frontiers
in Environmental Science

ORIGINAL RESEARCH
published: 05 December 2019
doi: 10.3389/fenvs.2019.00192

Food Web Structure and Trophic Dynamics of a Fish Community in an Ephemeral Floodplain Lake

Richard A. Peel[1,2,3], **Jaclyn M. Hill**[2,4*†], **Geraldine C. Taylor**[1,2] and **Olaf L. F. Weyl**[1,5†]

[1] Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa, [2] South African Institute for Aquatic Biodiversity, Grahamstown, South Africa, [3] Namibia Nature Foundation/European Union Community Conservation Fisheries in KAZA Project, Katima Mulilo, Namibia, [4] Department of Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, QC, Canada, [5] Department of Science and Technology/National Research Foundation Research Chair in Inland Fisheries and Freshwater Ecology, South African Institute for Aquatic Biodiversity, Grahamstown, South Africa

OPEN ACCESS

Edited by:
John Pascal Simaika,
IHE Delft Institute for Water
Education, Netherlands

Reviewed by:
Martin Paar,
University of Greifswald, Germany
Guillaume Grosbois,
Université du Québec à
Chicoutimi, Canada

***Correspondence:**
Jaclyn M. Hill
jaclyn.hill@dfo-mpo.gc.ca

†ORCID:
Jaclyn M. Hill
orcid.org/0000-0003-0703-3772
Olaf L. F. Weyl
orcid.org/0000-0002-8935-3296

Specialty section:
This article was submitted to
Freshwater Science,
a section of the journal
Frontiers in Environmental Science

Received: 04 September 2019
Accepted: 21 November 2019
Published: 05 December 2019

Citation:
Peel RA, Hill JM, Taylor GC and
Weyl OLF (2019) Food Web Structure
and Trophic Dynamics of a Fish
Community in an Ephemeral
Floodplain Lake.
Front. Environ. Sci. 7:192.
doi: 10.3389/fenvs.2019.00192

In Africa, wetlands, such as shallow, ephemeral lakes provide ecosystem services, such as water purification, food supply, and flood control but are subject to dynamic flooding/drying cycles which vary in duration from years to decades. The stochastic nature of drying events subjects ephemeral lake fauna to persistent disturbance regimes, therefore understanding how biota respond to flooding and drying events is essential for their conservation and management. Primary production sources supporting consumer biomass in the shallow ephemeral Lake Liambezi (upper Zambezi Ecoregion), were investigated using stable isotope analysis, mixing models and stomach content analysis to investigate the following hypotheses: (1) algal primary production supports a higher consumer biomass than aquatic macrophytes; (2) the lake food chain is short, because the majority of fish fauna are detritivorous/herbivorous cichlids that are consumed by top predators; (3) fish community trophic structure will be similar between years; and (4) with short food chains and stochastic resource availability, there will be substantial competition for food among fish species. Results showed that phytoplankton production supported substantial consumer biomass in Lake Liambezi, with important contributions from macrophytes and associated detritus and/or periphyton. While particulate organic matter (POM) contributed substantially to the diet of herbivorous/detritivorous tilapiine cichlids (the backbone of Lake Liambezi's commercial fishery), considerable dietary carbon was likely also derived from aquatic plants and associated detritus and/or periphyton compared to other fishes. Three major food chains were identified in the lake. The phytoplankton-based pelagic food chain was longest, involving up to four trophic transfers. The benthic food chain based primarily on detritus of planktonic origin (but may also include macrophyte associated detritus/periphyton) was characterized by high levels of omnivory and involved up to three trophic transfers. The macrophytic detritus-based food chain was shortest, involving just two trophic transfers. Predators fed across all three food chains, but predominantly on the two benthic food chains. A combination of dietary overlap (amongst piscivores/predators, amongst insectivores), dietary specialization (tilapiine cichlids, alestids), the integration of multiple food chains and behavioral adaptation to changing dietary resources underpins the ability of Lake Liambezi's fish community to thrive under the stochastic nature of ephemeral lake ecosystems.

Keywords: floodplains, stable isotopes, food webs, lakes, fish communities

INTRODUCTION

Wetlands are diverse and productive systems (Ward et al., 1999, 2002) providing many economically valuable goods and services, such as water purification, food supply, and flood control (Baron et al., 2002). Among the most productive and important wetlands in Africa are large, shallow lakes (<5 m average depth, e.g., Lakes Chad and Chilwa) (Kalk et al., 1979; Carmouze et al., 1983), many of which occur in the drier tropics where surface water is scarce, making them extremely important both ecologically and economically (Kolding et al., 2016). With a high surface area relative to their volume, water replacement time in shallow lakes is generally short, making them especially sensitive to changes in water inputs (Talling, 2001). As a consequence, water level fluctuations are a dominant force controlling ecological processes in shallow lakes (Dumont, 1992; Wantzen et al., 2008; Kolding and van Zwieten, 2012). Many other environmental factors vary concurrently with fluctuations in water level (Talling, 1992), with important consequences for lake biota (Dumont, 1992; Talling, 2001).

Seasonal variation in the hydrological regime of tropical lakes becomes more pronounced with increasing latitude (Talling, 2001), and many endorheic lakes in the drier tropics experience large interannual fluctuations. In extreme cases, these are characterized by flooding and drying cycles, which can vary widely in duration from years to decades (e.g., Lake Chilwa; Kalk et al., 1979, and to some extent Lake Chad; Carmouze et al., 1983). Drying is a major disturbance in ephemeral lake ecosystems with severe consequences for populations of aquatic biota, but may be necessary for the maintenance of species diversity in ephemeral lakes as it increases habitat diversity, and promotes species coexistence by mediating biotic interactions (Dumont, 1992; Ward et al., 2002; Wantzen et al., 2008). The frequency and stochastic nature of drying events subjects ephemeral lake fauna to a persistent disturbance regime (Dumont, 1992) and thus understanding how biota respond to flooding and drying in ephemeral lakes is essential for their conservation and management.

Lake Liambezi is a shallow ephemeral floodplain lake situated in north-eastern Namibia. It is fed on an irregular basis by the Upper Zambezi and Kwando rivers, which overflow into the lake during years of extremely high flooding (Peel et al., 2015). The lake dried up in 1985 following 5 years of low floods in the inflowing rivers (Grobler and Ferreira, 1990). It remained largely dry until 2007, when it received a larger flood, followed by major flood in 2009, filling for the first time since the late 1970s. The lake reached a peak surface area of around 370 km^2 during successive floods in 2010 and 2011 and remained inundated, despite receiving minimal inflow until 2017. The lake hosts a thriving fish community (Peel et al., 2015, 2019) and consequently supports an active subsistence fishery, based primarily on large cichlid species, particularly *Oreochromis andersonii* and *Oreochromis macrochir*, however, the ephemeral nature of Lake Liambezi also puts it at risk of overfishing (Simasiku et al., 2017). The lake also supports extensive areas of aquatic macrophytes (Seaman et al., 1978; Peel et al., 2015), including vast, fragmented stands of the emergent reeds *Phragmites australis* (Gramineae) and *Typha capensis* (Typhaceae), which| provide shelter from wind and wave action, enabling the submerged macrophytes *Lagarosiphon ilicifolius* (Hydrocharitaceae) and *Najas horrida* (Hydrocharitaceae) to flourish in shallower areas. Seaman et al. (1978) hypothesized that these macrophytes acted as a "nutrient sponge," limiting the availability of nutrients to microalgae in the open lake, resulting in low algal growth potential. Seaman et al. (1978) and van der Waal (1985) thus considered macrophytes to be the most important primary producers supporting invertebrates and fishes in Lake Liambezi, a view widely held at the time (Howard-Williams and Junk, 1976; Soares et al., 1986; Bayley, 1989). Seaman et al. (1978) concluded that macrophytes must enter the food web mainly as detritus, and although there is some evidence that herbivores can remove an average of 40–48% of macrophyte biomass in aquatic ecosystems (Bakker et al., 2016), the direct consumption of macrophytes is rare among the Upper Zambezi ichthyofauna (van der Waal, 1985; Winemiller, 2004). Studies employing stable isotopes have since revealed that, despite being major primary producers in floodplain ecosystems, macrophytes, with some exceptions (e.g., Winemiller, 1996; Hoeinghaus et al., 2007; Zeug and Winemiller, 2008), generally contribute relatively little to aquatic food webs (Hamilton et al., 1992; Bunn and Boon, 1993; Forsberg et al., 1993; Thorp and Delong, 1994; Thorp et al., 1998; Lewis et al., 2001) and/or may have only very localized effects (Grosbois et al., 2017a). While these studies indicated that phytoplankton and periphyton, which usually constitute a small fraction of the potentially available carbon in floodplain ecosystems, are the principal carbon sources supporting invertebrates and fishes (Winemiller, 2004; Douglas et al., 2005).

This paper aims to investigate which primary production sources support consumer biomass in Lake Liambezi, a shallow ephemeral lake located in the upper Zambezi Ecoregion, to describe the trophic structure of the fish community and assess the trophic interactions among fish species, in order to discuss their potential influences in shaping its fish community. Using stable isotope analysis, mixing models and complimentary stomach contents analysis (fish only), this study set out to investigate the following hypotheses: (1) algal primary

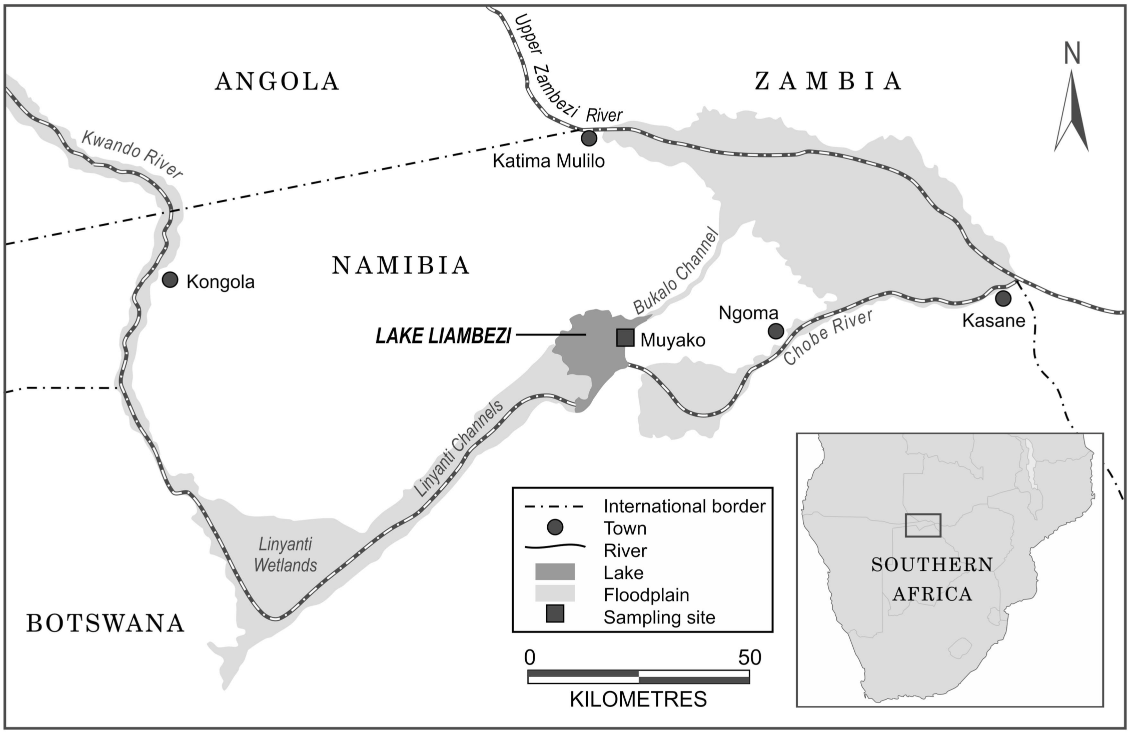

FIGURE 1 | Map of north-eastern Namibia illustrating the rivers and floodplains feeding into Lake Liambezi, and the location of the Lake Liambezi sampling site.

production (phytoplankton) supports a higher proportion of consumer biomass than aquatic macrophytes; (2) the lake food chain will be short, as a large component of the fish fauna comprises detritivorous and herbivorous fishes that may be consumed directly by top predators; (3) fish community trophic structure will be similar between years; and (4) with short food chains and the stochastic nature of resource availability in ephemeral systems, there will be substantial competition for food resources among fish species.

METHODS

Site Description

Lake Liambezi is a shallow ephemeral floodplain lake situated in the Zambezi Region of Namibia in southern Africa (**Figure 1**). With an average depth of ~2.5 m, and a maximum depth of 7 m at its peak in 2010, the lake is relatively shallow (Peel et al., 2015) and annual temperatures range between 16.7 and 28.0°C, with a mean of 24.1°C (Seaman et al., 1978; Peel, 2016; Simasiku et al., 2017). Rains fall during austral summer from October to April, and are highly variable, averaging ~700 mm in the north-east, declining gradually to 500 mm in the south-west (Mendelsohn and Roberts, 1997). The annual average evaporation rate is as high as 2,500 mm (Mendelsohn and Roberts, 1997). The composition of the Lake Liambezi fish community underwent a series of successional changes from its full inundation in 2007 until 2010, but remained largely the same from 2011 to 2014, suggesting the fish community may have reached maturity (Peel et al., 2019) and comprises 46 species from 10 families (**Supplementary Table 1**; Peel et al., 2015).

Stable Isotope Analysis

Stable isotope samples were collected during August 2011 and August 2012. Limited sampling of basal resources and fishes [*Oreochromis andersonii*, *Oreochromis macrochir*, *C. rendalli*, and *T. sparrmanii* (Cichlidae), $n = 11$ for each species] was additionally carried out in August 2014 to investigate dietary shifts in tilapiine cichlid species between years. Fishes and their potential food sources were collected across Lake Liambezi, including littoral areas, vegetated habitats and the open lake. Fish were sampled by D-netting (3 mm mesh), electrofishing, and using standardized multifilament gill nets (110 × 2.5 m, 11 panels) with stretched mesh sizes of 12, 16, 22, 28, 35, 45, 57, 73, 93, 118, and 150 mm and baited longlines (20 m long, 20 × 9/0 circle hooks on 80 lb monofilament snoods of 1 m in length). Nets were surface set between 18:00 and 19:00 and retrieved between 06:00 and 07:00 the following morning, in the eastern half of the lake, between the inflowing Bukalo Channel and Chobe River (**Figure 1**), in both open water and vegetated habitats. Fish were also purchased from local fishers. For most fishes, white muscle tissue was taken above the lateral line, for fish species <30 mm (e.g., *Micropanchax* spp, Poeciliidae family), whole bodies were used after removing the head, intestines and scales (skin however was not removed). Aquatic invertebrates were sampled using a scoop nets and by kick sampling, and whole bodies, and/or pooled individuals of the same species, were used for each sample. Zooplankton was collected using a Bongo net (500 µm mesh) towed on the water surface at night, sorted into the broadly defined groups of herbivorous or predatory zooplankton and then analyzed as bulk, pooled ($n = 10$) samples. Detritus was sampled using a cone dredge and aquatic macrophytes and filamentous algae were collected by hand. Particulate organic matter (POM) was collected by filtering between 1 and 2 L surface water, onto 0.45 μm pre-combusted (at 500°C for 4 h) glass fiber filters (Advantec).

All samples were oven dried at 50°C for 24–48 h, ground to a homogenous powder and then analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Europa Scientific 20-20 IRMS linked to an ANCA SL Prep Unit at IsoEnvironmental cc, South African Institute for Aquatic Biodiversity, Grahamstown, South Africa. Isotope values are expressed in delta notation according to:

$$\delta X = \left(R_{\text{sample}}/R_{\text{standard}} - 1\right) \times 1000,$$

where X is the element and R is the ratio of the heavy over the light isotope. The $\delta^{13}C$ and $\delta^{15}N$ values were reported as parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric nitrogen standards, respectively, and normalized to internal standards (casein and beet sugar), calibrated to the International Atomic Energy reference materials (IAEA-CH-3 and IAEA-CH-6 for $\delta^{13}C$, IAEA-N1 and IAEA-N2 for $\delta^{15}N$). Analytical precision was ± 0.07‰ for $\delta^{13}C$ and ± 0.12‰ for $\delta^{15}N$ for the 2011 samples and ± 0.08‰ for $\delta^{13}C$ and ± 0.12‰ for $\delta^{15}N$ for the 2012 samples.

Ethics approval was granted by the SAIAB Animal Ethics Committee (2013-07).

Food Web Structure

All fish samples were lipid corrected as described by Taylor et al. (2017a) and all isotope data collected in 2011 and 2012 were assessed separately, as baseline corrections for trophic positioning (e.g., Anderson and Cabana, 2007; Olsson et al., 2009) were not possible due to a lack of long-lived primary consumers living in the system. Aquatic insect and plant species were analyzed for $\delta^{13}C$ and $\delta^{15}N$ values and were then grouped into broad functional groups to ensure isotopically distinct resource assemblages for food-web interpretation and mixing model analyses (see below). Fishes were grouped according to a combination of taxonomic and feeding guilds as diets are often too flexible to be used solely for conclusive groupings (Yodzis and Winemiller, 1999; Jackson et al., 2001; Welcomme et al., 2006). The assessment of food web structure was based on a trophic enrichment of 1.5‰ for $\delta^{13}C$ (Sweeting et al., 2007a), and 3.2‰ for $\delta^{15}N$ (Sweeting et al., 2007b).

To investigate the proportional contribution of resources underpinning Lake Liambezi food webs separately for each year, Bayesian mixing models (MixSIAR; Stock and Semmens, 2016; Stock et al., 2018) were run using stable isotope data from all primary consumers (and some secondary consumers) (see **Table 1**) with $n \geq 10$ in both 2011 and 2012 (raw data), food sources (mean ± 1 SD) and discrimination factors of 1.5 ± 0.5‰ for $\delta^{13}C$ and 3.2 ± 0.5‰ for $\delta^{15}N$ as described above. The model was run with Markov chain Monte Carlo (MCMC) parameters of three chains of 300,000 iterations, a burn-in phase of 200,000 and a thinning of 100. Individuals as a random effect and both residual and process error were included in the model. The model generates posterior probability distributions that can be described by average estimates of the source contributions and their associated credible intervals. Convergence and diagnostic statistics were evaluated using the Gelman–Rubin test (all variables were $\leq$1.05). Note that while Bayesian mixing models can include some variability in predictions through the incorporation of error terms and informative priors (Parnell et al., 2010; Stock et al., 2018), there remains a mismatch in time integration between food resources and consumers, with the latter being typically more time integrated (Phillips et al., 2014). Thus, predicted proportional resource contributions to Lake Liambezi food webs will likely display some variation over time.

Because no long lived primary consumers were found in Lake Liambezi in order to baseline our datasets, variation in the isotope values ($\delta^{13}C$ and $\delta^{15}N$) of basal resources sampled in both years were assessed by multivariate statistical analyses performed using the PRIMER package, version 6 with PERMANOVA (Clarke and Gorley, 2006; Anderson et al., 2008). Analyses were performed on Euclidean distance measures of untransformed data. PERMANOVA were used to test for significant differences ($\alpha = 0.05$) between years and calculated using the Type III (partial) sums of squares with 9,999 unrestricted permutations and *post-hoc* pair-wise PERMANOVAs ($\alpha = 0.05$) were performed where appropriate. Important consumer species that showed large variation in $\delta^{13}C$ between 2011 and 2012 were also tested for significant differences ($\alpha = 0.05$) using univariate PERMANOVAs as described above. Here, the additional data collected in 2014 were used to determine whether the differences in $\delta^{13}C$ values of the tilapiine cichlids between years represented a permanent dietary shift, or simply inter-annual dietary variation.

Community Metrics

The trophic structure of the fish community was then compared between 2011 and 2012 using six quantitative isotope metrics (Layman et al., 2007; Jackson et al., 2011); nitrogen range (NR); carbon range (CR); mean distance to centroid (CD), providing a measure of trophic diversity; mean nearest neighbor distance (MNND), which estimates the density and clustering of species within the community; standard deviation of the nearest neighbor distance (SDNND), which gives a measure of the evenness of species packing in isotopic biplot space; and the sample size corrected standard ellipse area (SEA_c), which provides a bivariate measure of the mean core isotopic niche of a community. The degree of SEA_c overlap between communities was calculated to give a quantitative measure of dietary similarity (Jackson et al., 2012). Only fish species collected in both years with a sample size $\geq$3 were included in the analyses. All metrics were calculated using the Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al., 2011) package in the R statistical computing programme (R Core Team, 2013), and bootstrapped ($n = 10{,}000$) to allow comparisons of 2011 and 2012 datasets that differed in sample size.

Trophic Structure and Species Interactions

The trophic structure of the fish community sampled in 2011 only was further resolved by calculating the SEA_c of each

TABLE 1 | Carbon and nitrogen stable isotope values (mean ± standard deviation) of fish species, invertebrate groups and basal carbon sources sampled in Lake Liambezi in 2011 and 2012, and the taxonomic/feeding group to which species were assigned for broad food web analysis.

Species	***Family***	**2011**			**2012**			**Group**
		N	δ^{13}**C**	δ^{15}**N**	***N***	δ^{13}**C**	δ^{15}**N**	
FISH								
Brycinus lateralis	Alestidae	28*	−26.71 ± 1.40	9.82 ± 0.85	32*	−27.89 ± 2.20	9.81 ± 0.98	Alestids
Rhabdalestes maunensis	Alestidae	21*	−27.97 ± 0.93	9.89 ± 0.41	10*	−26.15 ± 1.31	9.64 ± 0.62	Alestids
Enteromius barnardi	Cyprinidae	1	−29.16	8.71	–	–	–	Cyprinids
Enteromius bifrenatus	Cyprinidae	3	−21.66 ± 1.19	7.36 ± 0.37	7	−31.31 ± 0.99	9.11 ± 0.88	Cyprinids
Enteromius haasianus	Cyprinidae	6	−24.45 ± 0.84	8.26 ± 0.39	–	–	–	Cyprinids
Enteromius poechii	Cyprinidae	8	−23.14 ± 2.96	8.25 ± 0.81	2	−27.10 ± 0.70	8.36 ± 0.03	Cyprinids
Enteromius radiatus	Cyprinidae	21*	−25.55 ± 2.01	8.38 ± 0.56	11*	−26.32 ± 0.46	8.50 ± 0.89	Cyprinids
Enteromius unitaeniatus	Cyprinidae	9	−27.07 ± 0.80	9.04 ± 0.36	–	–	–	Cyprinids
Coptostomobarbus wittei	Cyprinidae	3	−26.85 ± 2.21	9.90 ± 0.55	–	–	–	Cyprinids
Labeo cylindricus	Cyprinidae	1	−24.27	7.78	1	−24.54	8.03	Cyprinids
Pharyngochromis acuticeps	Cichlidae	21*	−26.94 ± 2.02	8.46 ± 0.76	16*	−27.60 ± 2.28	8.92 ± 1.17	Benthic cichlids
Pseudocrenilabrus philander	Cichlidae	17*	−24.00 ± 2.41	9.42 ± 0.73	5	−23.89 ± 1.05	8.54 ± 0.79	Benthic cichlids
Sargochromis codringtonii	Cichlidae	20*	−24.68 ± 2.12	8.30 ± 0.69	1	−23.93	8.82	Benthic cichlids
Sargochromis carlottae	Cichlidae	–	–	–	3	−25.37 ± 2.62	9.47 ± 1.66	Benthic cichlids
Schilbe intermedius	Schilbeidae	25	−25.26 ± 2.24	8.95 ± 1.04	29	−26.08 ± 1.82	9.50 ± 0.83	Generalist predators
Clarias ngamensis	Clariidae	11	−24.46 ± 2.20	8.92 ± 0.46	1	−24.23	9.8	Generalist predators
Clarias theodorae	Clariidae	1	−22.93	10.55	–	–	–	Generalist predators
Synodontis spp.	Mochokidae	17	−27.84 ± 2.01	9.25 ± 0.88	3	−26.81 ± 0.36	10.30 ± 0.51	Generalist predators
Marcusenius altisambesi	Mormyridae	13*	−25.67 ± 2.27	7.51 ± 0.76	2	−27.74 ± 3.52	7.70 ± 0.21	Mormyrids
Petrocephalus cf. *okavangensis*	Mormyridae	7	−26.08 ± 1.01	9.11 ± 0.55	6	−25.59 ± 1.74	8.93 ± 0.40	Mormyrids
Mormyrus lacerda	Mormyridae	1	−30.63	9.3	–	–	–	Mormyrids
Cyphomyrus cubangoensis	Mormyridae	–	–	–	1	−26	9.2	Mormyrids
Serranochromis macrocephalus	Cichlidae	16	−25.49 ± 2.21	10.35 ± 0.78	10	−25.56 ± 2.12	10.48 ± 1.33	Piscivores
Serranochromis robustus jallae	Cichlidae	3	−20.57 ± 0.65	9.37 ± 0.41	1	−21.59	9.37	Piscivores
Hepsetus cuvieri	Hepsetidae	11	−23.69 ± 1.99	9.91 ± 0.80	10	−24.61 ± 3.19	10.36 ± 1.32	Piscivores
Clarias gariepinus	Clariidae	5	−24.74 ± 2.36	9.88 ± 0.46	7	24.33 ± 1.62	10.04 ± 0.73	Piscivores
Oreochromis andersonii	Cichlidae	10*	−26.14 ± 4.09	6.34 ± 0.88	20*	−27.90 ± 1.97	7.73 ± 1.41	Tilapiine cichlids
Oreochromis macrochir	Cichlidae	12*	−22.46 ± 1.89	5.38 ± 0.68	14*	−24.49 ± 2.76	5.15 ± 0.90	Tilapiine cichlids
Coptodon rendalli	Cichlidae	18*	−21.92 ± 3.86	7.12 ± 0.98	10*	−25.75 ± 2.47	6.70 ± 1.14	Tilapiine cichlids
Tilapia sparrmanii	Cichlidae	16*	−24.55 ± 1.78	7.60 ± 1.38	18*	−26.95 ± 3.44	7.54 ± 1.35	Tilapiine cichlids
Tilapia ruweti	Cichlidae	2	−21.74 ± 1.08	8.18 ± 1.17	–	–	–	Tilapiine cichlids
Micropanchax johnstoni	Poeciliidae	11*	−26.20 ± 2.11	9.78 ± 0.50	6	−23.92 ± 1.00	8.34 ± 0.53	Topminnows
Micropanchax hutereaui	Poeciliidae	–	–	–	4	−22.06 ± 0.72	8.31 ± 0.38	Topminnows
INVERTEBRATES								
Aquatic insects	–	10	−28.32 ± 3.62	6.14 ± 2.79	24	−26.67 ± 2.40	5.95 ± 1.30	–
Decapods	–	10	−23.96 ± 0.94	7.22 ± 0.63	5	−25.43 ± 0.62	5.79 ± 0.21	–
Herbivorous zooplankton	–	3	−30.75 ± 0.97	6.08 ± 0.81	–	–	–	–
Predatory zooplankton	–	9	−30.16 ± 1.35	10.05 ± 0.68	2	−29.66 ± 0.08	9.89 ± 0.03	–
BASAL RESOURCES								
POM	–	17	−30.71 ± 1.63	4.02 ± 0.54	16	−29.62 ± 1.42	4.16 ± 0.87	–
Detritus	–	30	−17.68 ± 4.09	3.25 ± 1.14	–	–	–	–
Emergent plants**	–	–	–	–	15	−25.72 ± 1.28	2.46 ± 2.92	–
Submerged plants[†]	–	7	−21.47 ± 5.76	3.00 ± 2.82	25	−19.54 ± 3.62	0.93 ± 1.82	–
Filamentous algae[‡]	–	–	–	–	6	−23.20 ± 1.52	1.63 ± 0.43	–

**Indicate which fish species were included in the Bayesian mixing models (MixSIAR).*

***Emergent plants included Phragmites australis, Typha capensis, Nymphaea nouchali, Vossia cuspidate, and Ludwigia sp.*

[†] *Submerged plants included Potamogeton thunbergii, Potamogeton tiroides, Potamogeton schweinfurthii, Ceratophyllum demersum, Najas horrida, Lagarosiphon ilicifolius and Utricalaria sp.*

[‡] *Filamentous algae included Spirogyra sp. and Cladophora glomerta.*

taxonomic/feeding group, and the % of SEA_c overlap between groups (as fishes were more comprehensively sampled in 2011). The SEA_c and % overlap of individual species within important consumer groups were then calculated to elucidate interspecific trophic interactions and explore potential competition in the lacustrine fish community. The groups of species examined included the alestids, which have been a dominant component of the fish fauna in the lake since it filled, the tilapiine cichlids on which the fishery is based, generalist predators that include the highly abundant *Schilbe intermedius* (Schilbeidae), and piscivores which may influence community food web structure (van der Waal, 1985; Peel et al., 2015).

Stomach Content Analysis

To aid in interpreting the results of the stable isotope analyses, stomach contents were conducted the four most abundant, large piscivorous fish species in Lake Liambezi; *S. intermedius, Clarias gariepinus* (Clariidae), *Hepsetus cuvieri* (Hepsetidae), and *Serranochromis macrocephalus* (Cichlidae), which likely influenced food web structure *via* predation, and one small zooplanktivorous species, *Brycinus lateralis* (Alestidae), which was a major component of the Lake Liambezi fish fauna (Peel et al., 2015). Fish were sampled using standardized multifilament and baited longlines (see above). All fish caught were identified to species level according to Skelton (2001, 2016), measured to the nearest mm and weighed to the nearest gram. Samples of the piscivorous species were collected on five occasions between October 2013 and December 2014, and their stomach contents were examined in the field. *Brycinus lateralis* were sampled in February 2013, and preserved whole in the field in 10% buffered formalin. Stomach contents of *B. lateralis* were later examined under a dissecting microscope in the laboratory, identified to the lowest practical taxonomic level, counted and weighed to the nearest 0.1 gram after blotting dry. For *B. lateralis*, an indirect volumetric assessment of each food category was used (Booth and McKinlay, 2001), because food items could not be weighed with sufficient precision.

Dietary composition of the five study species was assessed by calculating the index of relative importance (IRI; Pinkas et al., 1971) of each prey item, as:

$$IRI = (\%N + \%W) \times \%FO,$$

where $\%N$ and $\%W$ are the number and weight of each prey item as a percentage of all prey, and $\%FO$ is the number of stomachs containing a specific prey item as a percentage of all sampled stomachs. For *B. lateralis* $\%V$, the volume of each prey item as a percentage of all prey, was used in place of $\%W$. The IRI for each prey item was then expressed as a percentage of the sum of IRI values for all prey items (%IRI).

RESULTS

Stable Isotope Analysis

Food Web Structure

In 2011, 424 samples were collected for stable isotope analysis, comprised of three basal carbon sources, four general invertebrate groups and 30 fish species (**Table 1**). In 2012, 318 samples were collected, comprising four basal carbon sources, three general invertebrate groups and 26 fish species. The $\delta^{13}C$ values of basal resources ranged between −33 and −9‰ in 2011, and between −32 and −13‰ in 2012 (**Table 1**; **Figure 2**). POM had the lowest $\delta^{13}C$ of all basal resources, averaging approximately −30‰ in both years. The $\delta^{13}C$ of emergent plants and filamentous algae, both of which were only collected in 2012, averaged −26 and −23‰, respectively. Submerged plants had average $\delta^{13}C$ values of −21 and −20‰ in 2011 and 2012, respectively. Detritus, which was only collected in 2011, was the most enriched with a $\delta^{13}C$ value of −18‰ but was not isotopically distinct from submerged plant samples, suggesting a substantial proportion of the detritus was of submerged plant origin. The $\delta^{15}N$ values of different basal resources sampled in 2011 were similar (∼3–4‰), but in 2012, plants and filamentous algae had much lower $\delta^{15}N$ values than POM. The isotope values of submerged plants (PERMANOVA; *Pseudo-F* = 2.04, $P = 0.145$) and POM (PERMANOVA; *Pseudo-F* = 3.51, $P = 0.053$) did not differ significantly between years. Note that although periphyton has been identified as one of the principal carbon sources supporting fish and invertebrate communities in floodplain ecosystems (Winemiller, 2004; Douglas et al., 2005), periphyton isotope data was not available for this study. However, as the isotopic values of macrophytes and associated periphyton (e.g., Neill and Cornwell, 1992; de Kluijver et al., 2015; Pettit et al., 2016) are often indistinguishable, for the purposes of interpretation, macrophytes and periphyton are considered together.

Overall, mixing model results for primary and secondary fish consumers showed that 58% of modeled fish species in 2011 and 87.5% in 2012 had substantial dietary POM contributions of >15%. In 2011 83% of fish species also had strong dietary contributions (>12.5%) of submerged plants. Briefly; topminnows and alestids relied almost exclusively on zooplankton and aquatic invertebrates in both years, *Coptodon rendalli* relied primarily on detritus and submerged plants in 2011 and decapods, POM and filamentous algae in 2012; mormyrids (data only available for 2011) were strongly opportunistic, feeding on a variety of sources including, aquatic invertebrates, zooplankton, POM, and submerged plants; tilapiine cichlids depended on submerged plants, POM and in some case zooplankton and aquatic invertebrates in 2011, vs. POM, zooplankton and filamentous algae in 2012; and benthic cichlids preferred POM, zooplankton in both years, as well as submerged plants and detritus in 2011 (**Figures 3**, **4**, **Supplementary Table 2**). The low contribution values of any food source to *Tilapia sparrmanii* diet in 2012 suggests some basal resources may have been missed.

Both 2011 and 2012 data suggest that POM was the ultimate driver of the Lake Liambezi food web (either directly or indirectly), with three potential energy pathways by which basal resources were assimilated into the food web. Firstly, in 2011, the isotopic position of herbivorous zooplankton indicated that their diets likely consisted exclusively of POM. Secondly, aquatic invertebrates (including decapods in 2012) were similarly positioned, but demonstrated more variable $\delta^{13}C$

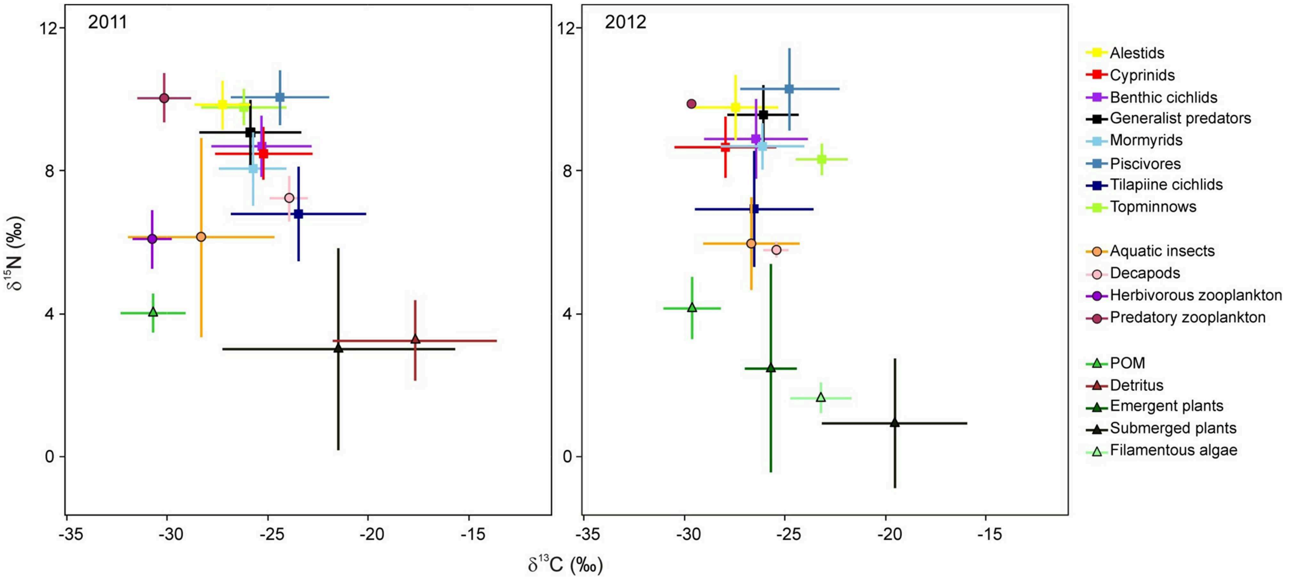

FIGURE 2 | Stable δ^{13}C-δ^{15}N isotopic bi-plots of fish groups and their potential food sources from Lake Liambezi in 2011 and 2012. Data points represent the mean ± standard deviation for each group.

values, indicating that while this diverse group relies primarily on POM, they likely also assimilate carbon from a range of other basal resources, including emergent plants and potentially their associated detritus and/or periphyton. The aquatic invertebrate group consisted mainly of benthic organisms, so their main source of POM likely settled out of the water column, possibly in the form of planktonic detritus (e.g., sinking phytoplankton). Thirdly, the relatively depleted values of δ^{15}N and slightly enriched δ^{13}C values (in 2012 only) of tilapiine cichlids relative to other fish species, suggest that although POM was a substantial contributor to tilapiine cichlid diet, considerable amounts of their dietary carbon were also derived from aquatic plants and detritus/periphyton compared to other consumers (**Figure 2**). However, as only *Coptodon rendalli* feed directly on macrophytes, this carbon was likely incorporated as detritus. As degradation does not often effect isotopic change in macrophytes (Macko and Estep, 1984; Currin et al., 1995; Fellerhoff et al., 2003; Hill and McQuaid, 2009), it is likely the sampled detritus was of submerged plant origin. All three of these primary consumers (herbivorous zooplankton; aquatic invertebrates/decapods and tilapiine cichlids) were regular dietary components for other fish species (**Table 2**).

The average δ^{13}C of tilapiine cichlids showed a 3‰ depletion in 2012, possibly indicating a shift to a more POM based diet. Further sampling of the tilapiine cichlids was carried out in 2014 to establish whether the shift to a lower δ^{13}C diet was permanent. δ^{13}C values did not differ significantly between years for *O. andersonii* (PERMANOVA; *Pseudo-F* = 1.53, *P* = 0.233) or *O. macrochir* (PERMANOVA; *Pseudo-F* = 2.33, *P* = 0.113). However, δ^{13}C values differed significantly between years for *C. rendalli* (PERMANOVA; *Pseudo-F* = 8.48, *P* = 0.001) and *T. sparrmanii* (PERMANOVA; *Pseudo-F* = 4.69, *P* = 0.015), with δ^{13}C significantly lower in 2012 compared to 2011 and 2014. Two other groups of fishes showed changes in trophic position between years; cyprinids showed a depletion in δ^{13}C, and topminnows an enrichment in δ^{13}C coupled with decrease in δ^{15}N between 2011 and 2012, however as minor components of the fish community, they were unlikely to alter major pathways of energy flow through the food web and were thus not investigated further. Community-wide stable isotope metrics were subsequently used to quantitatively assess the similarity of fish communities between years.

Community Metrics

The NR and CR of the fish community in 2012 were higher than in 2011, suggesting that both the trophic length and range of basal resources used by the fish community in 2012 was greater. However, the average degree of trophic diversity (CD), was similar between years. Lower MNND and SDNND in 2011 indicate greater density and evenness of species packing in bi-plot space (**Table 3**). For each metric, the difference between years was relatively small, and the overlap of 95% confidence intervals was substantial. The core isotopic niche area (SEA_c) of the whole fish community (**Figure 5A**) was slightly larger in 2012 compared to 2011, corroborating results of the other metrics. The degree of overlap between years was also significant; the 2011 fish community SEA_c overlapped with the 2012 fish community SEA_c by 68.3%, whereas the 2012 SEA_c overlapped with the 2011 SEA_c by an even greater 76.8%. Overall, the tropic structure of the fish communities sampled in 2011 and 2012 were thus very similar, however, the inter-annual variations in trophic positions of the tilapiine cichlids, cyprinids and topminnows precluded the combination of both datasets. As a result, further analyses on the fish community interactions were based only on the more comprehensive 2011 dataset.

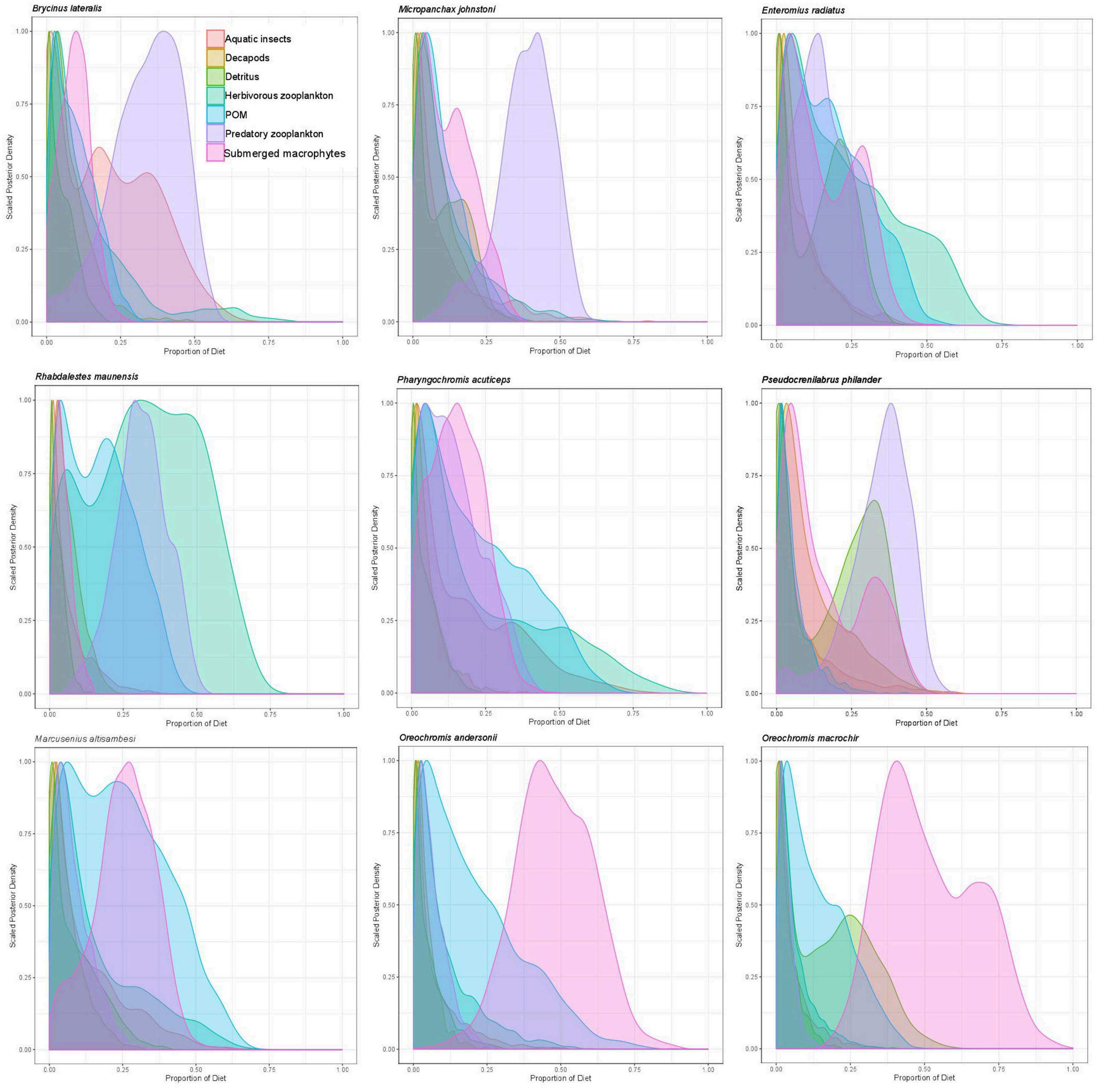

FIGURE 3 | Proportional resource contributions to primary and secondary fish consumers as determined by Bayesian MixSIAR mixing models for 2011.

Trophic Structure and Species Interactions

Tilapiine cichlids, despite being the backbone of the Lake Liambezi gill net fishery, made up only 4% of the CPUE (kg net^{-1} night^{-1}) (**Supplementary Table 1**). They occupied the lowest trophic position in the overall fish community and did not show much SEA$_c$ overlap with other groups, indicating that they are the only primary consumers in the fish community. Their SEA$_c$ was large, suggesting higher trophic diversity compared to other groups. At the next trophic level there was considerable overlap in isotopic space between cyprinids, benthic cichlids, mormyrids and generalist predators, all of which had similar sized SEA$_c$. These four groups were most likely primarily dependent upon aquatic invertebrates for their food. Alestids and topminnows occupied a slightly higher trophic level, with considerable SEA$_c$ overlap between the two groups. Alestids had the smallest SEA$_c$ of any group, indicative of dietary specialization. Their elevated trophic position and relatively low δ^{13}C reflects a diet composed of both herbivorous and predatory zooplankton. Piscivores occupied the highest trophic level in Lake Liambezi and overlapped relatively little with other groups (**Figure 5B**;

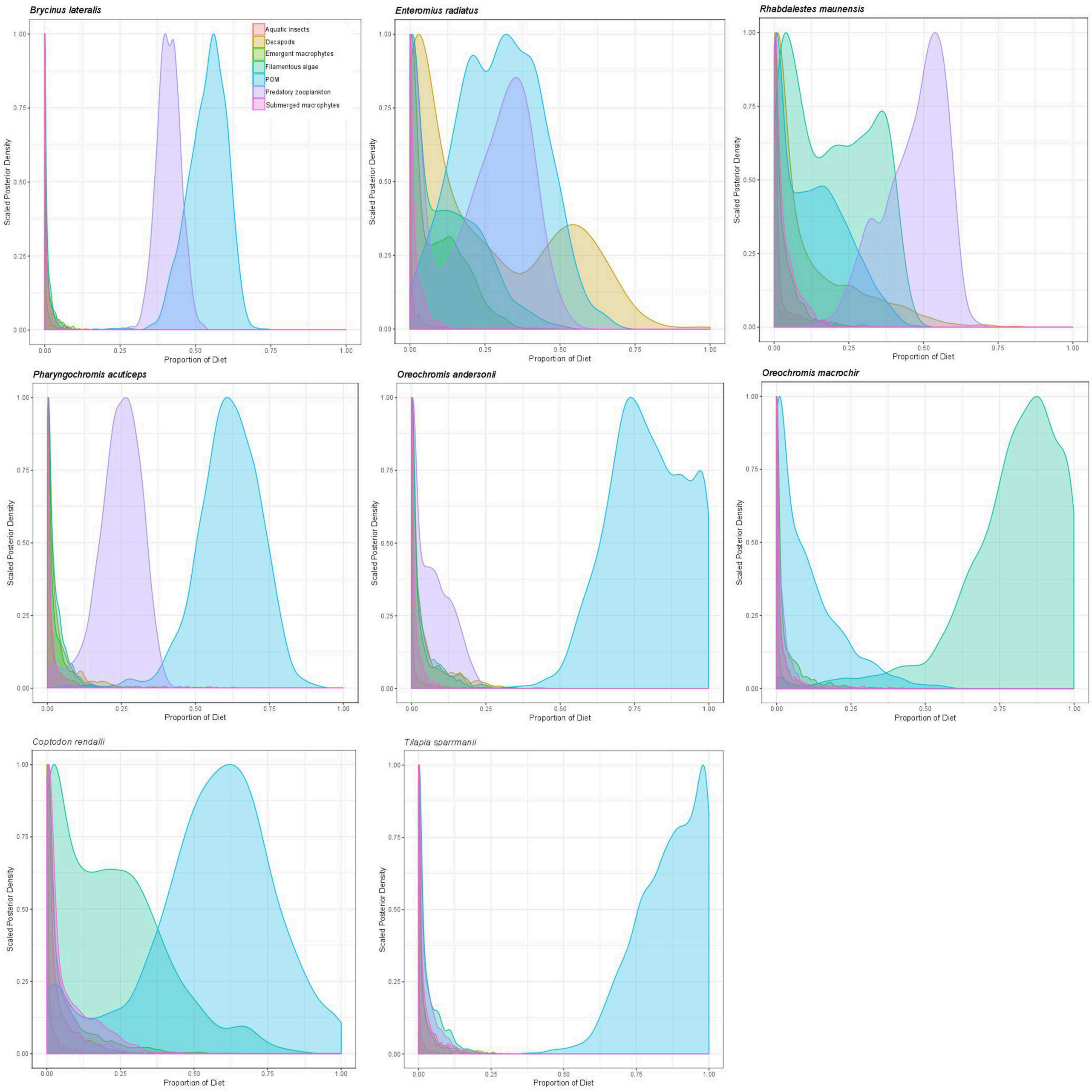

FIGURE 4 | Proportional resource contributions to primary and secondary fish consumers as determined by Bayesian MixSIAR mixing models for 2012.

Table 4). The trophic positions of individual fish species within important consumer groups were examined further to elucidate interspecific trophic interactions.

The trophic level of the alestids *B. lateralis* and *Rhabdalestes maunensis* was similar to that of the piscivores in Lake Liambezi. *Brycinus lateralis*, the larger of the two alestids, had a SEAc of 3.36‰^{2}. *Rhabdalestes maunensis* had a significantly smaller SEAc of 1.24‰^{2}, 48.9% of which was overlapped by *B. lateralis.* In contrast, only 18.1% of the core niche of *B. lateralis* was overlapped by *R. maunensis* (**Figure 5C**).

Of the four tilapiine cichlids, *O. macrochir* had the smallest SEAc and lowest trophic position, indicating this species was a highly specialized primary consumer (**Figure 5D**). The much larger isotopic niche of *O. andersonii* overlapped with that of *O. macrochir* by approximately one third (**Table 5**). *Oreochromis andersonii* generally had a lower δ^{13}C and higher δ^{15}N than *O. macrochir*. *Coptodon rendalli* had the largest SEAc of the four species, perhaps reflective of the extremely variable isotope values of submerged plants. *Coptodon rendalli* occupied a higher trophic level than both *Oreochromis* spp. and did not overlap

TABLE 2 | Stomach contents of fish species (no. of stomachs; % empty) and their length, by % number (*%N*), % weight (*%W*) and % frequency of occurrence (*%FO*), and the % index of relative importance (*%IRI*) of each prey category.

Species and prey category	TL/FL (mm)	*n*	ID	*%N*	*%W*	*%FO*	*%IRI*
Clarias gariepinus (63 stomachs; 75% empty)	434–1,220 TL	16					
Fish			Fish remains	23.53	8.27	6.35	5.50
			Cichlidae	76.47	91.73	20.63	94.50
Hepsetus cuvieri (125 stomachs; 72% empty)	195–386 TL	35					
Fish			Fish remains	26.32	8.22	8.00	7.91
			Cichlidae	71.05	89.66	20.00	91.98
			Alestidae	2.63	2.12	0.80	0.11
Serranochromis macrocephalus (72 stomachs; 81% empty)	120–302 TL	14					
Fish			Fish remains	35.29	30.00	8.11	40.48
			Cichlidae	17.65	13.79	4.05	9.75
			Alestidae	41.18	53.45	6.76	48.88
Aquatic invertebrates			Insect remains	5.88	2.76	1.35	0.89
Schilbe intermedius (241 stomachs; 43% empty)	90–273 FL	137					
Fish			Fish remains	9.73	10.45	15.35	12.54
			Cichlidae	13.57	69.36	19.09	64.08
			Alestidae	1.36	10.83	2.07	1.02
			Cyprinodontidae	0.45	0.24	0.41	0.01
Aquatic invertebrates			Insect remains	8.60	1.89	15.77	6.69
			Ephemeroptera	36.20	4.83	7.47	12.41
			Trichoptera	0.23	0.03	0.41	0.00
			Coleoptera	0.23	0.00	0.41	0.00
			Hemiptera	0.23	0.00	0.41	0.00
			Odonata	0.90	0.24	1.66	0.08
			Diptera	19.68	0.86	3.32	2.76
			Decapoda	1.13	0.37	1.24	0.08
			Gastropoda	0.23	0.02	0.41	0.00
Terrestrial invertebrates			Lepidoptera	0.23	0.07	0.41	0.00
			Orthoptera	0.90	0.29	1.66	0.08
			Araneae	0.23	0.03	0.41	0.00
			Insect eggs	5.66	0.17	0.83	0.20
			Detritus	0.45	0.31	0.83	0.03
Brycinus lateralis (29 stomachs; 23% empty)	24–127 FL	30			*%V*		
Fish			Fish remains	4.19	20.05	20.51	7.88
Aquatic invertebrates			Insect remains	9.95	27.11	46.15	27.09
			Ephemeroptera	2.62	4.33	7.69	0.85
			Trichoptera	2.09	4.10	7.69	0.75
			Odonata	0.52	1.67	2.56	0.09
			Diptera	53.93	18.73	41.03	47.22
			Zooplankton	18.85	0.75	25.64	7.96
			Insect eggs	4.71	12.99	23.08	6.47
			Plant matter	1.05	4.93	5.13	0.49

Note for Brycinus lateralis, % volume (%V) replaces %W.

with either. It did, however, overlap with *T. sparrmanii* which had a slightly smaller and more laterally compressed SEAc, suggesting a narrower range of basal resources, but large variation in trophic level.

The core niche areas of piscivores and generalist predators were examined together (**Figure 5E**), with the two most abundant generalist predators, *S. intermedius* and *Clarias ngamensis* occupying a lower trophic level than the top piscivores. *Schilbe intermedius* had the larger SEAc of the two species, which overlapped considerably with that of *C. ngamensis* (**Table 5**). There was also extensive SEAc overlap among the three piscivores. Half the SEAc of *H. cuvieri*, and two thirds the SEAc of *C. gariepinus* were overlapped by *S. macrocephalus*. *Serranochromis macrocephalus* had a similarly large SEAc size to that of *S. intermedius*. The large isotopic niche of *S. macrocephalus* revealed by stable isotope analysis is contrary to the dietary specialization inferred from stomach contents analysis. However, the smaller SEAc of *H. cuvieri* and *C. gariepinus* appear to confirm that they are relatively specialized piscivores. For both *H. cuvieri* and *C. gariepinus*, δ^{15}N tended to decrease with increasing δ^{13}C.

TABLE 3 | Stable isotope community metrics (mean with 95% CI in parentheses) comparing the trophic structure of fish communities sampled from Lake Liambezi in 2011 and 2012.

Metric	2011	2012
NR	5.03 (4.43–5.66)	5.67 (4.84–6.74)
CR	6.95 (5.59–8.89)	7.95 (6.72–9.49)
CD	2.12 (1.88–2.38)	2.05 (1.83–2.28)
MNND	0.87 (0.67–1.08)	0.98 (0.80–1.18)
SDNND	0.54 (0.33–0.79)	0.79 (0.53–1.06)
SEA_C	11.93 (10.07–14.15)	13.42 (11.89–15.23)
Sample size (*n*)	259	212

NR, δ^{15}N range; CR, δ^{13}C range; CD, mean distance to centroid; MNND, mean nearest neighbor distance; SDNND, standard deviation of nearest neighbor distance; SEA_C, core isotopic niche area of the community (‰^{2}).

Stomach Contents Analysis

Clarias gariepinus and *H. cuvieri* gut contents comprised exclusively fish, while *S. macrocephalus* also preyed on aquatic invertebrates (**Table 2**). Cichlidae were the only fish identified in the stomachs of *C. gariepinus*. In addition to cichlids, alestids were among the prey of *H. cuvieri* and *S. macrocephalus*. Cichlidae constituted the bulk of *H. cuvieri* prey, while alestids were more important to *S. macrocephalus*. The most frequently identified cichlid prey species were *Tilapia sparrmanii* and *Pharyngochromis acuticeps* but *Oreochromis* spp. also contributed substantially to the diet of *C. gariepinus*.

A diverse range of prey were recorded from full stomachs of *S. intermedius*, including fish, aquatic and terrestrial invertebrates, insect eggs, and detritus (**Table 2**). Fish, cichlids in particular, were the most important food source for *S. intermedius* in Lake Liambezi, with the most commonly identified cichlid species being *T. sparrmanii* and *P. acuticeps*. Ephemeroptera were the only insect order to contribute substantially to the diet of *S. intermedius*.

Identifiable items in full stomachs of *B. lateralis* included fish, aquatic invertebrates, insect eggs and plant matter (**Table 2**). A large portion of the aquatic invertebrate prey were masticated and could not be identified further. Dipteran larvae, primarily *Chaobrus* spp., were the most important prey item identified, accounting for nearly half of the diet of *B. lateralis*. Planktonic

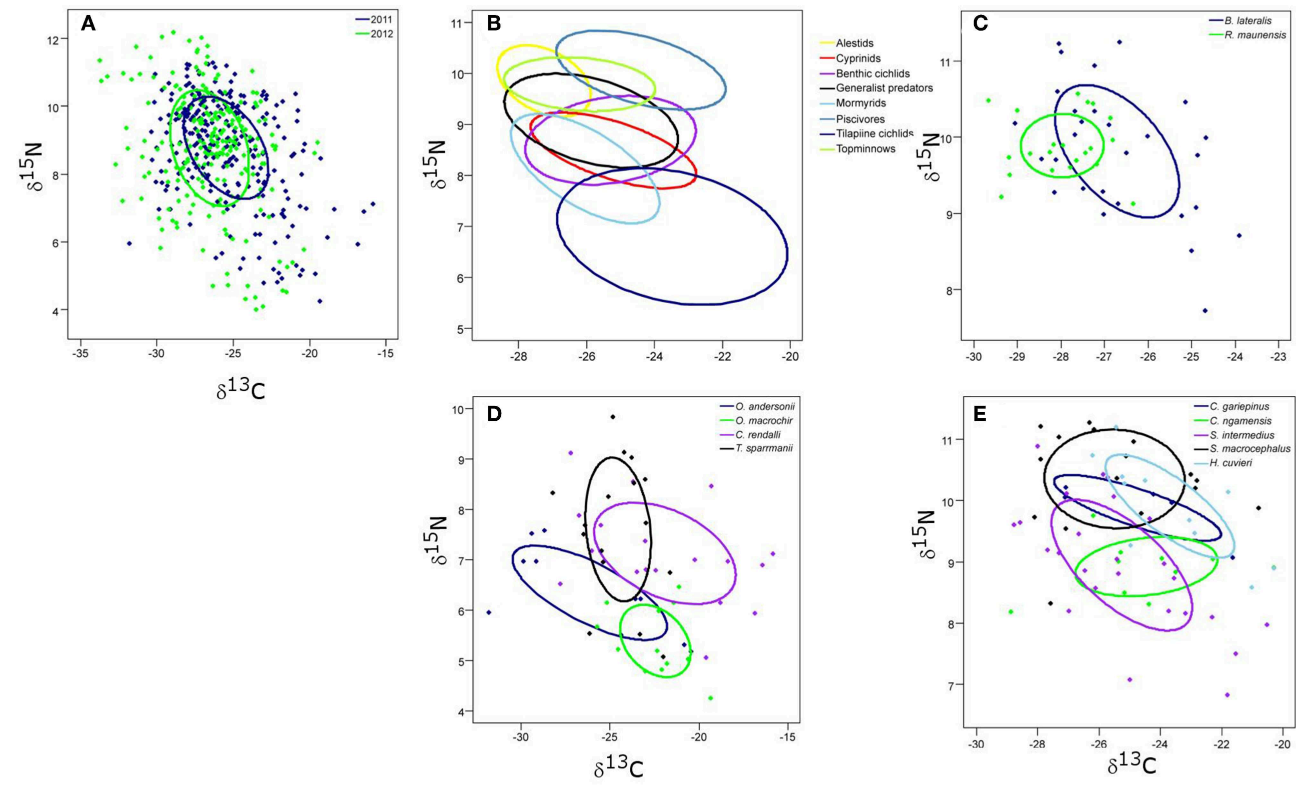

FIGURE 5 | The core isotopic niche areas (SEAc) of **(A)** 2011 and 2012 complete fish communities; **(B)** all fish groups; **(C)** alestid species; **(D)** the four tilapiine cichlid species; and **(E)** the predatory fish species in Lake Liambezi in 2011.

TABLE 4 | The core isotopic niche area (SEAc) and percent overlap between fish groups in Lake Liambezi in 2011.

	SEAc	Alestids	Cyprinids	Benthic cichlids	Generalist predators	Mormyrids	Piscivores	Tilapiine cichlids	Topminnows
Alestids	2.80		1.2	2.3	23.1	0.0	3.2	0.0	53.8
Cyprinids	4.47	1.9		55.1	45.5	41.9	0.0	5.6	0.0
Benthic cichlids	6.69	5.6	82.5		66.4	54.7	4.7	2.8	13.0
Generalist predators	6.78	56.0	69.0	67.2		34.1	8.2	0.0	55.7
Mormyrids	5.71	0.1	53.6	46.7	28.8		0.0	15.7	0.0
Piscivores	5.31	6.0	0.0	3.7	6.4	0.0		0.0	40.2
Tilapiine cichlids	13.77	0.0	17.3	5.9	0.0	37.8	0.0		0.0
Topminnows	3.64	70.0	0.0	7.1	29.9	0.0	27.5	0.0	

Columns indicate the group niche area being overlapped, e.g., 82.5% of the cyprinids niche is overlapped by benthic cichlids, while 55.1% of the benthic cichlids niche is overlapped by cyprinids.

TABLE 5 | The core isotopic niche area (SEAc) and percent overlap between (A) tilapiine cichlid species and (B) predatory fish species in Lake Liambezi in 2011.

(A)	**SEAc**	***O. andersonii***	***O. macrochir***	***C. rendalli***	***T. sparrmanii***
O. andersonii	8.9		35.7	0.1	12.0
O. macrochir	4.2	16.9		0.0	0.0
C. rendalli	11.4	0.1	0.0		49.6
T. sparrmanii	8.1	10.9	0.0	35.3	

(B)	**SEAc**	***C. gariepinus***	***C. ngamensis.***	***S. intermedius.***	***S. macrocephalus***	***H. cuvieri***
C. gariepinus	2.73		0.0	3.7	31.7	42.7
C. ngamensis	3.41	0.1		42.2	0.0	6.1
S. intermedius	5.83	7.9	72.1		11.6	0.0
S. macrocephalus.	5.77	67.0	0.0	11.5		50.3
H. cuvieri.	3.55	55.7	6.4	0.0	31.0	

crustacea and fish had similar contributions, followed by insect eggs.

DISCUSSION

Primary Production Sources Supporting Fishes

Stable isotopic values of POM indicated that it was composed primarily of freshwater phytoplankton (see Cloern et al., 2002; O'Reilly et al., 2002; Harding and Hart, 2013; Morana et al., 2015) and was clearly the primary carbon source supporting consumer biomass in Lake Liambezi, however substantial contributions from aquatic macrophytes (including associated detritus and periphyton), the most conspicuous source of primary production in the lake, were also present. This highlights the importance of algal (here phytoplankton and/or periphyton) carbon in aquatic food webs, even when aquatic macrophytes are the dominant primary producers (Araujo-Lima et al., 1986; Forsberg et al., 1993; Lewis et al., 2001; Herwig et al., 2004). Terrestrial C_3 macrophytes can also be important carbon sources in aquatic food webs (e.g., Berggren et al., 2014), particularly when algal growth is light limited (Zeug and Winemiller, 2008; Roach and Winemiller, 2015). However, the probability of a substantial contribution of terrestrial carbon in Lake Liambezi, except during the filling phase, was deemed small due to the large surface area of the lake relative to its circumference, and because benthic fish are not restricted to nearshore areas that would receive greater terrestrial carbon inputs. This differs considerably from riverine food webs which in this region are supported mainly by riparian vegetation from the floodplains and detritus from aquatic macrophytes (Taylor et al., 2017b).

Trophic Pathways

Carbon from phytoplankton and aquatic macrophytes was assimilated into the food web via three major pathways, one pelagic and two benthic. These are summarized visually in **Figure 6**.

In the pelagic food web phytoplankton was assimilated directly by herbivorous zooplankton, such as calanoid copepods (Grosbois et al., 2017b) or cladocerans (e.g., *Bosmina longirostis*, Seaman et al., 1978) that are preyed upon by larger zooplankton, such as cyclopoid copepods and chaoborid larvae, as well as small zooplanktivorous fishes that include the poecilid *Micropanchax johnstonii* and the alestids *B. lateralis* and *R. maunensis*. Stomach content analysis showed that zooplankton and Diptera larvae (aquatic invertebrates) made up a large portion of the diet of *B. lateralis*, yet while isotope data generally supported these observations, the $\delta^{15}N$ values revealed that *B. lateralis* and zooplankton occupied the same trophic level. This may be

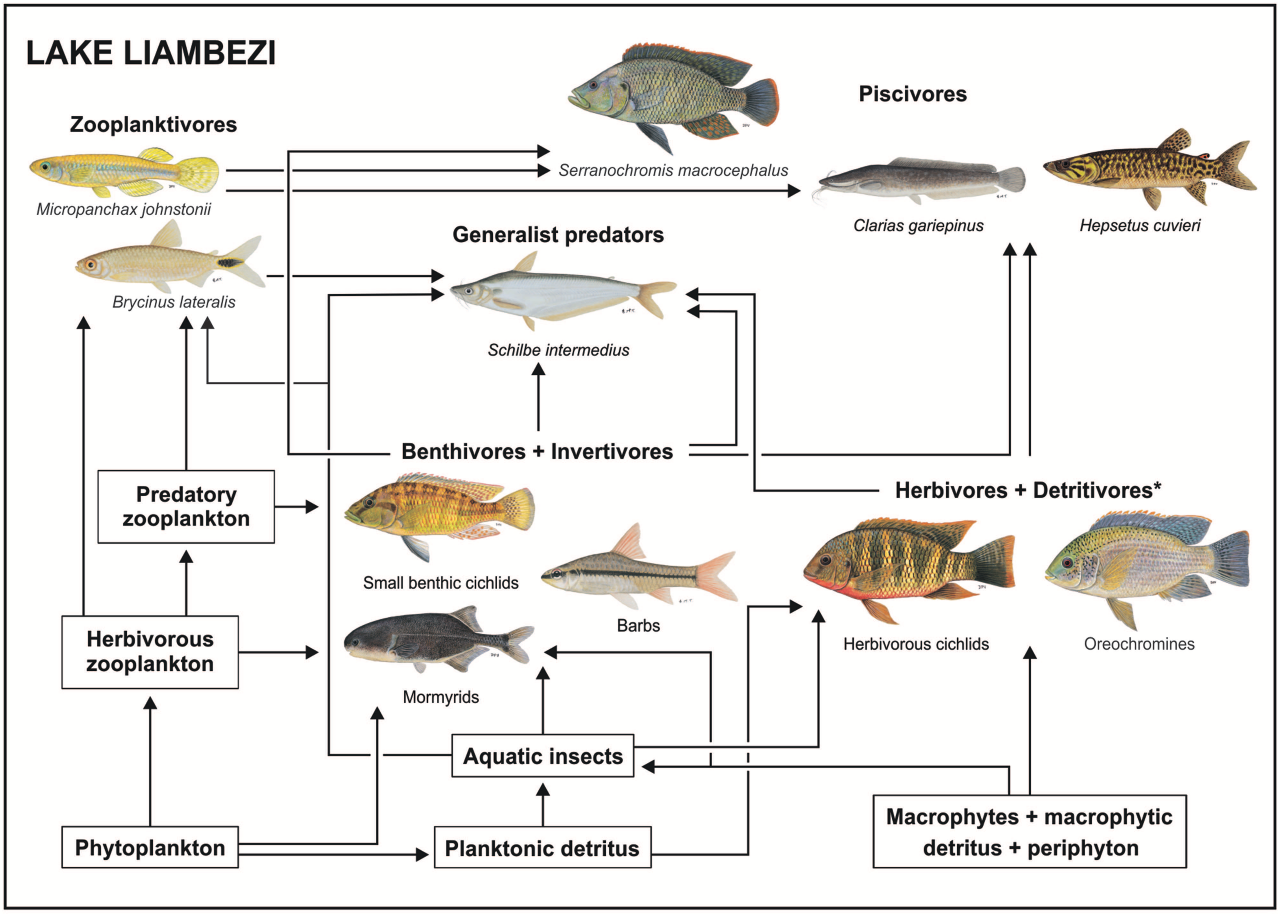

FIGURE 6 | Conceptual diagram of the food web in Lake Liambezi, illustrating the flow of energy through three major food chains, and their integration by generalist predators and piscivores in the mature lacustrine fish community. *Herbivores and detritivores incorporate all the tilapiine cichlids. All fish images are ©NRF-SAIAB.

due to several factors including different tissue turnover rates among species, variable δ^{15}N values among sampling periods, and seasonal variation in the abundance of zooplankton and dipteran larvae and/or their importance in the diet of *B. lateralis,* as seasonal variation in diet is well-documented for *Brycinus* species (e.g., Booth and McKinlay, 2001).

Thus, the second major pathway by which basal carbon was assimilated into the food web was via aquatic invertebrates that feed primarily on detritus of planktonic origin or potentially on emergent macrophytes and associated macrophytic detritus and/or periphyton. Among the most important aquatic invertebrates in Lake Liambezi are diptera larvae, ephemeroptera, trichoptera, and odonata nymphs (Seaman et al., 1978). These support benthic invertivorous mormyrids, cichlids, barbs, and to a lesser degree, generalist predators, such as *S. intermedius*. The mormyrids *Petrocephalus* cf. *okavangensis* and *Marcusenius altisambesi* are some of the most specialized insectivorous fishes in Lake Liambezi and feed primarily on the dominant aquatic insect groups mentioned above (van der Waal, 1985; Winemiller and Adite, 1997), but also showed a reliance on POM and submerged plants in the mixing models. The benthic invertivore cichlid group comprised four species, the small sized *P. acuticeps* and *Pseudocrenilabrus philander*, and two medium sized *Sargochromis* species. The diets of these cichlids were more diverse and flexible than those of the mormyrids (van der Waal, 1985; Winemiller, 1991; Zengeya and Marshall, 2007), incorporating substantial contributions from all available food resources. As members of this group are important prey species of the top piscivores (**Table 2**), they play an important role in moving energy up the food web.

The third major pathway involves the tilapiine cichlids which include *O. andersonii*, *O. macrochir, T. sparrmanii* and *C. rendalli*. This group occupies the lowest trophic level of all the fish in the lake, indicating that they were largely primary consumers. The isotopic positioning of the tilapiine cichlids indicated reliance on POM (particularly in 2012) as well as on submerged (in 2011) and emergent plants (2012) and/or detritus. *Coptodon rendalli* is regarded as being a specialized macrophyte feeder (van der Waal, 1985; Winemiller and Kelso-Winemiller, 2003) which is consistent with the relatively high average δ^{13}C values and supports the mixing model which showed a reliance on submerged plants, filamentous algae, detritus and

POM. *Tilapia sparrmanii* incorporated large contributions of POM into its diet, along with smaller amounts of zooplankton, aquatic invertebrates and submerged plants. In 2011, the isotopic niche of *T. sparrmanii* overlapped with that of *C. rendalli* by approximately one third, supporting mixing model results and previous dietary observations that *T. sparrmanii* consume a small amount of aquatic macrophytes (van der Waal, 1985; Winemiller and Kelso-Winemiller, 2003; Zengeya and Marshall, 2007). The higher average δ^{15}N value over other tilapiine cichlids suggests that *T. sparrmanii* is likely more omnivorous, feeding at multiple trophic levels, which is supported by van der Waal (1985) who recorded a variety of aquatic and terrestrial invertebrates, fish remains and zooplankton in the diet of *T. sparrmanii* in the lake. Data from 2011 also showed that the larger *Oreochromis* species had lower δ^{15}N values, and shared little isotopic niche space with *C. rendalli* and *T. sparrmanii, whereas Oreochromis andersonii* had a similarly wide δ^{13}C range to that of *C. rendalli* but was on average 4‰ more depleted. Mixing models suggested a reliance on POM in both years, as well as submerged macrophytes in 2011. *Oreochromis andersonii* with lower δ^{13}C values were probably more reliant on algal carbon sources, while those with higher δ^{13}C values probably consumed more detritus derived from the abundant aquatic macrophytes, demonstrating some degree of individual specialization (Gu et al., 1997; Benhaïm et al., 2017). In contrast, *O. macrochir* occupied a small isotopic niche, and a lower trophic position than *O. andersonii,* although mixing models suggested they also fed on POM, detritus and submerged plants (2011) as well as POM and filamentous algae (2012). The low levels of dietary overlap support observations by van der Waal (1985) who identified algae and zooplankton as the most important food sources for *O. andersonii* and fine detritus as the main food source for *O. macrochir*. Of note is that the tilapiine cichlids, despite being the backbone of the Lake Liambezi fishery, accounted for a minimal proportion of this study's CPUE. This is likely indicative of strong fishing pressure in Lake Liambezi, where subsistence fishers are capable of removing substantial biomass (i.e., 27 00 t/year in 2011–2012; Peel et al., 2015).

Integrating Trophic Pathways

While the three trophic pathways discussed above are by no means discrete (fishes may forage across pelagic and benthic food chains), predators occupying the highest trophic levels fully integrate all pathways (Vander Zanden and Vadeboncoeur, 2002). The dominant predator in Lake Liambezi in terms of biomass was *S. intermedius* (**Supplementary Table 1**; Peel et al., 2015, 2019), a generalist predator, which consumed a wide variety of prey items including fish, aquatic and terrestrial invertebrates, decapods and gastropods. The broad, but fish-dominated diet of *S. intermedius* observed during the present study was consistent with previous observations from Lake Liambezi (van der Waal, 1985) and with dietary (Merron and Mann, 1995; Winemiller and Kelso-Winemiller, 1996) and trophic (Taylor et al., 2017b) assessments in neighboring rivers. *Schilbe intermedius* shared a significant amount of isotopic niche space with *C. ngamensis*, which also feeds on a wide variety of fish, insects, molluscs, and decapods (Willoughby and Tweddle, 1978; van der Waal, 1985; Winemiller and Kelso-Winemiller, 1996). These two species occupied a lower trophic position than the top predators, overlapping more with benthic cichlids, cyprinids and mormyrids.

Stomach contents and stable isotope analysis revealed a significant level of dietary overlap among the three piscivores *C. gariepinus*, *H. cuvieri* and *S. macrocephalus*. *Clarias gariepinus* and *H. cuvieri* fed almost exclusively on cichlids, while *S. macrocephalus* fed predominantly on alestids. Although *C. gariepinus* is known to have a broad omnivorous diet (Willoughby and Tweddle, 1978; Bruton, 1979; van der Waal, 1985; Winemiller and Kelso-Winemiller, 1996), they often specialize on a fish prey (Merron, 1993; Weyl et al., 2016). Stable isotope analysis provided strong support for the high contribution of both benthic and tilapiine cichlids to the diets of *C. gariepinus* and *H. cuvieri*, and clearly illustrated how these species integrated the two benthic trophic pathways described above. Variation in trophic position of individual *C. gariepinus* and *H. cuvieri* suggests some degree of specialization. Individuals with depleted δ^{13}C values had high trophic positions, reflecting the greater number of trophic transfers involved in obtaining energy from omnivorous and insectivorous benthic cichlids. Individuals with enriched δ^{13}C values had lower trophic positions, as fewer trophic transfers were involved in obtaining energy from the detritivorous and herbivorous tilapiine cichlids. *Serranochromis macrocephalus* were, on average, slightly more enriched in δ^{15}N and depleted in δ^{13}C compared to *C. gariepinus* and *H. cuvieri*, as they fed more evenly across all three trophic pathways indicating a more diverse diet than the alestid-dominated gut content analysis would suggest. As a result, *B. lateralis* the most abundant species in the lake (Peel et al., 2015), appears relatively poorly utilized as a prey resource and its occupation of the pelagic food web may be facilitated by predator release.

The use of the pelagic food chain, even if on a small scale, by *B. lateralis* may well have been facilitated by the absence of *Hydrocynus vittatus*, a large pursuit predator, from the lake (Peel et al., 2015). Where it occurs, *H. vittatus* exerts top-down control on fish communities, restricting smaller fishes to shallow littoral refugia and to macrophyte beds (Jackson, 1961). Comparing the food web of Lake Liambezi with that developed by Taylor et al. (2017b) for the upper Zambezi River demonstrates this idea (**Figure 7**). While the Zambezi River fish community is richer because it includes several species that were unable to colonize Lake Liambezi, zooplanktivory is only represented by *M. johnstonii*, a small poecilid that is strongly associated with aquatic vegetation (Skelton, 2001). In the Zambezi River *B. lateralis* occupies a benthic insectivore niche (**Figure 7**). This is different to Lake Liambezi, where we propose that, in the absence of *H. vittatus* resulted in predation release which facilitated the use of pelagic space by *B. lateralis* allowing it to make use of an unexploited niche and exit the more competitive food chain driven by benthic invertebrates.

In summary, the investigations into trophic and food web structure supports the hypothesis that phytoplankton production supports a high amount of consumer biomass in Lake Liambezi, however substantial contributions by periphyton/emergent plants are also likely. These results add to the large body of evidence highlighting the importance of algal production

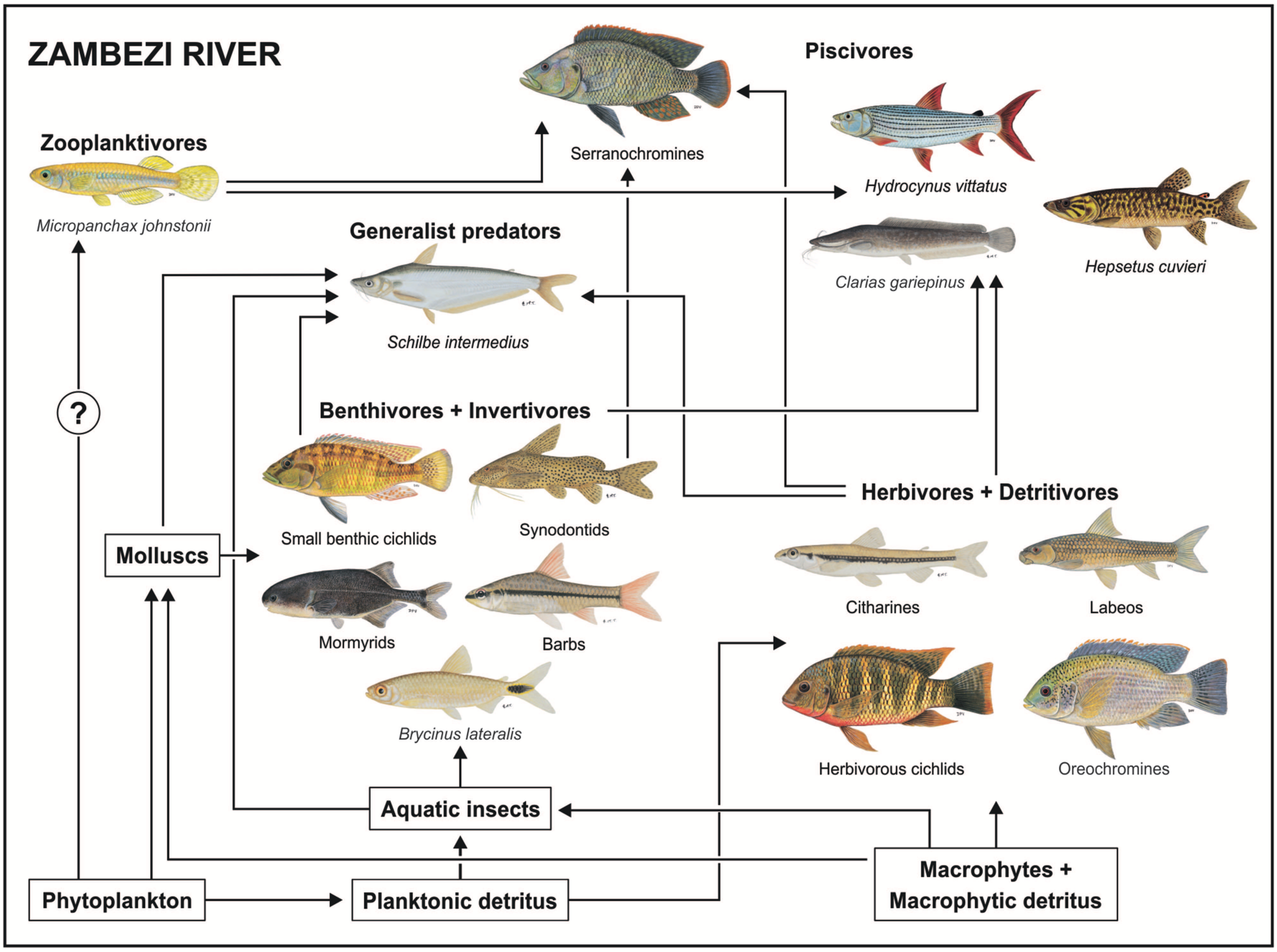

FIGURE 7 | Conceptual diagram of the food web in the Zambezi River as described by Taylor et al. (2017b), illustrating the flow of energy through three major food chains, and their integration by generalist predators and piscivores in the riverine fish community. All fish images are ©NRF-SAIAB.

sources to fishes, even where macrophytes appear to be the dominant source of primary production (Winemiller, 2004; Douglas et al., 2005). Submerged and emergent macrophytes (including associated detritus and potentially periphyton) do however, contribute to the assimilated diets of the tilapiine cichlids, which are the mainstay of the commercial gillnet fishery on the lake (Peel et al., 2015). Of the three major food chains, the phytoplankton based pelagic food chain was longest. The benthic food chain based on detritus of planktonic origin was characterized by high levels of omnivory and the macrophytic detritus-based food chain was shortest. Predators fed across all three food chains, but more so on the two benthic food chains. A combination of dietary overlap, dietary specialization, the integration of multiple food chains and the behavioral adaptation to changing dietary resources, underpins the ability of Lake Liambezi's fish community to thrive under the stochastic nature of ephemeral ecosystems. Unfortunately, the development of a substantial subsistence tilapiine fishery on Lake Liambezi (Peel et al., 2015, 2019) combined with the recession of lake water after 2014 resulted in the collapse of the cichlid fishery in 2016 (Peel et al., 2019; Tweddle, personal observation). The management of Lake Liambezi during its next cycle of inundation should likely focus on monitoring size and abundance of fish species involved in the longer phytoplankton based pelagic food chain, as its length and complexity would contribute to ecosystem stability. Management of catch quotas and acceptable fishing gears may also be needed in future to prevent fishery collapse (and its knock-on economic effects on subsistence livelihoods, see Simasiku et al., 2017) before the start of the subsequent drying cycle.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by South African Institute for Aquatic Biodiversity Animal Ethics Committee.

AUTHOR CONTRIBUTIONS

RP and OW: ideas, data collection, analysis, manuscript preparation, and funding. JH: ideas, analysis, and manuscript preparation. GT: ideas, data collection, and analysis.

FUNDING

This research collaboration was facilitated by a South African–Namibia Research Partnership Programme Grant (National Research Foundation NRF Grant No.: UID 74015). Fieldwork was funded through the Namibia Nature Foundation (NNF) managed Integrated Community-Based Ecosystem Management (ICEMA) Project, the Nedbank Namibia Go-Green Fund, the Southern African Science Service Center for Climate Change and Adaptive Land Management (SASSCAL), NNF/WWF Zambezi/Chobe Fisheries Project, the EU/NNF Community Conservation Fisheries in KAZA project, Rhodes University, Department of Environmental Affairs: National Resource Management Programme, Working for Water Programme, and the South African Research Chairs Initiative of the Department of Science and Technology (Grant No. 110507).

ACKNOWLEDGMENTS

We gratefully acknowledge the Ministry of Fisheries and Marine Resources, Namibia, for granting permission to carry out this research and for providing technical and logistic support. We acknowledge use of infrastructure and equipment provided by the SAIAB Research Platform and the funding channelled through the NRF-SAIAB Institutional Support system. Special thanks to Denis Tweddle for logistical, technical and intellectual support. Thank you to Susan Abraham for drawing our stylized food web diagrams

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2019.00192/full#supplementary-material

REFERENCES

Anderson, C., and Cabana, G. (2007). Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. *J. North Am. Benthol. Soc.* 26, 273–285. doi: 10.1899/0887-3593(2007)26[273:ETTPOA]2.0.CO;2

Anderson, M. J., Gorley, R. N., and Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth: PRIMER-E.

Araujo-Lima, C. A., Forsberg, B. R., Victoria, R., and Martinelli, L. (1986). Energy sources for detritivorous fishes in the Amazon. *Science* 234, 1256–1258. doi: 10.1126/science.234.4781.1256

Bakker, E. S., Wood, K. A, Pagès, J. F. Veen, G. F., Christianen, M. J. A., Santamaría, L., et al. (2016). Herbivory on freshwater and marine macrophytes: a review and perspective. *Aquat. Bot.* 135, 18–36. doi: 10.1016/j.aquabot.2016.04.008

Baron, J. S., Poff, N. L., Angermeier, P. L., Dahm, C. N., Gleick, P. H., Hairston, N. G., et al. (2002). Meeting ecological and social needs for freshwater. *Ecol. Appl.* 12, 1247–1260. doi: 10.1890/1051-0761(2002)012[1247:MEASNF]2.0.CO;2

Bayley, P. B. (1989). Aquatic environments in the Amazon basin, with an analysis of carbon sources, fish production, and yield. *Can. Spec. Publ. Fish. Aquat. Sci.* 106, 399–408.

Benhaïm, D., Akian, D. D., Ramos, M., Ferrari, S., Yao, K., and Bégout, M.-L. (2017). Self-feeding behaviour and personality traits in tilapia: a comparative study between Oreochromis niloticus and Sarotherodon melanotheron. *Appl. Anim. Behav. Sci.* 187, 85–92. doi: 10.1016/j.applanim.2016.12.004

Berggren, M., Ziegler, S. E., St-Gelais, N. F., Beisner, B. E., and del Giorgio, P. A. (2014). Contrasting patterns of allochthony among three major groups of crustacean zooplankton in boreal and temperate lakes. *Ecology* 95, 1947–1959. doi: 10.1890/13-0615.1

Booth, A. J., and McKinlay, B. W. (2001). Spatial aspects of the reproductive and feeding biology of the striped robber, *Brycinus lateralis* (Pisces: Characidae), in the Okavango Delta, Botswana. *Afr. Zool.* 36, 31–40. doi: 10.1080/15627020.2001.11657111

Bruton, M. N. (1979). The food and feeding behaviour of *Clarias gariepinus* (Pisces: Clariidae). in Lake Sibaya, South Africa, with emphasis on its role as a predator of cichlids. *Trans. Zool. Soc. Lond.* 35, 47–114. doi: 10.1111/j.1096-3642.1979.tb00057.x

Bunn, S. E., and Boon, P. I. (1993) What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. *Oecologia* 96, 85–94.

Carmouze, J. P., Durand, J. R., and Leveque, C. (1983). *Lake Chad: Ecology and Productivity of a Shallow Tropical Ecosystem*. The Hague: Dr. W. Junk Publishers, 575. doi: 10.1007/978-94-009-7266-7

Clarke, K. R., and Gorley, R. N. (2006). *PRIMER v6: User Manual/Tutorial*. Plymouth: PRIMER-E.

Cloern, J. E., Canuel, E. A., and Harris, D. (2002). Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnol. Oceanogr.* 47:713–729. doi: 10.4319/lo.2002.47.3.0713

Currin, C., Newell, S., and Paerl, H. (1995). The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Mar. Ecol. Prog. Ser.* 121, 99–116. doi: 10.3354/meps121099

de Kluijver, A., Ning, J., Liu, Z., Jeppesen, E., Gulati, R. D., and Middelburg, J. J. (2015). Macrophytes and periphyton carbon subsidies to bacterioplankton and zooplankton in a shallow eutrophic lake in tropical China. *Limnol. Oceanogr.* 60, 375–385. doi: 10.1002/lno.10040

Douglas, M. A., Bunn, S. E., and Davies, P. M. (2005). River and wetland food webs in Australia's wet–dry tropics : general principles and implications for management. *Mar. Freshw. Res.* 56, 329–342. doi: 10.1071/MF04084

Dumont, H. J. (1992). The regulation of plant and animal species and communities in African shallow lakes and wetlands. *Rev. Hydrobiol. Trop.* 25, 303–346.

Fellerhoff, C., Voss, M., and Wantzen, K. M. (2003). Stable carbon and nitrogen isotope signatures of decomposing tropical macrophytes. *Aquatic Ecol.* 37, 361–375. doi: 10.1023/B:AECO.0000007049.25535.12

Forsberg, B. R., Araujo-Lima, C. A. R. M., Martinelli, L. A., Victoria, R. L., and Bonassi, J. A. (1993). Autotrophic carbon sources for fish of the central Amazon. *Ecology* 74, 643–652. doi: 10.2307/1940793

Grobler, M., and Ferreira, J. (1990). The dying of Lake Liambezi. *Custos* 19, 39–47.

Grosbois, G., Del Giorgio, P. A., and Rautio, M. (2017a). Zooplankton allochthony is spatially heterogeneous in a boreal lake. *Freshw. Biol.* 62, 474–490. doi: 10.1111/fwb.12879

Grosbois, G., Mariash, H., Schneider, T., and Rautio, M. (2017b). Under-ice availability of phytoplankton lipids is key to freshwater zooplankton winter survival. *Sci. Rep.* 7:11543. doi: 10.1038/s41598-017-10956-0

Gu, B., Schelske, C. L., and Hoyer, M. V. (1997). Intrapopulation feeding diversity in blue tilapia: evidence from stable isotope analysis. *Ecology* 78, 2263–2266. doi: 10.1890/0012-9658(1997)078[2263:IFDIBT]2.0.CO;2

Hamilton, S. K., Lewis, W. M., and Sippel, S. J. (1992). Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. *Oecologia* 89, 324–330. doi: 10.1007/BF00317409

Harding, W. R., and Hart, R. C. (2013). Food-web structure in the hypertrophic Rietvlei Dam based on stable isotope analysis: specific and general implications for reservoir biomanipulation. *Water SA* 39, 611–614. doi: 10.4314/wsa.v39i5.5

Herwig, B. R., Soluk, D. A., Dettmers, J. M., and Wahl, D. H. (2004). Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes. *Can. J. Fish. Aquat. Sci.* 61, 12–22. doi: 10.1139/f03-139

Hill, J. M., and McQuaid, C. D. (2009). Variability in the fractionation of stable isotopes during degradation of two intertidal red algae. *Estuar. Coast. Shelf Sci.* 82, 395–405. doi: 10.1016/j.ecss.2009.02.001

Hoeinghaus, D. J., Winemiller, K. O., and Agostinho, A. A. (2007). Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. *Ecosystems* 10, 1019–1033. doi: 10.1007/s10021-007-9075-2

Howard-Williams, C., and Junk, W. J. (1976). The decomposition of aquatic macrophytes in the floating meadows of a Central Amazonian Várzea lake. *Biogeographica* 7, 115–123.

Jackson, A. L., Inger, R., Parnell, A. C., and Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80, 595–602. doi: 10.1111/j.1365-2656.2011.01806.x

Jackson, D. A., Peres-Neto, P. R., and Olden, J. D. (2001). What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* 58, 157–170. doi: 10.1139/cjfas-58-1-157

Jackson, M. C., Donohue, I., Jackson, A. L., Britton, J. R., Harper, D. M., and Grey, J. (2012). Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. *PLoS ONE* 7:e31757. doi: 10.1371/journal.pone.0031757

Jackson, P. B. N. (1961). The impact of predation, especially by the tiger-fish (*Hydrocyon vittatus* Cast.). on African freshwater fishes. *Proc. Zool. Soc. Lond.* 136, 603–622. doi: 10.1111/j.1469-7998.1961.tb05895.x

Kalk, M., McClachlan, A.J., and Howard-Williams, C. (eds.). (1979). *Lake Chilwa: Studies of Change in a Tropical Ecosystem*. The Hague: Dr. W. Junk Publishers.

Kolding, J., and van Zwieten, P. A. M. (2012). Relative lake level fluctuations and their influence on productivity and resilience in tropical lakes and reservoirs. *Fish. Res.* 115–116, 99–109. doi: 10.1016/j.fishres.2011.11.008

Kolding, J., van Zwieten, P. A. M., Marttin, F., and Poulain, F. (2016). *Fisheries in the Drylans of sub-Saharan Africa–"Fish Come With the Rains". Building Resilience for Fisheries-Dependent Livelihoods to Enhance Food Securty and Nutrition in the Drylands*. Technical Report, FAO Fisheries and Aquaculture Circular, Rome.

Layman, C. A., Arrington, D. A., Montaña, C. G., and Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88, 42–48. doi: 10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Lewis, W. M. J., Hamilton, S. K., Rodríguez, M. A., Saunders, J. F., and Lasi, M. A. (2001). Foodweb analysis of the Orinoco Floodplain based on production estimates and stable isotope data. *J. North Am. Benthol. Soc.* 20, 241. doi: 10.2307/1468319

Macko, S., and Estep, M. (1984). Microbial alteration of stable nitrogen and carbon isotopic compositions of organic matter. *Org. Geochem.* 6, 787–790. doi: 10.1016/0146-6380(84)90100-1

Mendelsohn, J., and Roberts, C. (1997). *An Environmental Profile and Atlas of Caprivi*. Windhoek: Ministry of Environment and Tourism.

Merron, G. S. (1993). Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis*, in the Okavango Delta, Botswana. *J. Fish Biol.* 43, 575–584. doi: 10.1006/jfbi.1993.1160

Merron, G. S., and Mann, B. Q. (1995). The reproductive and feeding biology of *Schilbe intermedius* Riippell in the Okavango Delta, Botswana. *Hydrobiologia* 308, 121–129. doi: 10.1007/BF00007397

Morana, C., Darchambeau, F., Roland, F. A. E., Borges, A. V., Muvundja, F., Kelemen, Z., et al. (2015). Biogeochemistry of a large and deep tropical lake (Lake Kivu, East Africa: insights from a stable isotope study covering an annual cycle. *Biogeosciences* 12, 4953–4963. doi: 10.5194/bg-12-4953-2015

Neill, C., and Cornwell, J. C. (1992). Stable carbon, nitrogen, and sulfur isotopes in a prairie marsh food web. *Wetlands* 12, 217–224. doi: 10.1007/BF03160612

Olsson, K., Stenroth, P., Nystr€om, P., and Granéli, W. (2009). Invasions and niche width: does niche width of an introduced crayfish differ from a native crayfish? *Freshw. Biol.* 54, 1731–1740. doi: 10.1111/j.1365-2427.2009.02221.x

O'Reilly, C. M., Hecky, R. E., Cohen, A. S., and Plisnier, P.-D. (2002). Interpreting stable isotopes in food webs: recognizing the role of time averaging at different trophic levels. *Limnol. Oceanogr.* 47, 306–309. doi: 10.4319/lo.2002.47.1.0306

Parnell, A. C., Inger, R., Bearhop, S., and Jackson, A. L. (2010). Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672. doi: 10.1371/journal.pone.0009672

Peel, R. A. (2016). Colonisation and succession of fishes in lake Liambezi, a shallow ephemeral floodplain lake in southern Africa. Retrieved from the Rhodes University Thesis Repository. 196.

Peel, R. A., Hill, J. M., Taylor, G. C., Tweddle, D., and Weyl, O. L. F. (2019). Species succession and the development of a lacustrine fish community in an ephemeral lake. *J. Fish Biol.* doi: 10.1111/jfb.14081

Peel, R. A., Tweddle, D., Simasiku, E. K., Martin, G. D., Lubanda, J., Hay, C. J., et al. (2015). Ecology, fish and fishery of Lake Liambezi, a recently refilled floodplain lake in the Zambezi Region, Namibia. *Afr. J. Aquat. Sci.* 40, 417–424. doi: 10.2989/16085914.2015.1105779

Pettit, N. E., Warfe, D. M., Close, P. G., Pusey, B. J., Dobbs, R., Davies, C., et al. (2016). Carbon sources for aquatic food webs of riverine and lacustrine tropical waterholes with variable groundwater influence. *Mar. Freshw. Res.* 68, 442–45. doi: 10.1071/MF15365

Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., et al. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.* 92, 823–835. doi: 10.1139/cjz-2014-0127

Pinkas, L., Oliphant, M. S., and Iverson, I. L. K. (1971). Food habits of albacore, bluefin tuna and bonita in Calaforninan waters. *Calif. Fish Game* 152, 1–105.

R Core Team (2013). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing. Available online at: http://www.R-project.org/

Roach, K. A., and Winemiller, K. O. (2015). Hydrologic regime and turbidity influence entrance of terrestrial material into river food webs. *Can. J. Fish. Aquat. Sci.* 72, 1099–1112. doi: 10.1139/cjfas-2014-0459

Seaman, M. T., Scott, W. E., Walmsley, R. D., van der Waal, B. C. W., and Toerien, D. F. (1978). A limnological investigation of Lake Liambezi, Caprivi. *J. Limnol. Soc. Southern Africa* 4, 129–144. doi: 10.1080/03779688.1978.9633164

Simasiku, E. K., Weyl, O. L. F., Kopij, G., and Mafwila, S. K. (2017). Assessment of Lake Liambezi gillnet fishery in the Zambezi region, Namibia. *Int. J. Fish. Aquat. Stud.* 5, 490–495. Available online at: http://www.fisheriesjournal.com/archives/2017/vol5issue1/PartG/4-6-53-460.pdf

Skelton, P. H. (2001). *A Complete Guide to the Freshwater fishes of Southern Africa*. Cape Town: Struik Publisher.

Skelton, P. H. (2016). Name changes and additions to the southern African freshwater fish fauna. *Afr. J. Aquat. Sci.* 1–7. doi: 10.2989/16085914.2016.1186004

Soares, M. G. M., Almeida, R. G., and Junk, W. J. (1986). The trophic status of the fish fauna in Lago Camaleão, a macrophyte dominated floodplain lake in the middle Amazon. *Amazoniana* 9, 511–526.

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., and Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ.* 6:e5096. doi: 10.7717/peerj.5096

Stock, B. C., and Semmens, B. S. (2016). *MixSIAR GUI User Manual. Version 3.1.* https://github.com/brianstock/MixSIAR

Sweeting, C. J., Barry, J., Barnes, C., Polunin, N. V. C., and Jennings, S. (2007b). Effects of body size and environment on diet-tissue δ^{15}N fractionation in fishes. *J. Exp. Mar. Biol. Ecol.* 340, 1–10. doi: 10.1016/j.jembe.2006.07.023

Sweeting, C. J., Barry, J. T., Polunin, N. V. C., and Jennings, S. (2007a). Effects of body size and environment on diet-tissue δ^{13}C fractionation in fishes. *J. Exp. Mar. Biol. Ecol.* 352, 165–176. doi: 10.1016/j.jembe.2007.07.007

Talling, J. F. (1992). Environmental regulation in African shallow lakes and wetlands. *Rev. Hydrobiol. Trop.* 25, 87–144.

Talling, J. F. (2001). Environmental controls on the functioning of shallow tropical lakes. *Hydrobiologia* 458, 1–8. doi: 10.1023/A:1013121522321

Taylor, G. C., Hill, J. M., Jackson, M. C., Peel, R. A., and Weyl, O. L. F. (2017a). Estimating δ^{15}N fractionation and adjusting the lipid correction equation using Southern African freshwater fishes. *PLoS ONE* 12:e0178047. doi: 10.1371/journal.pone.0178047

Taylor, G. C., Weyl, O. L. F., Hill, J. M., Peel, R. A., and Hay, C. J. (2017b). Comparing the fish assemblages and food-web structures of large floodplain rivers. *Freshw. Biol.* 62, 1891–1907. doi: 10.1111/fwb.13032

Thorp, J. H., and Delong, M. D. (1994). The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* 70, 305–308. doi: 10.2307/3545642

Thorp, J. H., Delong, M. D., Greenwood, K. S., and Casper, A. F. (1998). Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia* 117, 551–563. doi: 10.1007/s004420050692

van der Waal, B. C. W. (1985). Aspects of the biology of larger fish species of Lake Liambezi, Caprivi, South West Africa. *Madoqua* 14, 101–144.

Vander Zanden, M. J., and Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83, 2152–2161. doi: 10.2307/3072047

Wantzen, K. M., Junk, W. J., and Rothhaupt, K. (2008). An extension of the floodpulse concept (FPC). for lakes. *Hydrobiologia* 613, 151–170. doi: 10.1007/s10750-008-9480-3

Ward, J. V., Tockner, K., Arscott, D. B., and Claret, C. (2002). Riverine landscape diversity. *Freshw. Biol.* 47, 517–539. doi: 10.1046/j.1365-2427.2002.00893.x

Ward, J. V., Tockner, K., and Schiemer, F. (1999). Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regul. Rivers Res. Manage.* 15, 125–139. doi: 10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E

Welcomme, R. L., Winemiller, K. O., and Cowx, I. G. (2006). Fish environmental guilds as a tool for assessment of ecological condition of rivers. *River Res. Appl.* 22, 377–396. doi: 10.1002/rra.914

Weyl, O. L. F., Daga, V. S., Ellender, B. R., and Vitule, J. R. (2016). A review of *Clarias gariepinus* invasions in Brazil and South Africa. *J. Fish Biol.* 89, 386–402. doi: 10.1111/jfb.12958

Willoughby, N. G., and Tweddle, D. (1978). The ecology of the catfish *Clarias gariepinus* and *Clarias ngamensis* in the Shire Valley, Malawi. *J. Zool. Soc. Lond.* 184, 507–534. doi: 10.1111/j.1469-7998.1978.tb03936.x

Winemiller, K. O. (1991). Comparative ecology of Serranochromis species (Teleostei: Cichlidae). in the Upper Zambezi River floodplain. *J. Fish Biol.* 39, 617–639. doi: 10.1111/j.1095-8649.1991.tb04393.x

Winemiller, K. O. (1996). "Factors driving temporal and spatial variation in aquatic floodplain food webs," in *Food Webs: Integration of Patterns and Dynamics*, eds G.A. Polis and K.O. Winemiller (New York, NY: Chapman and Hall), 298–312. doi: 10.1007/978-1-4615-7007-3_29

Winemiller, K. O. (2004). "Floodplain river food webs: generalizations and implications for fisheries management," in *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries Vol. 2,* eds R.L. Welcomme and T. Petr (Bangkok: FAO Regional Office for Asia and the Pacific), 285–309.

Winemiller, K. O., and Adite, A. (1997). Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America. *Environ. Biol. Fishes* 49, 175–186. doi: 10.1023/A:1007376826609

Winemiller, K. O., and Kelso-Winemiller, L. C. (1996). Comparative ecology of catfishes of the Upper Zambezi River floodplain. *J. Fish Biol.* 49, 1043–1061. doi: 10.1111/j.1095-8649.1996.tb01777.x

Winemiller, K. O., and Kelso-Winemiller, L. C. (2003). Food habits of tilapiine cichlids of the Upper Zambezi River and floodplain during the descending phase of the hydrologic cycle. *J. Fish Biol.* 63, 120–128. doi: 10.1046/j.1095-8649.2003.00134.x

Yodzis, P., and Winemiller, K. O. (1999). In search of operational trophospecies in a tropical aquatic food web. *Oikos* 87, 327–340. doi: 10.2307/3546748

Zengeya, T. A., and Marshall, B. E. (2007). Trophic interrelationships amongst cichlid fishes in a tropical African reservoir (Lake Chivero, Zimbabwe). *Hydrobiologia* 592, 175–182. doi: 10.1007/s10750-007-0790-7

Zeug, S. C., and Winemiller, K. O. (2008). Evidence supporting the importance of terrestrial carbon in a large-river food web. *Ecology* 89, 1733–1743. doi: 10.1890/07-1064.1

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.