes et al. 2019), there is some evidence that $C_4$ grasses may be the foundation of food chains that support the biomass of at least some fishes in tropical river-floodplain systems. For example, $C_4$ 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, $C_4$ 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).

Okavango fishes are unable to forage in floodplains during the dry season; however, other animals may import floodplain resources to river channels. Hippopotamuses were frequently observed in the Boteti River throughout our study, and these megaherbivores could have transferred material derived from $C_4$ 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 $C_4$ grass that supports aquatic food webs (Masese et al. 2015). Therefore, both terrestrial $C_4$ grass and $C_3$ plants could have entered aquatic food chains during the dry season in the Boteti River 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).

Our findings indicate that seasonal changes in connectivity and aquatic habitat size likely drove changes in basal resource availability to aquatic organisms and the predominant energy pathways supporting fish biomass in the Lower Okavango Delta. Notable is the major role of aquatic macrophytes and terrestrial $C_3$ plants in supporting food chains that maintain the biomass of fishes in the Boro River, which agrees with a prediction from the river wave concept (Humphries et al. 2014). Under low-flow conditions during the dry season, aquatic food webs are supported mostly by local instream autochthonous production, in this case aquatic macrophytes, whereas allochthonous inputs predominate during the wet season. Adaptive foraging is one mechanism that could enhance food web resilience to fluctuations caused by extreme seasonal hydrology in the lower Okavango Delta. Our 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 Jepsen 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 greatly expands aquatic habitat in the lower Okavango Delta and provides fish and other aquatic organisms with access to abundant autochthonous and allochthonous resources. Heterotrophy and the brown food web seem to be predominant in the oligotrophic aquatic habitats of the Okavango Delta. In theory, the extensive multi-channel foraging that results from these temporal and spatial dynamics enhances the stability of these complex ecological systems (Kondoh 2003; Wolkovich et al. 2014; McMeans et al. 2019).

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