Flooding affects food web structure and basal sources supporting fish guilds in a subtropical wetland and shallow lake

Rodrigo Ferreira Bastos (✉ bio.rfbastos@gmail.com)

Universidade Federal de Pernambuco <https://orcid.org/0000-0002-9692-4237>

Alexandre Miranda Garcia

Universidade Federal do Rio Grande

Kirk O. Winemiller

Texas A&M University

Nelson Ferreira Fontoura

PUCRS: Pontificia Universidade Catolica do Rio Grande do Sul

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Abstract

Aquatic ecosystems exchange nutrients and organic matter with surrounding terrestrial ecosystems, and floods import allochthonous material from riparian areas into fluvial systems. We surveyed food web components of a wetland and shallow lake in a subtropical coastal region of Brazil to examine how community trophic structure and the entrance of allochthonous material into the food web were affected by floods. Stable isotope analysis was performed for samples of terrestrial and aquatic basal production sources and aquatic animals to trace the origin of organic matter assimilated by aquatic animals and estimate vertical trophic positions and food chain length. Lake and wetland trophic structures were compared for cool/wet and warm/dry seasons. Food web structure was hypothesized to differ based on hydrology, with the more stable lake having greater food web complexity, and seasonal flooding resulting in greater allochthonous inputs to the aquatic food web. We compared spatial and temporal variation in assemblage trophic structure using an adapted isotopic ellipse approach that plots assemblage elements according to $\delta^{13}\text{C}$ on the x-axis and estimated TP on the y-axis. Lake trophic structure was more complex with longer food chains compared to that of the wetland. A greater contribution from terrestrial resources to animal biomass was observed in the wetland during the cool/wet period, and food chains in both habitats tended to be longer during the cool/wet period. Findings supported the hypothesis of greater assimilation of allochthonous sources during floods and greater trophic complexity in the more hydrologically stable system.

Introduction

A major issue in aquatic ecology is energy dynamics and the production and transfer of organic materials that sustains the communities and drives ecosystem functioning. Transfer of organic material between terrestrial and aquatic habitats is bidirectional, especially in fluvial systems subject to hydrologic variation. Hydrologic variation affects geomorphology, sediment dynamics, habitat availability and connectivity, and resource and population dynamics. Several conceptual models predict the origin of organic matter supporting aquatic communities along lateral and longitudinal gradients of rivers (Vannote et al 1980; Junk et al 1989; Thorp and Delong 1994; Junk and Wantzen 2008), however, similar models are generally lacking for lakes and wetlands. Lakes vary in size, shape, depth, hydrology, thermal regime, productivity, as well as in the degree to which they exchange organic material, including organisms, with adjacent terrestrial systems.

Variation among these factors yields between-lake variation in trophic state (Carlson 1977) and food web structure (Wetzel 2001). Aquatic communities of small, shallow lakes tend to be supported by aquatic macrophytes, whereas in larger, deeper lakes, food webs are mostly supported by phytoplankton, with macrophytes contributing to variable degrees within littoral zones (Vander Zanden and Vadeboncoeur 2002; Kruger et al 2015). The major production sources supporting aquatic food webs may vary spatially within a lake. For example, Rodrigues et al. (2015) found different trophic states on northern and southern limits of a long and shallow lake in southern Brazil. They attributed those differences to wind-driven water currents affecting water quality and the dominant types of primary producers (i.e., macrophytes vs. phytoplankton) (Rodrigues et al 2015).

Terrestrial organic matter enters aquatic food webs via direct consumption of terrestrial animals (Nakano et al 1999) and plant material (Correa and Winemiller 2014) or as detritus (Vannote et al 1980). Allochthonous inputs usually are greater when flooding transports material or allows access for aquatic organisms between terrestrial and aquatic habitats (Junk et al 1989; Thomaz et al 2007; Davidson et al 2012). The degree to which allochthonous material enters the aquatic food web is influenced by its availability, degree of habitat connectivity, and the ability of aquatic consumers to exploit it (Hoeinghaus et al 2011; Abrantes et al 2013).

By increasing physical connections between habitats, floods also affect vertical trophic structure, or the food chain length (Sabo et al 2018). Two major hypotheses have been proposed regarding the vertical trophic structure: the productivity hypothesis (Pimm and Lawton 1977; Briand and Cohen 1987) and the ecosystem size hypothesis (Cohen and Newman 1991; Post et al 2000). A relationship between average food chain length and community stability also has been proposed (Pimm 1982; Sabo et al 2010). There is some evidence that average food chain length is positively correlated with ecosystem productivity, size, and stability (Pimm and Lawton 1977; Post et al 2000; Sabo et al 2010). Based on analysis of data from diverse ecosystems, Takimoto and Post (2013) found a strong but variable effect of ecosystem size on food chain length, no consistent effect of disturbance (inverse of stability), and a weak but fairly consistent effect of resource availability (productivity).

Ratios of stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$, reported as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, reported as $\delta^{15}\text{N}$) have been used to describe food web structure (DeNiro and Epstein 1978; DeNiro and Epstein 1981). Consistent carbon isotopic differences have been shown between primary producers in pelagic and littoral zones of lakes and between hydrological conditions in wetlands (Wantzen et al 2002). The nitrogen isotopic ratio undergoes a fairly consistent shift between adjacent trophic levels and, therefore, provides a means to estimate trophic positions of consumers and the length of food chains (Post et al 2000; Post 2002). Therefore, the positions of organisms in biplots of isotopic space (e.g., $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) have been used to compare trophic niche, similarity and breadth (Newsome et al 2007).

To test if seasonal floods are associated with assimilation of organic matter of terrestrial origin by aquatic animals and if maximum food chain length and community trophic structure are related to ecosystem size, we surveyed aquatic and riparian food web components during cool/wet and warm/dry seasons in a shallow lake and nearby wetland in a coastal region of southern Brazil. The lake is more stable hydrologically with much less temporal variation in area and perimeter/area ratio) compared to the wetland that can sometimes lack surface water entirely during periods of drought. We hypothesized that (1) trophic structure is more complex in the lake compared to the wetland because of its greater area and greater hydrologic stability, (2) terrestrial input to the aquatic food web is greater during flood period, and (3) the influence of flooding is greater in the wetland, where the aquatic/terrestrial interface (i.e. wetted perimeter/area ratio) is greater.

Materials And Methods

Study area and sampling design

To investigate potential effects of the flood pulse on aquatic food web structure, we conducted field sampling during cool/wet (Winter – W) and warm/dry (Summer – S) periods at two locations of Taim Hydrological System: Caçapava wetland (hereafter ‘wetland’) and Nicola Lake (hereafter ‘lake’) (Figure 1). The Taim Hydrological System lies within a coastal landscape of forests, grasslands, dunes, lakes and wetlands that supports high biological diversity (Motta-Marques et al 2013). The region is subtropical, and patterns of precipitation, temperature and wind produce strongly seasonal variation the hydrological cycle. During austral winter, high rainfall and low evaporation result in accumulation of water within the wetland, which in turn promotes connectivity with riparian habitats. The opposite tends to occur during austral summer, when lower precipitation and higher evaporation reduce water levels and exchanges of material and organisms with terrestrial habitats (Bastos et al 2014). The magnitude of the seasonal flood pulse varies interannually due to *El Niño* and *La Niña* climatic events, which respectively produce positive and negative rainfall anomalies in southern Brazil (Grimm et al 1998). In addition to floods, wind can promote exchange of organic matter, nutrients and organisms between adjacent habitats (Bastos et al 2014; Rodrigues et al 2015) by causing wind-driven tides on the 90-km long Mangureira Lake, connected to the Caçapava wetland.

The wetland site is a system of ephemeral water bodies covering an area of approximately of 2 km². Average water depth is 0.3 m with a maximum depth of 1 m during the cool/wet period. The lake is a perennial with an area of approximately 2 km² and average water depth of 0.6 m, but depth can reach 1.3 m during the cool/wet period. Both aquatic systems are surrounded by grasslands dominated by species of Poaceae (C4 grasses). Aquatic macrophytes in both habitats are mostly plants that use the C3 photosynthesis pathway. This distinction is important, because $\delta^{13}\text{C}$ values are usually distinct between plants using the C3 or C4 pathway. Aquatic macrophytes (C3) in these systems are characterized by relatively low $\delta^{13}\text{C}$ values, whereas the most abundant terrestrial grasses (C4) have relatively high $\delta^{13}\text{C}$ (Garcia et al 2006; Rodrigues et al 2014).

Surveys were conducted during December 2012 (austral summer) and September 2013 (austral winter). Each site was sampled on two consecutive days. Samples were stored on ice in the field and then transferred to a freezer in the laboratory until processing. Clippings were obtained of leaves of the most common terrestrial plants (mostly Poaceae) along the margins and surrounding grasslands of both the wetland and lake during both seasons. Aquatic basal food sources, including dominant macrophytes and algae, were collected by hand. Suspended particulate organic matter (SPOM) samples were taken from 0.5 to 4 L of water, depending on the amount of suspended particles at each site/season after previous filtering through a 200 μm mesh to remove zooplankton and other large organic debris. Benthic particulate organic matter (BPOM) was collected by taking the top layer (~1 cm) of sediment using a spatula. Samples of an additional basal resource, capybara feces (*Hydrochoerus hydrochaeris*, Rodentia), were also collected. Fecal pellets usually were common along the water margins at both study sites and were often found floating in the water, especially during the cool/wet period.

Fish and macroinvertebrates were sampled using a rapid assessment method (Price and Harris 2009) involving several methods as described in (Bastos et al 2014). To collect fish, three sets of gillnets (8 x 2 m each, each set with adjacent meshes sizes of 30 mm) were placed in the water overnight. Insects, snails and clams were collected by hand from littoral and surrounding areas at both sites. A plankton net (250 μm) was used to obtain zooplankton samples at both sites during the cool/wet period. This method could not be employed during the warm/dry period when there was little water in the wetland and suspended detritus in the lake quickly filled the plankton net.

Sample processing and data compilation

Samples of primary producers (bulk samples), macroinvertebrates and fish (muscle tissue) were prepared for isotopic analyses by first drying (60° C for 48 h) and then grinding them into a fine powder. After being weighed (approximately 0.01 and 0.5 mg for animal and plants, respectively) and packaged within tin capsules, the dried and powdered samples were sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, for measurement of stable isotope ratios of carbon and nitrogen. Results were reported as parts per mil (‰) deviations from the corresponding standard: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 10^3$. Standards were PeeDee Belemnite (C) and molecular nitrogen in air (N). Standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ based on analysis of samples replicates were 0.70 $\pm$ 0.65‰ and 0.32 $\pm$ 0.51‰, respectively.

Fish were classified into six trophic functional guilds (TG) based on the literature (Moresco and Bemvenuti 2005; Corrêa and Piedras 2008; Kutter et al 2009; Bastos et al 2011; Corrêa et al 2012; Rodrigues et al 2012; Bastos et al 2013) plus analysis of gut contents of specimens collected during the field surveys. The six trophic guilds (TG) were: (1) detritivore, (2) omnivore, (3) invertivore, (4) zooplanktivore, (5) invertivore/piscivores (i.e., invertivores that also consume minor fractions of fish) and (6) piscivores (i.e., fish dominate the diet). Invertebrates were classified according to six functional groups: (1) microcrustacean, (2) macrocrustacean, (3) bivalve mollusc, (4) snail, (5) aquatic

insect, and (6) terrestrial arthropod. Basal resources were grouped and categorized as: (1) aquatic primary producers (C_3 macrophytes and algae), (2) terrestrial plants (C_4 grasses), (3) capybara feces, (4) SPOM, and (5) BPOM.

Data analysis

The average $\delta^{15}N$ of aquatic invertebrates identified as primary consumers ($\lambda = 2$) was used as baseline to estimate consumer trophic positions using the following equation:

$$TP = \lambda + ((\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}}) / TDF),$$

where λ is the baseline trophic level; $\delta^{15}N_{\text{consumer}}$ is the $\delta^{15}N$ value of each consumer species of category; $\delta^{15}N_{\text{baseline}}$ is the average $\delta^{15}N$ value of the second trophic level baseline collected in the same location and period as the consumer; and TDF is the trophic discrimination factor for $\delta^{15}N$ (Post 2002). The second trophic level was used as the baseline in this equation instead of the first trophic level, because (1) there was significant $\delta^{15}N$ variation among primary producers, whereas (2) the community of primary consumers assimilates material from all of these sources and thereby integrate this variation (Vander Zanden and Rasmussen 2001; Post 2002). Invertebrates considered as primary consumers for estimation of $\delta^{15}N$ baseline were amphipods, zooplankton, bivalves (*Corbicula fluminea*), snails (*Heliovia australis* and *Pomacea canaliculata*), beetles (Coleoptera), and crickets (Gryllidae).

Trophic position (TP) estimates were computed for each macroinvertebrate and fish specimen and then averaged for functional categories as described above. Average $\delta^{15}N$ values of the primary consumers used as baseline for TP estimates were compared among sites and periods using analysis of variance (ANOVA) after evaluating normality and homocedasticity. The same analysis was performed for the average values for TP of consumer functional categories. Only baseline and consumer samples obtained at all sites and seasons and in sufficient number ($n > 5$ per site and period) were included in this analysis. When data assumptions were not achieved, non-parametric ANOVA (Kruskal-Wallis) was performed (Zar 2010). When the main effect was significant, multiple comparisons (Tukey post-hoc test) were performed for parametric data.

To estimate relative contributions of terrestrial (allochthonous) vs. aquatic (autochthonous) primary producers to consumer biomass, Bayesian stable isotope mixing models were applied using the package SIAR (Parnell et al 2008) in R. To achieve higher resolution and better ecological inferences from mixing models, primary producers with similar isotopic composition were grouped *a priori* as suggested by Phillips et al. (2005). Hence, algae and macrophytes were considered as aquatic primary producer sources and terrestrial C_4 grasses as the principal terrestrial primary producer source in all models.

Because it is difficult to obtain pure samples of phytoplankton, samples of suspended particulate organic matter (SPOM) are usually used as a proxy for isotopic composition of algae and organic matter in the water column (Kaehler et al 2000; Cresson et al 2012). In shallow (<1.5 m) wetlands and lakes in the subtropics, winds frequently stir the entire water column (De Vicente et al 2006; Dubois et al 2012). Therefore, SPOM samples from both locations likely were composed of a mixture of pelagic and benthic particles. Because SPOM, BPOM and capybara feces were of uncertain origin, they were excluded from this analysis. The TDF (trophic discrimination factor defining isotopic shifts between adjacent trophic levels) was set at 2.54 ± 1.59 for nitrogen ($\delta^{15}N$) (Vanderklift and Ponsard 2003) and 0.40 ± 1.3 for carbon ($\delta^{13}C$) (Post 2002).

Isotopic spaces occupied by fish assemblages at the two sites during each period were estimated using Bayesian standard ellipse areas (SEA_B ; Jackson et al. 2011) calculated using SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) within the SIAR package (Parnell et al 2008). SEAs are comparable to the univariate standard

deviation and contain approximately 40% of the data compared with other isotopic space metrics, such as convex hull, and therefore provide a better and more standardized description of population/community trophic structure (Jackson et al 2011). Moreover, SEAs are not affected by bias associated with the number of groups, allowing comparisons among assemblages or guilds with different members (Jackson et al 2011). The small sample size-corrected SEA (SEA_C) and its overlap also were calculated for each site and period (Jackson et al 2011). Overlap between any given pair of sites/seasons (SEA_{C1}) was given as percentage of SEA_{C1} and SEA_{C2} . It is important to note that relative positions in isotopic space provides an estimate of trophic niches occupied by species, guilds or assemblages, but does not necessarily provide an accurate and precise description of trophic ecology (Newsome et al 2007). Hence, isotopic space metrics provide a proxy allowing of trophic niche relationships (Jackson et al 2011). Although there has been considerable debate about assumptions and ecological inferences based on isotopic space metrics (e.g., Layman et al 2007; Layman and Post 2008; Hoetinghaus and Zeug 2008), they have been used increasingly in studies of trophic ecology (Newsome et al 2012; Layman et al 2012; Abrantes et al 2014; Santos et al 2020). The $\delta^{15}N$ values of taxa used as baselines for estimation of consumer TP (e.g., primary producers or primary consumers) can change over space and time (Newsome et al 2007; Hoetinghaus and Zeug 2008). This potential source of error can cause overestimate of consumer TP, whereby elevated $\delta^{15}N$ at the baseline yields underestimation of consumer TP, and low $\delta^{15}N$ at the baseline yields overestimation. Baseline standardization approaches have been proposed to correct this problem (Catry et al 2016; Huckembeck et al 2020). Consequently, we used TP estimates instead of $\delta^{15}N$ values on the y-axis when plotting isotopic ellipses (i.e., plotting TP vs. $\delta^{13}C$ to infer trophic niche space).

Results

Among all studied food web components, basal food sources revealed greatest variation on $\delta^{15}N$ values. Basal sources from the wetland had $\delta^{15}N$ values ranging from

-4.1 to 6.4‰ during the cool/wet period, and from -4.4 to 6.6‰ during the warm/dry period (Table S1). A similar pattern was observed for basal sources from the lake, with a $\delta^{15}N$ ranging from -1.9 to 7.2‰ during the cool/wet period, and from -1.96 to 5.82‰ during the warm/dry period (Table S1, Figure 2). Fishes tended to reveal greater variation in $\delta^{15}N$ values during the cool/wet period at both sites (Table S2, Figure 2).

Omnivore and piscivore were the most common fish guilds at both sites during both seasons, and this allowed for spatiotemporal comparisons of trophic positions, estimates of basal source contributions to fish biomass, and the size and similarity of isotopic ellipses. The Kruskal-Wallis test indicated that $\delta^{15}N$ of primary consumers (invertebrates at the second trophic level) was not significantly different between sites, but significantly higher during the warm/dry period (lake: 4.5 ± 1.6 ‰; wetland: 3.9 ± 1.9 ‰) than the cool/wet period (lake: 3.14 ± 0.9 ‰; wetland: 2.64 ± 1.4 ‰) ($p = 0.023$). Average TP of fish guilds showed the opposite pattern (Figure 3, Table 1). ANOVA revealed no interaction between site and season; therefore, TP of omnivores and piscivores was tested separately by site and season. Omnivores had higher average TP during the cool/wet period (3.9) than warm/dry period (3.5) ($p = 0.001$). The piscivore guild revealed the same pattern, with higher average TP during the cool/wet (4.8) than warm/dry period (3.9) ($p = 0.001$) (Figure 3). TP was not significantly different between sites for piscivores ($p = 0.145$), but omnivores had higher values in the lake (3.9) than wetland (3.6) ($p = 0.001$).

Table 1

Sample size (N), mean trophic position (TP) and standard deviation (s.d.) of main consumers in the Taim Hydrological System, southern Brazil. Bold values represent mean and standard deviation values by functional group.

CONSUMERS	Wetland						Lake					
	Cool/wet			Warm/dry			Cool/wet			Warm/dry		
	N	TP	s.d.	N	TP	s.d.	N	TP	s.d.	N	TP	s.d.
FISHES												
Piscivorous	8	4.6	0.2	9	3.9	0.3	8	4.9	0.4	14	3.9	0.3
<i>Hoplias cf. malabaricus</i>	8	4.6	0.2	9	3.9	0.3	3	5.0	0.2	4	3.9	0.2
<i>Oligosarcus jenynsii</i>							5	4.9	0.5	10	4.0	0.3
Invertivorous/piscivorous	12	4.2	0.2	2	3.6	0.4	7	4.8	0.4	10	3.6	0.3
<i>Charax stenopterus</i>										1	3.7	-
<i>Crenicichla lepidota</i>	2	4.0	0.1	2	3.6	0.4	1	4.3	-	1	3.5	-
<i>Pimelodella australis</i>										1	4.2	-
<i>Pimelodus pintado</i>							3	5.2	0.3			
<i>Rhamdia quelen</i>	1	4.4	-				2	4.4	0.3	7	3.5	0.3
<i>Tracheleopterus lucenai</i>	9	4.2	0.2				1	4.7	-			
Zooplanktivorous										8	4.1	0.2
<i>Odontesthes spp.</i>										2	4.0	0.1
<i>Platanichthys platana</i>										6	4.2	0.2
Invertivorous	1	3.8	-	12	3.5	0.3	12	3.7	0.4	14	3.3	0.7
<i>Bunocephalus iheringii</i>										5	3.5	0.4
<i>Characidium rachovii</i>				4	3.1	0.1						
<i>Geophagus brasiliensis</i>							3	4.2	0.1	1	3.4	-
<i>Hyphessobrycon igneus</i>	1	3.8	-	6	3.7	0.1	9	3.5	0.4	1	3.1	-
<i>Microglanis cottoides</i>										3	2.4	1.1
<i>Mimagoniates inequalis</i>										2	3.8	0.4
<i>Pseudocorynopoma doriae</i>										2	3.6	0.2
<i>Synbranchus marmoratus</i>				2	3.6	0.0						
Omnivorous	79	3.7	0.3	35	3.4	0.3	82	4.1	0.3	35	3.6	0.3
<i>Astyanax eigenmanniorum</i>	19	3.7	0.3	5	3.7	0.1	24	4.2	0.2	6	3.9	0.3
<i>Astyanax fasciatus</i>							2	4.6	0.5			

CONSUMERS	Wetland						Lake					
	Cool/wet			Warm/dry			Cool/wet			Warm/dry		
	N	TP	s.d.	N	TP	s.d.	N	TP	s.d.	N	TP	s.d.
<i>Australoheros acaroides</i>				11	3.3	0.3						
<i>Cheirodon interruptus</i>	7	3.5	0.1	6	3.6	0.1	24	4.2	0.2	8	3.6	0.2
<i>Cichlasoma portalegrense</i>				5	3.1	0.2						
<i>Cnesterodon decemmaculatus</i>	5	3.8	0.2	2	3.5	0.1						
<i>Corydoras paleatus</i>										7	3.5	0.5
<i>Hyphessobrycon luetkenii</i>							27	4.0	0.4			
<i>Jenynsia multidentata</i>	48	3.8	0.3	6	3.4	0.2	5	3.8	0.4	12	3.6	0.3
<i>Loricariichthys</i> spp.										2	3.9	0.1
Detritivorous	2	4.6	0.1				4	4.3	0.8	12	2.6	0.3
<i>Cyphocharax voga</i>	2	4.6	0.1				2	4.7	1.2	4	2.8	0.3
<i>Hypostomus commersonii</i>							2	4.0	0.0	8	2.5	0.3
INVERTEBRATES												
Macrocrustaceans							15	4.0	0.1	12	3.7	0.3
<i>Cyrtograpsus angulatus</i>										3	3.3	0.2
<i>Macrobrachium</i> spp.										3	3.9	0.1
<i>Palaeomonetes argentinus</i>							15	4.0	0.1	6	3.8	0.2
Microcrustaceans	5	2.0	0.6				8	1.9	0.1			
Amphipoda*							8	1.9	0.1			
Zooplankton*	5	2.0	0.6									
Aquatic filter clam										4	2.3	0.7
<i>Corbicula fluminea</i> *										4	2.3	0.7
Aquatic grazer snails				8	2.0	0.8	10	2.2	0.2	3	1.8	0.5
<i>Heliobia australis</i> *				2	3.2	0.0	6	2.0	0.1	1	2.3	-
<i>Pomacea canaliculata</i> *				6	1.6	0.2	4	2.5	0.2	2	1.5	0.0
Aquatic insects				1	2.5	-				2	2.4	0.7
Belostomatidae										1	2.0	-

CONSUMERS	Wetland						Lake					
	Cool/wet			Warm/dry			Cool/wet			Warm/dry		
	N	TP	s.d.	N	TP	s.d.	N	TP	s.d.	N	TP	s.d.
Ephemeroptera				1	2.5	-						
Odonata										1	2.9	-
Terrestrial arthropods							7	2.2	0.8	2	1.7	0.1
Araneae							1	2.7	-			
Coleoptera*										2	1.7	0.1
Formicidae							1	2.7	-			
Gryllidae*							5	2.0	0.8			

Because trophic discrimination factors are assumed to be different for omnivores and piscivores, source contributions to consumer biomass were estimated separately for these groups using the isotopic mixing model (Table S3). The models revealed spatial and temporal differences in the proportional assimilation of sources among fish trophic guilds (Figure 4, Table 2). Overall, aquatic basal sources (C_3 plants + algae) rather than terrestrial sources (C_4 plants) were assimilated by omnivorous and piscivorous fishes in greatest proportions (ranging from 3 to 77%, for the 95th percentile confidence interval of model estimates). Estimated contribution of C_3 plants to these fish guilds ranged from 29% in the wetland during the cool/wet period to 77% in the wetland during the warm/dry period. Algae also were important contributors to these fish guilds, with greater contributions in the wetland during the warm/wet period (16 - 62%) compared the warm/dry period (3 - 41%). C_4 plants seemed to contribute little to fish biomass in the lake, with estimates ranging from 0% during the cool/wet period to 45% during the warm/dry period. In general, the contribution of C_4 plants to piscivorous fish in the wetland was slightly greater during the warm/dry period compared with the cool/wet period; the opposite pattern was observed for omnivorous fish from the lake (Figure 4, Table 2). C_3 plants were estimated to be the dominant source supporting both omnivorous and piscivorous fishes in the wetland during the warm/dry period (Figure 4, Table 2).

Table 2

Stable isotope mixing models contribution estimates of predominantly primary producers of aquatic (C_3 plants and Algae) and terrestrial (C_4 plants) habitats for each fish consumer group, site and season. Samples taken in the Nicola Lake and Caçapava wetland, Taim Hydrological System, southern Brazil.

GUILD	Wetland				Lake			
	Cool/wet		Warm/dry		Cool/wet		Warm/dry	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
Piscivorous								
Algae	0.16	0.62	0.03	0.41	0.05	0.54	0.04	0.50
C_3 Plant	0.31	0.62	0.55	0.74	0.35	0.68	0.33	0.54
C_4 Plant	0.02	0.27	0.01	0.25	0.02	0.32	0.01	0.45
Omnivorous								
Algae	0.31	0.45	0.05	0.32	0.27	0.47	0.09	0.46
C_3 Plant	0.29	0.38	0.63	0.77	0.52	0.66	0.33	0.49
C_4 Plant	0.25	0.32	0.01	0.20	0.00	0.09	0.18	0.45

Standard ellipses (SEA_C) of fish assemblages varied in size, shape, position and overlap within $\delta^{13}C$ x TP biplots (Figure 5) in relation to sites and periods. Ellipse area of the local fish assemblage was greater in the lake than wetland (Figure 5A), and greater during the warm/dry period (lake = 4.07; wetland = 2.24) than the cool/wet period (lake = 2.99, wetland = 1.69). Isotopic areas occupied by the lake fish assemblage was larger in both dimensions ($\delta^{13}C$ and TP), and fish from the lake tended to have lower $\delta^{13}C$ values than those from the wetland (Figure 5A). Between-site overlap of isotopic ellipses was higher during the warm/dry period, with 93% of the wetland area overlapping with 52% of the lake area. During the cool/wet period, 19% of the lake ellipse area overlapped with 25% of the wetland ellipse area. Inter-season ellipse overlap was higher for the wetland, with 30% of the warm/dry area overlapping with 40% of the cool/wet area; in the lake, 19% of the warm/dry area overlapped with 25% of the cool/wet area (Figure 5A).

Although the standard ellipse area occupied by omnivores (lake warm/dry = 2.23; lake cool/wet = 1.93; wetland warm/dry = 1.71; wetland cool/wet = 1.10) was smaller than the area occupied by the entire fish assemblage, both revealed similar patterns of spatiotemporal variation (Figure 5B). Within a given season, TP and $\delta^{13}C$ dimensions of ellipses for fish assemblages spanned similar ranges at the two sites. The exception was the cool/wet sample from the wetland with relatively narrow $\delta^{13}C$ range. For assemblages at both sites, the TP dimension had a greater range during the cool/wet period. Conversely, the $\delta^{13}C$ dimension of the lake fish assemblage had a smaller range during the cool/wet period, and that of wetland fish assemblage was greater during that same period. Within-site, inter-season ellipse overlap was higher for the wetland fish assemblage (19% of warm/dry, 30% of cool/wet) than the lake assemblage (6% of warm/dry, 7% of cool/wet) (Figure 5B). Ellipse overlap between sites was higher during the warm/dry period (62% of wetland, 47% lake) than cool/wet period (17% of wetland, 10% of lake).

Standard ellipse areas differed between seasons to greater extent for wetland piscivores (warm/dry = 1.08, wetland cool/wet = 0.65) when compared to piscivores from the lake (warm/dry = 1.44, cool/wet = 1.14) (Figure 5C). The range of $\delta^{13}\text{C}$ was relatively narrow for piscivores from the lake during the cool/wet period and for the wetland during the warm/dry period. The TP dimension was broadest for piscivores from the lake and narrow for piscivores from the wetland during the cool/wet period. Piscivore SEA_C had no overlap between the warm/dry and cool/wet periods at both sites, and this was largely due to separation in the vertical dimension (TP axis) (Figure 5C). Piscivore SEA_C had higher overlap during the warm/dry period, when overlap was 84% for the wetland sample and 66% for the lake sample. During the cool/wet period, overlap was 27% of the ellipse of wetland piscivores and 15% of the ellipse for lake piscivores.

Discussion

Between-habitats differences in food-web structure

Findings corroborated our hypothesis of higher complexity in the trophic structure of the lake compared with the wetland. For instance, omnivorous fishes had higher trophic positions in the lake, suggesting higher food chain lengths in this system. Fish assemblage isotopic niches were larger in the lake, and this likely was influenced by the greater range of values in the vertical dimension (i.e., trophic levels). These patterns could be explained by the fact that the lake, in contrast with the wetland, did not completely dry during prolonged periods of water deficit. Lake water volume and quality does not appear to be greatly impacted by severe droughts (Motta-Marques et al 2013), allowing for persistence of aquatic species. Greater ecosystem size and resilience to hydrological perturbations may explain greater food web complexity in the lake compared to the more ephemeral wetland. Similar environmental drivers of food web complexity and stability have been reported for other ecosystems (Sturner et al 1997; Post et al 2000; McHugh et al 2010).

Contrary to our initial expectation, the overall isotopic niche of local fish assemblages did not enlarge during the cool/wet period, but instead was smaller when compared with the summer/dry period. A possible explanation could be related to the greater habitat size and connectivity when water levels were higher during the cool/wet period, especially in the wetland. Under these conditions, fish may have access to seasonally abundant resources, which might result in exploitation of the most profitable and available resources by diverse fish species, resulting in a reduction in interspecific trophic niche differences (Winemiller 1989). An increase in spatial similarity of aquatic community structure in tropical floodplains during the annual flood pulse was previously reported (Thomaz et al 2007), and it is known that complexity of trophic structure in streams is related to environmental heterogeneity (Zeni and Casatti 2014). Although the isotopic space of local fish assemblages decreased during the flood period, we cannot necessarily assume that trophic niches of individual species had shifted. As pointed out earlier, isotopic ellipses are only proxies for trophic niches and should not be interpreted as highly accurate and reliable indicators (Newsome et al 2007). In some cases, communities assimilating material from a greater diversity of sources can have smaller isotopic spaces than those using fewer but more isotopically distinct sources. In other scenarios, spatiotemporal shifts in isotopic baselines may hinder comparisons of isotopic spaces (Hoeinghaus and Zeug 2008). Although we could not control for the influence of seasonal changes in water level on isotopic signatures of basal sources, our approach using trophic position (instead of $\delta^{15}\text{N}$ values) should have reduced potential influences of temporal and between-habitats differences in isotopic baselines on fish isotopic ellipses, at least in the vertical position. Future studies employing complementary approaches (e.g., stomach contents analysis) with isotopic analysis based on surveys across relevant spatial and temporal scales and sources with sufficient isotopic discrimination will be in need to better understand the effects of hydrology on the trophic niche of aquatic organisms.

Basal sources and assimilation of allochthonous matter under high water conditions

Our finding corroborated the initial hypothesis that terrestrial input to the aquatic food web is greater during the cool/wet period when water levels are higher, especially in the wetland. An increase in the interface between aquatic and terrestrial habitats promotes great contribution of terrestrial sources to the aquatic food web (Reid et al 2008; Abrantes et al 2013; Correa and Winemiller 2018). Additional evidence of greater terrestrial input under high water conditions was the more ^{13}C -enriched carbon signature of BPOM during the cool/wet period at both sites. This could be explained by the increased contribution from terrestrial C4 grasses in the form of detritus when riparian areas are inundated, especially in the wetland. It is important to note that we did not include dissolved organic carbon (DOC) in our isotopic mixing models. DOC, much of which may originate from terrestrial primary producers, has been shown to be an important basal source in tropical coastal lagoons (Marinho et al 2010). Further research is needed to estimate contributions of terrestrial sources to both dissolved and particulate organic matter entering aquatic food webs.

Our isotope mixing models estimated that aquatic C3 plants were the most important carbon source supporting fishes in both lake and wetland. Algae also were estimated to be an important source supporting the biomass of omnivorous and piscivorous fishes, and some fish species could be strongly supported by food chains originating from algae. In at least one other study, algae (periphyton) was estimated to be the most important carbon source for benthivorous fishes in a tropical floodplain (Lopes et al 2015).

Vertical trophic structure changed seasonally in fish assemblages at both sites. Fish $\delta^{15}\text{N}$ tended to be higher and more variable during the cool/wet period. Most fish guilds had higher average TP during this period. These findings suggest an overall expansion of the vertical trophic structure during the cool/wet period, possibly in response to greater foraging options within expanded aquatic habitats. For omnivores, a greater variety of available food resources can lead to an expansion in horizontal structure at the same time of a contraction in the vertical structure of food webs (Akin and Winemiller 2006).

Conclusions

Seasonal hydrological pulsing in a shallow lake and wetland in coastal southern Brazil was associated with shifts in both vertical and horizontal aspects of fish assemblage trophic structure. Findings corroborated our hypotheses of higher complexity in the trophic structure of the lake compared with the wetland, and this was largely due to elevated trophic positions of omnivorous fishes and an overall expansion of trophic niches. We also found an increase the contribution of terrestrial basal sources to fish biomass during the cool/wet season, especially in the wetland. By plotting consumer TP instead of $\delta^{15}\text{N}$ in relation to $\delta^{13}\text{C}$, we obtained more reliable estimates of assemblage trophic niche spaces (ellipses). This approach should strengthen inferences from comparisons of community metrics using stable isotope data.

Declarations

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Author Contributions

RFB, AMG, KOW and NFF contributed to study conception, design and data analysis RFB contributed field sampling, RFB and AMG funding acquisition, AMG, KOW, NFF supervision, RFB drafted the manuscript.

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Data Availability

Data available on request to the corresponding author

Code availability (software application or custom code): Not applicable.

The software used Rstudio is an open source.

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication We fully adhere to its Code of Conduct and to its Best Practice Guidelines

Conflict of Interest The authors declare no conflicts of interest.

Ethics approval: Not applicable.

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Figures

Figure 1

Map showing sites surveyed, Nicola Lake and Caçapava wetland inside the TAIM Hydrological System, which is located inside the Patos-Mirim hydrological system, southern Brazil, South America.

Figure 2

Average $\pm$ standard deviation (s.d.) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of primary producers (black open boxes), basal sources (gray open boxes) and macroinvertebrate and fish functional groups (symbols as defined in figure) from Nicola Lake and Caçapava wetland.

Figure 3

Average of estimated trophic positions (TP) and standard deviations (s.d.) of invertebrate functional groups and fish trophic guilds from Nicola Lake and Caçapava wetland during two seasons.

Figure 4

Relative contributions of basal production sources to omnivorous and piscivorous fishes in the wetland and lake during cool/wet and warm/dry periods. Bayesian credible intervals of the feasible contributions of each basal production source to the fish guilds: 50 (darkest gray), 75 (medium gray) and 95% (lightest gray).

Figure 5

Left column: Estimated trophic position and $\delta^{13}\text{C}$ values of fishes. Solid lines enclose the standard ellipse area corrected for small samples (SEAc) containing c. 40% of the data, showing the isotopic space for the entire fish assemblage (A), omnivores (B), and piscivores (C) by site and season (Wetland Warm/Wry – black ellipses; Wetland Cool/Wet – red ellipses; Lake Warm/Dry – green ellipses; Lake Cool/Wet – blue ellipses). Right column: Density plots showing the credibility intervals (50 (darkest gray), 75 (medium gray) and 95% (lightest gray)) and modes (black dots) of the estimated standard ellipse areas (SEAB) and the mode (red squares) of the estimated standard ellipse area corrected for small samples (SEAC) by site and season.

Supplementary Files

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