

## Seasonal increases in fish trophic niche plasticity within a flood-pulse river ecosystem (Tonle Sap Lake, Cambodia)

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**Abstract.** Species' responses to seasonal environmental variation can influence trophic interactions and food web structure within an ecosystem. However, our ability to predict how species' interactions will vary spatially and temporally in response to seasonal variation unfortunately remains inadequate within most ecosystems. Fish assemblages in the Tonle Sap Lake (TSL) of Cambodia—a dynamic flood-pulse ecosystem—were studied for five years (2010–2014) using stable isotope and Bayesian statistical approaches to explore both within- and among-species isotopic niche variation associated with seasonal flooding. Roughly 600 individual fish specimens were collected during 19 sampling events within the lake. We found that fishes within the same species tended to have a broader isotopic niche during the wet season, likely reflecting assimilation of resources from either a wider range of isotopically distinct prey items or a variety of habitats, or both. Furthermore, among-species isotopic niches tended to overlap and range more broadly during the wet season, suggesting that floodplain inundation promotes exploitation of more diverse and similar resources by different species in the fish community. Our study highlights that the flood-pulse dynamic that is typical of tropical aquatic ecosystems may be an essential element supporting freshwater fish community structure and the fish diversity that underpins the TSL food web. This flow regime is currently threatened by regional dam development, which may in turn impact the natural function and structure of the fishery food web.

**Key words:** flood-pulse; food webs; Mekong; omnivory; stable isotopes; trophic dynamics.

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### INTRODUCTION

An organism's trophic niche is the evolutionary result of its morphological, physiological, and behavioral adaptations to its environment (Winemiller and Jepsen 1998). At a broader community scale, identifying disparities in species'

trophic roles can delineate the unique scaffolding that forms an ecosystem in terms of energy transfer and resource utilization. Studying spatial and temporal variation in species' trophic niches within a community is also of conservation interest because that variation is often related to the stability of ecosystem functions and resulting

ecosystem services (Hooper et al. 2005). For example, high redundancy in species' trophic niches may reduce the likelihood that natural or human-caused disturbances may alter ecosystem processes. In environments that have a complex mosaic of habitat types and/or substantial seasonal variability, an improved understanding of how species' trophic roles shift within food webs may be useful for devising management strategies to preserve biodiversity and ecosystem services (Tallis et al. 2010).

Current approaches for characterizing species' trophic niche dimensions have advanced from static dietary profiles (Grimm 1995, Tilman et al. 1997) to dynamic and highly parameterized food web models that incorporate multiple interactions among species across complex habitats. Quantifying trophic niche overlap between species can provide an estimate of resource segregation within an environment, as well as provide a descriptive measure of assemblage organization (Corrêa et al. 2011). For example, some isotope tracer studies have broadly shown that omnivore species commonly share dietary items with other species within a community, in contrast to feeding specialists whose diets tend to overlap less with other species (Tillberg and Breed 2004). Interestingly, additional studies using isotope tracers have shown that seasonal variation in the overlap of species' niches can occur within some systems (Jaeger et al. 2010, Pokharel et al. 2015). As a result, there have been renewed efforts to explore species' trophic plasticity and the influence natural and/or human factors have on the adaptability of food web structures (Corrêa et al. 2011).

Omnivory is a common feeding strategy for many fish species in freshwater ecosystems, as many consumers utilize a range of prey items (Prejs and Prejs 1987, Mérona and Rankin-de-mérona 2004, Pouilly et al. 2006). Fishes, in particular, tend to have high dietary adaptability, which makes them useful model organisms for exploring how seasonal changes in aquatic environments may impact food web structure. Furthermore, fish are widely documented to influence overall ecosystem structure, including a food web's trophic interactions (e.g., Carpenter and Kitchell 1993), nutrient cycling (e.g., Vanni 2002), and primary productivity (e.g., Schindler et al. 1997). The structure of fish communities in tropical freshwater ecosystems is of particular

interest because they seasonally experience strong and predictable high flow events that inundate floodplain areas (i.e., the flood pulse; Zaret and Rand 1971, Junk et al. 1989, Ortega et al. 2015), increasing habitat complexity and potentially altering resource availability. As a result, increases in habitat availability and type during the wet season might provide important low trophic-level foraging opportunities for fishes (i.e., plants and insects), in contrast to the dry season when piscivory may be the more dominant strategy (Wantzen et al. 2002). Therefore, seasonal shifts in the physical, chemical, and biological environment have the potential to "reshuffle" fishes' trophic architecture within tropical river and lake ecosystems.

In the field of trophic ecology, scientists strive to understand resource partitioning as a mediator of species coexistence within ecosystems. The partitioning of resources within a food web can manifest as consumers feeding on distinctive prey items within a single habitat or consumers feeding on similar prey items across multiple habitats. Quantifying species' isotopic niches (a representative proxy for their trophic niche; Layman et al. 2007, Boecklen et al. 2011) has proven to be an effective approach to study resource partitioning, reflecting both a consumer's habitat and resource use demands within an ecosystem. Isotopic tracer analysis therefore provides insight associated with basal production, predation, and competition within an ecosystem by enumerating species' trophic roles (Bearhop et al. 2004). Particularly within freshwater ecosystems, isotopic niche approximations have assisted with defining species' roles within complex food web communities, nested in dynamic biogeochemical aquatic landscapes (Jepsen and Winemiller 2002, Willson et al. 2010).

The Lower Mekong River Basin in Southeast Asia is an archetypal seasonal flood-pulse ecosystem, one of the few large tropical river basins that is currently undammed for a large proportion of its length. Within the heart of this system, the Tonle Sap Lake (TSL) is a seasonal wetland in central Cambodia that undergoes substantial annual flooding from the Mekong River mainstem (Appendix S1). As observed in many tropical freshwater systems, the TSL has a diverse fish fauna that supports a highly productive fishery that provides food security for the region, but

substantial gaps remain in our understanding of the TSL's basic ecology (but see Lim et al. 1999). Furthermore, concomitant with increasing agricultural and urban development, numerous water infrastructure projects (i.e., dams and canals) are proposed throughout the Lower Mekong Basin for hydropower, irrigation, flood control, and municipal use (MRC 2009; Lauri et al. 2012). Unfortunately, lessons learned from other flood-pulse systems underscore the importance of natural river flow dynamics in supporting ecosystem function (Junk et al. 1989, Thomaz et al. 2007, Wantzen et al. 2008). With this understanding, there is strong indication that dam development in the TSL region may alter the timing and extent of seasonal flooding with negative consequences on the lake's fishery (Arias et al. 2013, 2014). Therefore, quantitatively establishing the influence of seasonal flood cycles on the food web structural plasticity is needed for the current and future management of the TSL ecosystem (Zarfl et al. 2014, Benchimol and Peres 2015).

In this study, we used carbon (C), nitrogen (N), and sulfur (S) stable isotope tracers and a Bayesian niche breadth model (Swanson et al. 2015) to explore seasonal within- and among-species isotopic niche variation in the TSL. There are four scenarios that depict how species' isotopic niche spaces might change from the dry (Fig. 1a) to wet season (Fig. 1b–e): (1) increased niche breadth with increased niche overlap (Fig. 1b), (2) increased niche breadth with decreased niche overlap (Fig. 1c), (3) decreased niche breadth with increased niche overlap (Fig. 1d), and (4) decreased niche breadth and decreased niche overlap (Fig. 1e). We hypothesize that floodplain inundation during the wet season provides additional food resources for fishes across a more diverse array of habitats, increasing both the total available niche range for individual species and the isotopic range for the entire fish community (Fig. 1b or c). Although previous freshwater fish research has provided some evidence that increased resource partitioning may seasonally

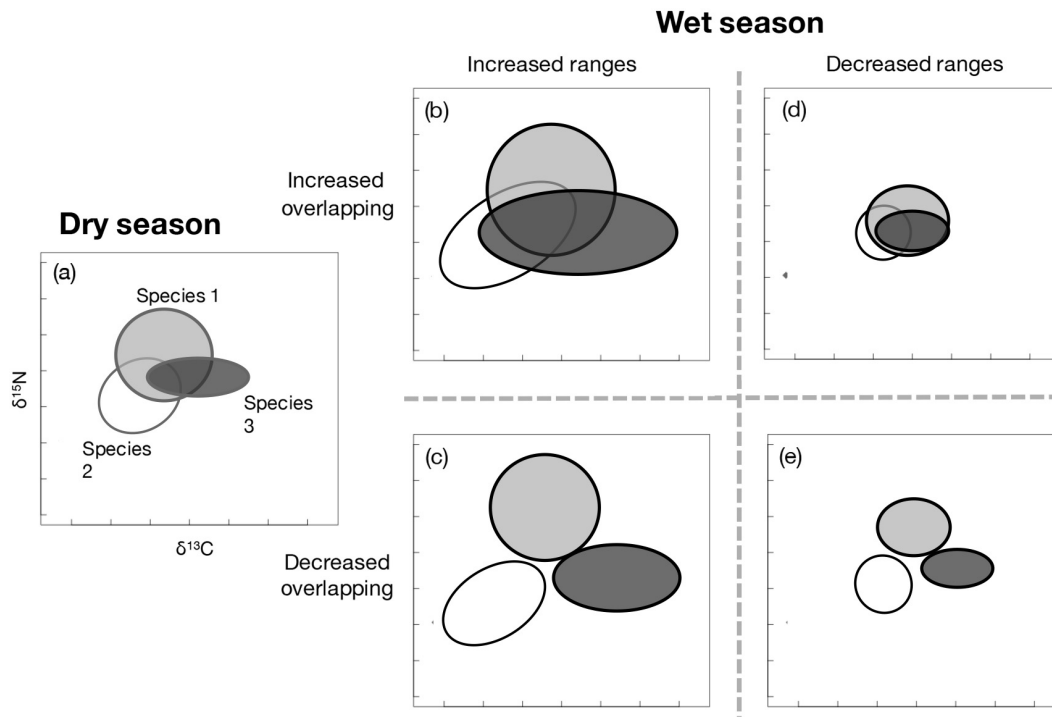


Fig. 1. Conceptual model of four possible scenarios associated with changes in species' trophic niche breadths from the dry season (part a) to the wet season (parts b–e). As flooding occurs during the wet season, species may display an increase (part b or c) or a decrease (part d or e) in trophic niche ranges. Regardless of the change in niche ranges, species can also display an increase (part b or d) or a decrease (part c or e) in niche overlap with other species.

occur in some systems (i.e., niche differentiation; Zaret and Rand 1971), we further hypothesize that increased niche overlap is common for TSL fishes during the wet season when resources are more abundant (Fig. 1b), consistent with observed decreases in resource partitioning by fish in other tropical freshwater environments (Goulding 1980, Meschiatti 1995). Our analyses provide an enhanced understanding of the resource structure of this poorly studied fish community and offers insight into how the fish community may respond to future anthropogenic disturbances within the basin.

## METHODS

### *Study system*

The TSL is the largest lake and wetland system in the Mekong River Basin (UNESCO 2010). As an integrated aquatic and terrestrial landscape influenced by flooding from the mainstem Mekong River, the lake's surface area increases from approximately 2000 km<sup>2</sup> in the dry season (typically May–July), to over 10,000 km<sup>2</sup> during the wet season (typically September–February; MRC 2005). The average lake depth increases from less than one meter in the dry season, to more than 8 m at high water (MRC 2005). There is a diverse set of natural and agricultural habitats within the TSL floodplain, including forests, shrublands, grasslands, and cleared fields. This landscape is exceedingly important for Cambodian people economically, supporting a substantial proportion of Cambodia's rice production and ~60% of its total fishery production (Bonheur and Lane 2002). Evidence also suggests the lake's dynamic flood-pulse cycle is the primary driver supporting numerous plant, reptile, and bird species, many of which are of conservation interest for the region (Davidson 2006).

### *Field sampling*

The TSL fish community is highly diverse and varies seasonally. There are at least 120 species targeted by the fishery, as well as numerous non-fishery species. This creates considerable logistical challenges for obtaining a representative sample using independent survey methods. To illustrate, local fishermen utilize over 200 gear types—including gill nets, basket traps, trawl and seine nets in numerous habitats throughout

the lake and floodplain (Deap et al. 2003). To address this difficulty, we employed a multi-tiered sampling approach to acquire fish specimens from a diverse array of habitats. First, we collected specimens from five regional markets and/or associated fish landing areas located around the perimeter of the TSL (Appendix S1). Second, we approached fishermen and fish traders directly on the fishing grounds and within floating and stilted villages during daily peak trading periods to acquire additional samples that were not collected in the regional markets. Third, we acquired incidental specimens from multi-panel gill netting at six locations around the basin (Appendix S1). All these specimens were then pooled to characterize the fish community within the TSL. This combination of approaches ensured that substantial fishing effort was consistently incorporated spatially around the lake, as well as across seasons. In total, specimen collection involved 19 sampling events over 89 d during both dry (May–August) and wet seasons (September–March), from 2010 to 2014. During field collections, we also attempted to acquire specimens across the observed range of lengths for each species. Sampling efforts for our different collection methods were not balanced across space and time (i.e., extensive multi-panel netting took place exclusively during 2014 to increase the diversity of species included in our study). However, we are confident our approach provides a representative sampling of the most abundant fishery species in the lake during the dry and wet seasons (see Appendix S2 for sample size and collection details).

For this study, we included 18 common species utilizing at least five specimens per season, resulting in a minimum of 10 specimens per species (mean across all species = 21 specimens), with a range of life-history characteristics (i.e., max size, trophic position, and diet breadth), representing 14 families of fishes (Table 1). After collection, the fish were immediately stored on ice until processing at the Inland Fisheries Research and Development Institute of Cambodia. Specimens were measured to the nearest 1 mm for standard and total lengths and then weighed to the nearest 0.1 g total weight. Roughly 1 g dorsal muscle tissue was removed and frozen until the sample could be processed for stable isotope analysis. Samples were oven-dried (–60°C for 24 h) or

Table 1. The mean overlap of each species ( $n = 17$ ) standard Bayesian ellipsoid ( $SEA_b$ ) with all species ellipsoids using carbon ( $\delta^{13}C$ ), nitrogen ( $\delta^{15}N$ ), and sulfur ( $\delta^{34}S$ ) data in three-dimensional (C–N–S) and two-dimensional space during the dry and wet seasons.

Species	C–N–S Overlap (%)		C–N Overlap (%)		C–S Overlap (%)		N–S Overlap (%)	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
<i>Anabas testudineus</i>	21.2	14.2	34.5	8.6	54.3	9.5	66.9	30.9
<i>Barbonymus gonionotus</i>	<b>3.2</b>	<b>27.8</b>	<b>8.2</b>	<b>43.7</b>	<b>31.7</b>	<b>70.1</b>	<b>33.5</b>	<b>51.3</b>
<i>Boesemania microlepis</i>	<b>3.4</b>	<b>11.4</b>	<b>7.8</b>	<b>17.2</b>	80.4	63.8	28.0	22.3
<i>Channa micropeltes</i>	<b>3.1</b>	<b>17.4</b>	<b>15.2</b>	<b>23.1</b>	<b>5.0</b>	<b>21.2</b>	<b>25.6</b>	<b>71.1</b>
<i>Channa striata</i>	<b>13.1</b>	<b>49.3</b>	<b>41.2</b>	<b>58.0</b>	<b>54.7</b>	<b>81.1</b>	60.9	57.2
<i>Cirrhinus siamensis</i>	<b>7.8</b>	<b>9.6</b>	23.7	12.1	44.1	39.8	25.7	21.5
<i>Clarias macrocephalus</i>	8.0	1.9	<b>11.6</b>	<b>32.6</b>	31.5	10.6	29.7	4.9
<i>Cylocheilichthys enoplos</i>	12.3	11.1	21.8	21.4	36.0	35.4	46.4	30.4
<i>Hemibagrus spilopterus</i>	<b>1.3</b>	<b>33.7</b>	<b>16.8</b>	<b>52.2</b>	<b>25.1</b>	<b>54.1</b>	<b>1.5</b>	<b>44.3</b>
<i>Kryptopterus apogon</i>	<b>3.1</b>	<b>6.7</b>	8.8	8.7	<b>47.5</b>	<b>56.9</b>	<b>23.7</b>	<b>38.1</b>
<i>Macrogathus siamensis</i>	<b>17.2</b>	<b>77.9</b>	<b>69.6</b>	<b>83.3</b>	<b>54.9</b>	<b>89.8</b>	<b>60.9</b>	<b>83.1</b>
<i>Notopterus notopterus</i>	<b>18.1</b>	<b>48.6</b>	<b>22.5</b>	<b>56.9</b>	<b>65.9</b>	<b>87.4</b>	<b>64.2</b>	<b>82.3</b>
<i>Pangasius larnaudii</i>	<b>6.0</b>	<b>10.2</b>	<b>9.1</b>	<b>31.3</b>	49.7	24.1	61.5	26.1
<i>Parambassis wolffii</i>	<b>3.3</b>	<b>11.3</b>	<b>12.7</b>	<b>19.8</b>	<b>16.3</b>	<b>41.3</b>	<b>7.3</b>	<b>18.6</b>
<i>Pristolepis fasciata</i>	<b>4.5</b>	<b>52.8</b>	<b>6.8</b>	<b>62.1</b>	<b>33.7</b>	<b>79.8</b>	<b>27.6</b>	<b>68.5</b>
<i>Puntioplites proctozystron</i>	<b>15.0</b>	<b>19.2</b>	48.5	31.9	<b>32.9</b>	<b>47.0</b>	<b>54.0</b>	<b>54.7</b>
<i>Thynnichthys thynnoides</i>	<b>1.3</b>	<b>3.2</b>	<b>2.8</b>	<b>6.3</b>	8.6	8.5	<b>15.6</b>	<b>59.9</b>

Notes: Bold cells identify increases in species' isotopic overlap from the dry to wet season. We removed *Mystus albolineatus* since there were not enough data for this type of analysis.

freeze-dried ( $-80^{\circ}C$  for 24 h) in Cambodia prior to shipping to the University of Washington (UW) for further processing and analysis.

### Stable isotope analysis

We used the distribution of carbon ( $^{13}C/^{12}C$ ), nitrogen ( $^{15}N/^{14}N$ ), and sulfur ( $^{34}S/^{32}S$ ) stable isotopes to explore food web structure within the TSL. Carbon stable isotopes indicate the origin of C sources consumed by an organism, providing insight into primary and secondary production. Nitrogen stable isotopes can reveal the trophic positioning of species, with elevated  $^{15}N/^{14}N$  being suggestive of species higher in the trophic pyramid. Sulfur stable isotopes assist with identification of the habitats that species are utilizing because they differentiate benthic and pelagic producers, as well as marsh and phytoplankton producers. We included  $^{34}S/^{32}S$  to allow us to discriminate between detrital and living algae resources, because it is more sensitive than  $^{13}C/^{12}C$  (France 1996) and there is very little enrichment of  $^{34}S$  over  $^{32}S$  between trophic levels (McCutchan et al. 2015). Taken together, this suite of tracers provides information about the type of food items being consumed and spatial

variability in where those resources are located across an aquatic landscape.

Upon arrival to UW, samples were again freeze-dried to remove any residual water and homogenized to a fine powder. Subsequently, between 0.4 and 6 mg of material was packed into tin or silver capsules, depending on the specific analysis. We then performed stable isotope analysis in the UW  $\Delta \times$  IsoLab by standard combustion and subsequent reduction (N), using a Costech ECS 4010 Elemental Analyzer coupled to Thermo Finnigan MAT 253 (Costech Analytical Technologies Inc., Valencia, California, USA) in continuous flow mode. Lipid extraction or correction of  $^{13}C/^{12}C$  was not needed because the sample C:N ratios (muscle tissue = 3.47) were below the suggested cutoff of 3.5 by Post et al. (2007). Stable isotope compositions throughout our study are expressed in terms of delta values ( $\delta$ ) in per mil (‰) relative to the international standards of Vienna Pee Dee Belemnite, atmospheric air, and Vienna Canyon Diablo Troilite for C, N, and S, respectively.

Quantifying variation in species' trophic niche space across time and space using isotopes can be challenging because of variation in "baseline" values (i.e., specimens at the base of the food

chain that provide a comparable starting point for higher trophic-level assessments of feeding position for species such as fish). If “trophic expansion” is observed for a particular species, using stable isotope values across seasons, that variation could be explained due to natural seasonal variation in the  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  incorporated into baseline specimens in addition to genuine changes in prey items consumed by higher trophic-level species. In our study, we pooled together fish collections spanning multiple years and locations but baseline information was not available to incorporate into our analyses. Despite our inability to account for the possibility of resource baseline expansion across seasons, we believe our numerous and diverse collection of specimens from this region is extensive enough to identify general patterns of resource use for fishes within the TSL.

### Statistical analyses

In the past decade, considerable progress has been made in quantifying species’ trophic niches utilizing stable isotope data (Layman et al. 2007, Jackson et al. 2011). Researchers often use convex hulls to define the maximum isotopic area in two-dimensional space, but concern associated with the sensitivity of this approach to outliers and differences in sample size has led to the increased use of standard ellipse approaches (Jackson et al. 2011). We calculated standard ellipses with a standard sample size correction ( $\text{SEA}_c$ ; Jackson et al. 2011), using pairwise combinations of  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  data to estimate species’ isotopic area in two-dimensional space (e.g.,  $\delta^{13}\text{C}$  with  $\delta^{15}\text{N}$ , and  $\delta^{13}\text{C}$  with  $\delta^{34}\text{S}$ ). First, we calculated within-species ellipse centroids for the dry and wet seasons to assess the mean shift in occupied isotopic space for each species. A two-tailed  $t$  test was used to determine whether the seasonal change in species’ mean isotopic values (i.e.,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$ ) was significant for the community. Second, we used within-species ellipses to calculate niche range expansion and the significance of seasonal change for each species using all three isotopic tracers (two-tailed  $t$  tests). Third, we calculated a within-season beta-diversity value (i.e., the amount of dissimilarity) for species’ ellipses, using the Jaccard’s index (Villéger et al. 2008) to determine the extent of seasonal niche overlap within the community. Within the context of our study,

the beta-diversity metric calculated for each species determined its overlap with all other species’ isotopic ellipses, with lower beta-diversity values indicating reduced niche overlap and higher values indicating increased niche overlap. For each species, we assessed whether their mean niche overlap with all other species significantly increased from the dry to wet season.

Lastly, complementing the two-dimensional standard ellipse approach, we incorporated isotope data into a Bayesian framework that calculates species’ ellipses in three-dimensional space (Swanson et al. 2015) for the dry and wet seasons. Using Bayesian ellipsoids ( $\text{SEA}_b$ ) to explore the overlap between species allowed us to simultaneously incorporate the data from all three isotopes. This meant we could maximize our ability to infer how fish use habitat and resources seasonally. For each species, we calculated a mean overlap value with all other species to identify whether they were occupying unique or shared isotopic niche space within the community. Following the protocol established by Swanson et al. (2015), we used a default prior to construct a trophic niche region and utilized 10,000 samples from the normal distribution to obtain a single Monte Carlo estimate. Given that this approach expresses uncertainty about unknown parameters probabilistically, significance tests were not appropriate for these data. We removed *Mystus albolineatus* since there were not enough data for this type of analysis. We completed all analyses in R (R Development Core Team 2017) and used the following packages: ape, base, BiodiversityR, Geometry, Mvtnorm, nicheROVER, Pastecs, plyr, siar, and vegan.

## RESULTS

Seasonal shifts in species’ mean  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  values were not significant for the fish community as a whole ( $\delta^{13}\text{C}$ :  $t_{17} = -1.866$ ,  $P = 0.300$ ;  $\delta^{15}\text{N}$ :  $t_{17} = -1.545$ ,  $P = 0.141$ ;  $\delta^{34}\text{S}$ :  $t_{17} = -0.709$ ,  $P = 0.487$ ; see Fig. 2 for paired display of species shifts). However, within-species isotopic variation expanded significantly ( $\delta^{13}\text{C}$ :  $t_{17} = 1.847$ ,  $P = 0.041$ ;  $\delta^{15}\text{N}$ :  $t_{17} = 2.930$ ,  $P = 0.003$ ;  $\delta^{34}\text{S}$ :  $t_{17} = 6.501$ ,  $P < 0.001$ ) from the dry to wet season for most species (see Fig. 3 for all species; see Fig. 4 for selected species-specific  $\delta^{13}\text{C}$  with  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  with  $\delta^{15}\text{N}$  examples of

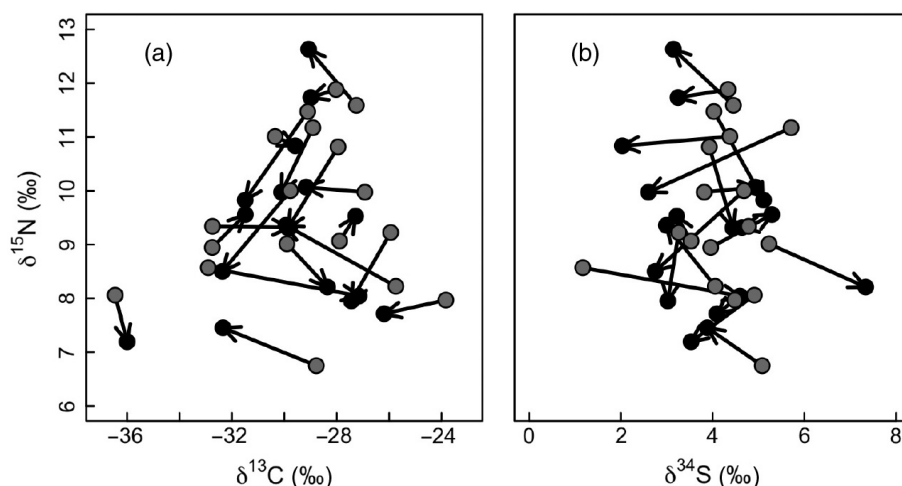


Fig. 2. Fish species' ( $n = 18$ ) isotopic values for carbon, nitrogen, and sulfur. Points are mean values for each species and are linked via arrows displaying their temporal shift in trophic space from the dry season (gray) to the wet season (black).

seasonal niche expansion). Among all species and individuals,  $\delta^{13}\text{C}$  values ranged by  $>20\text{‰}$ , from  $-39.4\text{‰}$  to  $-18.4\text{‰}$  during the dry season and increased from  $-41.0\text{‰}$  to  $-18.3\text{‰}$  during the wet season.  $\delta^{15}\text{N}$  showed a smaller range among samples, with values from  $5.5\text{‰}$  to  $13.0\text{‰}$  during the dry season and increasing to a range of  $4.8\text{‰}$  to  $13.5\text{‰}$  during the wet season.  $\delta^{34}\text{S}$  values spanned from  $0.1\text{‰}$  to  $7.9\text{‰}$  during the dry season, and subsequently increased to a range of  $4.8\text{‰}$  to  $13.5\text{‰}$  during the wet season. For many species, their niche range expansion encompassed more depleted isotopic tracer values (Fig. 3), although there were also examples of wet season niche range expansion along other axes (enriched  $\delta^{15}\text{N}$  range, Fig. 4a; enriched  $\delta^{13}\text{C}$  range, Fig. 4d; or  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  range enrichment and depletion, Fig. 4b, c). When comparing the beta-diversity of species between seasons (i.e., the similarity of all species' isotopic niches), we found a greater overlap of species' standard ellipses ( $\text{SEA}_c$ ) in the wet season relative to the dry (see Fig. 5a–d for  $\delta^{13}\text{C}$  with  $\delta^{15}\text{N}$  and  $\delta^{15}\text{N}$  with  $\delta^{34}\text{S}$  pairings; see Fig. 5e displaying 12 of 18 species as significantly increasing ( $P > 0.05$ ) in  $\delta^{13}\text{C}$  with  $\delta^{15}\text{N}$   $\text{SEA}_c$  overlap and Fig. 5f displaying 10 of 18 species significantly increasing ( $P > 0.05$ ) in  $\delta^{13}\text{C}$  with  $\delta^{15}\text{N}$   $\text{SEA}_c$  overlap).

Dry season, Bayesian isotopic niche ellipsoids ( $\text{SEA}_b$ ) incorporating  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  data

displayed a mean C–N–S overlap of 8.1% in contrast to 25.7% during the wet season among all species. Individual species' overlaps—the proportion of a species' isotopic niche overlapping with all other species' isotopic niches—ranged from 1.3% (*Hemibagrus spilopterus* and *Thynnichthys thynnoides*) to 21.2% (*Anabas testudineus*) during the dry season and 1.9% (*Clarias macrocephalus*) to 77.9% (*Macrognathus siamensis*) during the wet season (Table 1). For some species, particular isotopic dimensions contributed more substantially than others to the three-dimensional overlap of species' niche ellipsoids (Table 1), but all three stable isotopes contributed significantly to the C–N–S overlap values (i.e., C:  $R^2 = 0.515$ ,  $P < 0.001$ ; N:  $R^2 = 0.598$ ,  $P < 0.001$ ; S:  $R^2 = 0.205$ ,  $P < 0.001$ ; see Appendix S3).

## DISCUSSION

Our study explored seasonal shifts in the within- and among-species isotopic niche variation of TSL fishes in wet vs. dry periods to elucidate the complex species habitat and resource associations that characterize flood-pulse river systems. Changes in a consumer's seasonal isotopic niche reflect an isotopically expanded or contracted prey base, which can arise from either utilizing more diverse prey items or accessing prey from different habitats with distinct isotopic

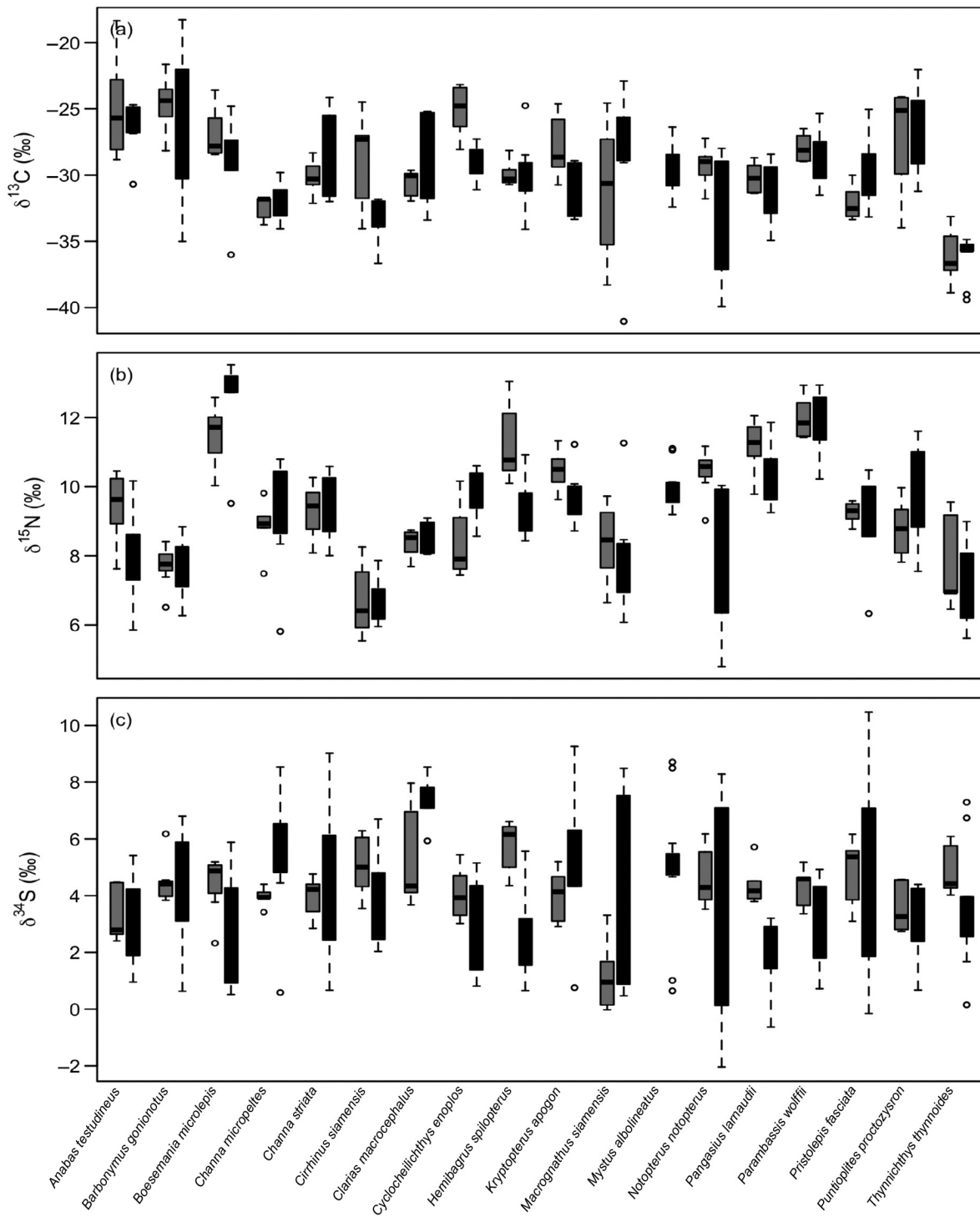


Fig. 3. Each species  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  range of values during the dry (gray) and wet (black) seasons. For all 18 species, the maximum and minimum isotope values along with the first and third quartiles for nitrogen and carbon are displayed (outliers are identified with circles).



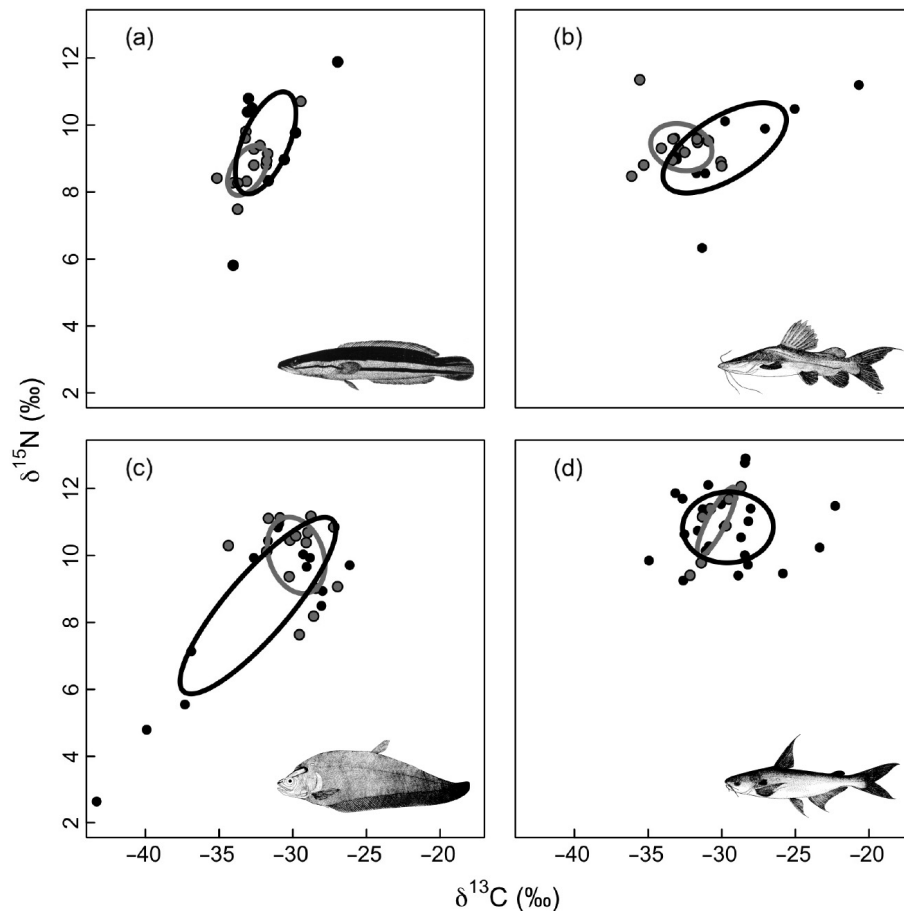


Fig. 4. Four species in the Tonle Sap Lake with points representing individual specimen  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic values for each species. Standard ellipses ( $\text{SEA}_c$ ) identify the trophic niche space for (a) *Channa micropeltes*, (b) *Hemibagrus spilopterus*, (c) *Notopterus notopterus*, and (d) *Pangasius larnaudii* during the dry (gray) and wet (black) seasons. Sulfur data are not displayed here but display a similar pattern when plotted with the nitrogen isotope values.

signatures, or both (Newsome et al. 2007). In either case, a wider or narrower isotopic niche space reflects changes in available resources in response to environmental drivers. Our finding of generally higher isotopic niche widths during the wet season suggests that while omnivory appears to be widespread throughout the year, individuals within the same species appear to expand their resource base through consuming a broader range of prey items and/or utilizing a wider variety of habitats during the wet season in contrast to the dry season. Furthermore, among-species isotopic niches tend to overlap more during the wet season, suggesting that floodplain inundation promotes an increase in

species utilization of similar resources and/or habitats within the fish community. Taken together, species' isotopic niche range and overlap increase during seasonal flooding (Fig. 1b). While most species' mean trophic positions did not substantially change between seasons, as indicated by their mean  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  values, the isotopic variation we observed (i.e., species' isotopic ellipses) indicates a dynamic seasonal relationship between fishes' trophic structure and their freshwater environments.

The flood-pulse concept posits that fish will have access to a greater diversity of aquatic habitats and novel food sources during floodplain inundation within tropical freshwaters because of

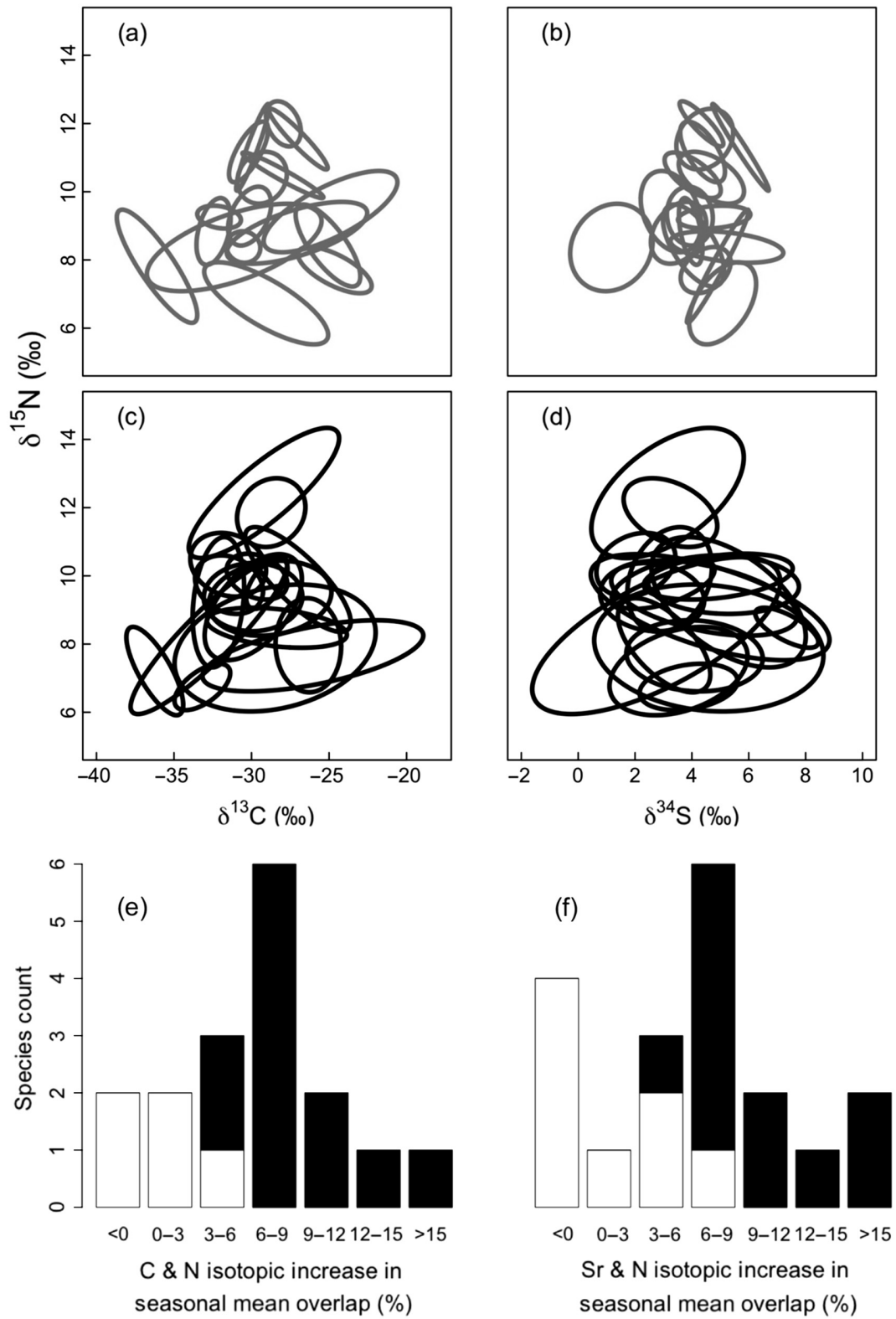


Fig. 5. Species ( $n = 18$ ) isotope niches are represented by standard ellipses ( $\text{SEA}_c$ ) for the dry (gray ellipses)

(Fig. 5. *Continued*)

and wet (black ellipses) seasons. The bivariate relationship between nitrogen and carbon isotope values (a, c), as well as nitrogen and sulfur isotopes values (b, d) is represented. The percentage increase in overlap of each species with all other species that occurred seasonally (dry to wet season) is displayed for each isotopic pairing (e, f) along with the significance of overlap change for each species (white bars are non-significant and black bars are significant; paired *t* test  $P < 0.05$ ).

the inclusion of terrestrial food sources from the floodplain (Junk et al. 1989, Amoros and Bornette 2002, Galacatos et al. 2004). Within the TSL, an increase in resource availability during the wet season is highly likely, given that a substantial amount of terrestrial organic plant matter is annually submerged around the lake (Arias et al. 2013). Relatively nominal estimates of primary production within the TSL (Holtgrieve et al. 2013) paired with its high fishery output (MRC 2005) also support the theory that additional resources are seasonally derived from floodplain habitats and that these allochthonous resources are critical in maintaining fish/fishery productivity. In step with those observations, the total range in isotopic C values among all our samples ( $-39.4$  to  $-18.4$   $\delta^{13}\text{C}$ ) was greater than the typical range for fishes in other ecosystems ( $-29$  to  $-20$   $\delta^{13}\text{C}$  in Hesslein et al. 1991, Vander Zanden and Casselman 1999, Fuller et al. 2012). Such an increase in the TSL within- and among-species isotopic ranges could be associated with reduced competitive interactions between species, due to greater resource availability in the floodplain during the wet season. Conversely during the dry season, specialized foraging strategies such as exclusive piscivory may be more common because of reduced basal resource availability (i.e., zooplankton and cyanobacteria may be the primary energy sources during low water periods; Samal 2009). While there are certainly advantages associated with dietary specialization at any time of the year, the diverse and abundant resources accessible to fish during the wet season may counterbalance the benefits of specialization for some fish.

In addition to the more typical C and N tracers incorporated into our study, S was also a significant contributor to the overlap of fishes' trophic niches during the wet season. Variation in  $\delta^{34}\text{S}$  is driven primarily by redox conditions among habitats (Peterson and Howarth 1987), which suggests that many of the fishes are capitalizing not only on increased prey availability within floodplain

habitat patches, but are also foraging across a variety of habitat locations or types. Although local assemblages of fishes and macroinvertebrates can characterize particular habitat types (Arrington and Winemiller 2006), the range in our  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  results suggests that fish species consume a diversity of prey items and/or forage in disparate habitat patches. Building on our understanding that the fish community utilizes floodplain habitat heterogeneity to support a diverse array of life-history strategies (such as reproduction and seasonal dormancy; Rainboth 1996), we infer that a mosaic of habitats may be required to support TSL fishes. However, while the S isotope results indicate that the fish community is exploiting resources from a range of habitats, they do not indicate the relative importance of specific habitats as dietary sources for each species. For example, the broad range in S isotope values found in *Notopterus notopterus* could be a result of individuals feeding on prey items in two different habitat types or feeding in the same habitat type in two different locations. Further work mapping the relationship between  $\delta^{34}\text{S}$  of sulfur and lower trophic levels is necessary before we can use this tracer to identify specific habitat types within the TSL. Similarly, additional research exploring species seasonal dietary dependency on particular habitat types, such as flooded gallery forest and shrublands, is needed because those habitats may be disproportionately impacted by future anthropogenic disturbances associated with flow regime change (Arias et al. 2012).

Ellipsoid overlap (i.e., all three isotopic tracers combined) and the relative contribution of each tracer varied between species. However, integrating the ellipsoid results with existing knowledge about specific fishes permitted some speculation about the relative influence of foraging behavior vs. habitat use on explaining their niche breadth and overlap with other species. Using all the tracer data simultaneously also allowed us to infer additional details about species within a

community context. For example, *Thynnichthys thynnoides* had a low C–N–S overlap value with other species across both seasons, suggesting that it occupies a unique trophic niche within the community, consistent with its classification as a periphyton grazer. However, this species had a relatively high N–S overlap value with the other fishes, suggesting it may be utilizing resources from similar habitats as many other species in the fish community. In contrast, *N. notopterus* overlapped substantially across all tracers, suggesting this species has a broad trophic niche utilizing common resources and habitats with numerous fishes in the community, consistent with its classification as a broad omnivore that displays movements between many floodplain habitat types. This improved understanding of TSL species, informed by our trophic niche overlap findings, provides a solid foundation for further studies of fish species' interactions within this region.

Understanding species' interactions within the TSL is further complicated because the biogeochemistry of the region appears to be spatially and temporally dynamic, potentially influencing our stable isotope values. Modeling, theory, and field data indicate changing redox conditions both horizontally and vertically through the floodplain, while the permanent lake maintains a generally mixed oxic conditions (Lamberts and Koponen 2008, Holtgrieve et al. 2013; B. Miller and G. Holtgrieve, *unpublished data*). Conditions of extreme hypoxia/anoxia can have pronounced effects on nutrient biogeochemistry and resource pathways, therefore confounding the standard interpretation of these isotopes in a food web context. For example, some individuals of *N. notopterus* show pronounced depletion of both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  during the wet season. The low C values suggest a methanogenic resource pathway, and the associated depletion of N indicates a source other than nitrate for this resource pathway (such as ammonium). Nevertheless, these complexities do not change the general result that most species display broader trophic niche variation during the wet season, suggesting that the seasonal inundation of the complex network of floodplain habitats is sustaining the current food web structure of TSL fish community.

Throughout the tropics, freshwater flood-pulse systems are experiencing increased levels of human alteration (i.e., dam construction,

channelization, water extraction, and wetland development) threatening the seasonal connectivity between terrestrial and aquatic environments and consequently the flora and fauna that they support. Reductions in the amount or length of floodplain inundation in the TSL are particularly concerning because our findings suggest the high fish diversity within the system is at least partially supported by increased resource availability during the wet season (see Taphorn and Lilyestrom 1985). Altering the composition, location, or quantity of seasonally available resources to fish may negatively impact the coexistence of resident species that appear to support this systems' food web structure (Chesson and Warner 1981). A reduction in the lake's floodplain connectivity may also influence the distribution and abundances of migratory fishes entering the system during the wet season that are believed to be subsidizing resident predatory fishes (Winemiller and Jepsen 1998). Curiously, previous tropical river studies exploring whether human alteration of the seasonal flow regime impacts fishes' ecological niches have produced equivocal results (Zaret and Rand 1971, Goulding 1980, Meschiatti 1995, Corrêa et al. 2011, Sá-Oliveira et al. 2014). Each river basin's unique environmental and human disturbance landscape undoubtedly regulates the impact that flow regime change has on the structure of aquatic food webs which, at least in part, accounts for the range of literature conclusions on this topic. As such, it remains unknown what the cumulative impact of the over 200 dams in development or scheduled for construction in the Mekong River Basin will have on the fishes of the TSL (MRC 2009). Ultimately, our research highlights that an assortment of floodplain habitats, potentially providing pathways for terrestrially derived C sources, may be critical for the preservation of species diversity and productivity in the TSL. Additional insights associated with the seasonal connectivity of habitat types are needed to successfully target species and habitats for protection within the ecosystem.

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