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Consumer trophic positions respond variably to seasonally fluctuating environments

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Abstract. The effects of environmental seasonality on food web structure have been notoriously understudied in empirical ecology. Here, we focus on seasonal changes in one key attribute of a food web, consumer trophic position. We ask whether fishes inhabiting tropical river–floodplain ecosystems behave as seasonal omnivores, by shifting their trophic positions in relation to the annual flood pulse, or whether they feed at the same trophic position all year, as much empirical work implicitly assumes. Using dietary data from the Tonle Sap Lake, Cambodia, and a literature review, we find evidence that some fishes, especially small piscivores, increased consumption of invertebrates and/or plant material during the wet season, as predicted. However, nitrogen stable isotope (δ^{15}N) data for 26 Tonle Sap fishes, spanning a broader range of functional groups, uncovered high variation in seasonal trophic position responses among species (0 to ±0.52 trophic positions). Based on these findings, species respond to the flood pulse differently. Diverse behavioral responses to seasonality, underpinned by spatiotemporal variation at multiple scales, could be central for rerouting matter and energy flow in these dynamic ecosystems. Seasonally flexible foraging behaviors warrant further study given their potential influence on food web dynamics in a range of fluctuating environments.

Key words: aquatic; environmental variation; fishes; food webs; omnivory; stable isotopes; stomach contents; tropical river–floodplain ecosystem.

Introduction

Most ecosystems are characterized by seasonal variation in temperature, light, or precipitation that influences resource availability for organisms. Despite early interest and recognition that seasonal variation influences animal communities (Elton 1927), the consequences of seasonality for food web patterns and processes remain poorly documented. However, this topic has recently garnered increasing interest among both aquatic and terrestrial ecologists (e.g., CaraDonna et al. 2017, Hampton et al. 2017).

Temporal food web studies can be informed by existing spatial food web theory (McMeans et al. 2015, 2016). For example, flexible foraging by mobile predators, which feed across different trophic levels to track abundant or accessible prey, promotes food web stability by weakening interaction strengths and releasing low-density prey from predation pressure (Kondoh 2003, McCann et al. 2005). Consistent with this theory, empirical work suggests that spatial heterogeneity weakens interaction strengths in river floodplains (Bellmore et al. 2015) and that stream food webs vary across spatial gradients (Thompson and Townsend 2005). In freshwater lakes, the trophic position of piscivorous fish varies across systems (Vander Zanden et al. 2000) and can decline from large to small lakes as the relative availability of inshore invertebrate prey increases (Post and Takimoto 2007, Tunney et al. 2012). While much of this work implicitly assumes that the

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extent of omnivory within any given system remains static through time, emerging evidence indicates that consumer trophic position can change on an interannual (Ruiz-Cooley et al. 2017) and seasonal basis (Akin and Winemiller 2006). Changes in omnivory through time, whereby a consumer shifts its trophic position to flexibly track different prey during different time periods (Takimoto et al. 2002, Křivan and Diehl 2005, Kratina et al. 2012), could have equally important consequences for food web structure and stability as those recognized in space (McCann et al. 2005, Thompson et al. 2007, Cross et al. 2013). Therefore, it remains important to explore if and how consumer trophic positions respond to temporal variation in nature, especially given that climate change is already altering existing seasonal signals in many of Earth's ecosystems (Wolkovich et al. 2014).

Here, we use tropical river–floodplain systems as a model system to investigate the response of fish trophic position to seasonal variation in the environment. Seasonal diet data for freshwater fishes are more common for tropical systems with wet-dry seasonality than for temperate and Arctic systems with summer-winter seasonality due to the paucity of winter data (McMeans et al. 2015, Hampton et al. 2017). Physical, chemical, and biological processes in tropical floodplains are governed by the flood pulse (Junk et al. 1989). Rising water of the "moving littoral zone" expands outward from the permanent open water into surrounding floodplain habitats (Fig. 1), providing new aquatic habitat that supports plant and invertebrate production (Junk et al. 1989, Arias et al. 2013). Flood pulse recession, on the other hand, strands aquatic vegetation (Bayley 1988) and increases per-unit-area densities of fishes, which increases foraging efficiency of piscivores (Winemiller 1989).

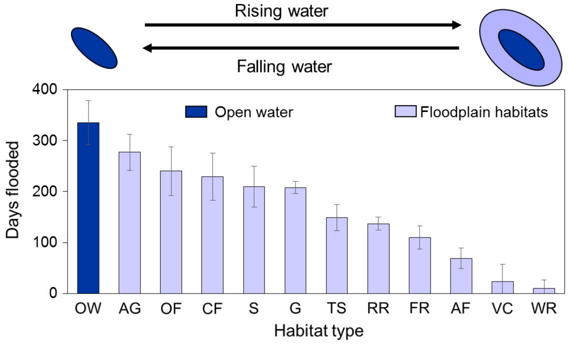

FIG. 1. The number of days per year with standing water (days flooded; mean ± SD) for open water and flood plain habitats in the Tonle Sap modeled for an average year from survey transect plots (data are from Table 1 of Arias et al. 2013). Flood plain habitats fill and empty as rising and falling water expands and contracts from the center open water of the lake. Habitats are abbreviated as follows: OW, open water; AG, aquatic grassland; OF, open forest; CF, closed forest; S, shrubland; G, grassland; TS, tall shrub land; RR, receding rice; FR, floating rice; AF, abandoned field; VC, village crop; WR, wet season rice.

Given these seasonal dynamics, the availability of floodplain-derived plant and invertebrate prey to consumers should peak in the wet season (Winemiller 1989, Wantzen et al. 2002, Correa and Winemiller 2014). Recent work using stable isotopes (δ^{15}N and δ^{13}C) supports this idea by demonstrating that fishes can become more generalized feeders during the wet season, likely reflecting increased access to a wider range of habitats and food resources while floodplains are inundated (Costa-Pereira et al. 2017, Pool et al. 2017). Some evidence argues for consistent increases in trophic position across the fish assemblage during the dry season (Wantzen et al. 2002), whereas other studies report diverse foraging strategies with no apparent seasonal pattern generalizable across species (Novakowski et al. 2008). Patterns and potential consequence of seasonal omnivory (i.e., food chain omnivory that results in a shift in trophic position) for tropical flood plain food webs therefore remain unclear.

We combined dietary (stomach content) and nitrogen stable isotope data (δ^{15}N) to explore the extent of seasonal omnivory in tropical floodplain fishes. We first test the hypothesis that piscivorous fish broaden their diet to consume greater proportions of food items at lower trophic levels during the wet season. To do so, we analyzed available dietary data for four common piscivorous fishes from the Tonle Sap Lake in Cambodia combined with a literature review of piscivore dietary data to broaden our findings to other floodplain fishes and ecosystems. We then explored whether seasonal trophic position shifts are consistent across a broader range of fish functional groups and body sizes using δ^{15}N data for 26 fish species sampled from the Tonle Sap Lake. Given the high biogeochemical complexity of tropical floodplain ecosystems and mobility of tropical floodplain fishes (Junk et al. 1989, Pettit et al. 2017), both of which could bias temporal trophic position estimates based exclusively on δ^{15}N or dietary data, combining these approaches should provide a more comprehensive trophic assessment (Rybczynski et al. 2008). Although focused on fishes in tropical floodplains, our findings are broadly relevant for consumers in other seasonal ecosystems.

METHODS

The Tonle Sap Lake in Cambodia is the largest lake in the Mekong River Basin and Southeast Asia. This relatively shallow lake (maximum depth 15 m) experiences a single flood pulse annually (Arias et al. 2013, Kong et al. 2017). During the wet season, rising waters in this system expand outward from the 2,600-km^2 permanent water at the lake's center and expand into 12,876 km^2 of surrounding natural and agricultural habitats (Fig. 1), stimulating aquatic primary production (Arias et al. 2013). Stable isotope and stomach contents data were collected as part of a broader research effort involving surveys at multiple locations around the Tonle Sap (Siem

Reap, Kampong Chhnang, Kampong Thom, and Pursat Provinces; see Pool et al. 2017) during both seasons. Fish samples were assigned to either the wet or dry season according to previous research on the Tonle Sap Lake. For dietary data, the wet season was considered July to October and the dry season November to June (Arias et al. 2013, Kong et al. 2017). To account for tissue turnover time for stable isotope analysis, fish sampled for stable isotopes during July were assigned to the dry season, and those captured during November, December, and January were assigned to the wet season (details provided in Appendix S1 and see Pool et al. [2017]). We define a "piscivore" as a fish that mostly feeds on fish, but that also may consume other types of food items (e.g., invertebrates and plants). An "omnivore" is defined as a fish that normally consumes both plant and animal (mostly invertebrate) biomass, but little or no fish. "Invertivores" and "herbivores" feed nearly exclusively on invertebrates or plant matter, respectively. Assigning tropical floodplain fishes into functional groups is challenging because diet composition may change during ontogeny or according to spatiotemporal variation in habitat conditions (Winemiller 1989, Novakowski et al. 2008), and fish considered to be piscivorous can feed as omnivores (e.g., the *Channa* spp. in our study, see *Results*). We therefore opted to place fish species into these four broad functional groups.

To explore dietary shifts in piscivores, stomach content data were analyzed for four Tonle Sap fish species that consume fish as well as invertebrates and plants (Table 1). These data were obtained from specimens sampled during July 2014–April 2015 (Kong et al. 2017) and reported as proportions of fish, invertebrate, and plant material by mass relative to total stomach contents mass. Fish with empty stomachs were excluded. Seasonal changes in proportional weight of invertebrate, fish, and plant material consumed by each species were analyzed using zero-inflated beta regression (due to the presence of zeros in the data) in R package zoib (Liu and Kong 2015; see Appendix S1 for detail). We included season (wet, dry) and total body length as explanatory variables and included species identity as a random intercept. To determine whether dietary findings from the Tonle Sap are consistent with evidence from other tropical floodplains, we reviewed literature accounts to obtain dietary data recorded during different phases of the annual flood pulse for piscivores (i.e., fish classified as piscivores plus any omnivores with stomach contents that included significant fractions of fish). Each report for a single species or trophic guild constituted a single "evidence item," with a total of 34 evidence items extracted from the 11 data sources that met our inclusion criteria (see Appendix S1 for details).

To explore trophic shifts in a broader range of functional groups, tissues for stable isotope analysis were obtained from 26 fish species (Table 2) collected from the Tonle Sap between November 2010 and April 2015 using multi-panel gill nets or purchased from local fishers or lakeside markets. To account for seasonal isotopic variation at the base of the food web (Post 2002, Dalerum and Angerbjorn 2005), aquatic invertebrate taxa were used as baseline indicators of benthic (snails, crabs) and pelagic (zooplankton, clam, mussel) production and were sampled with dip nets and plankton nets (see Appendix S1 for details). All samples were dried, homogenized, and weighed into tin capsules before being analyzed for δ^{15}N via a Costech ECS 4010 Elemental Analyzer (Valencia, CA, USA) coupled to a Thermo Finnigan MAT 253 isotope ratio mass spectrometer (Bremen, Germany). Stable isotopes are expressed as delta values (δ) in permil (‰) relative to the international standard for nitrogen (atmospheric air).

We applied the following single source equation to calculate fish trophic positions

$$\mathrm{TP}_{\mathrm{consumer}} = 2 + \delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{baseline}}/\mathrm{TDF} \quad (1)$$

TABLE 1. Sample size (*n*), total body length, and dietary proportions of fish, invertebrate, and plant material in stomach contents (by mass) of four Tonle Sap fishes sampled in both wet and dry seasons.

			Stomach contents data		
Species and season	*n*	Length (mm)	Fish	Invertebrate	Plant
Anabas testudineus (climbing perch)					
Dry	13	122 ± 14	0.52 ± 0.22	0.10 ± 0.22	0.12 ± 0.17
Wet	22	118 ± 24	0.48 ± 0.33	0.25 ± 0.29	0.11 ± 0.16
Notopterus notopterus (bronze featherback)					
Dry	12	197 ± 25	0.42 ± 0.26	0.27 ± 0.23	0.17 ± 0.07
Wet	6	148 ± 107	0.20 ± 0.31	0.56 ± 0.35	0.10 ± 0.07
Channa striata (striped snakehead)					
Dry	5	282 ± 55	0.57 ± 0.08	0.01 ± 0.00	0.08 ± 0.04
Wet	10	256 ± 90	0.47 ± 0.13	0.09 ± 0.24	0.13 ± 0.04
Channa micropeltes (giant snakehead)					
Dry	25	367 ± 45	0.68 ± 0.14	0.01 ± 0.04	0.11 ± 0.08
Wet	7	395 ± 89	0.70 ± 0.10	0.03 ± 0.06	0.10 ± 0.05

Note: All values are mean ± SD.

TABLE 2. Total mean body length, seasonal shift (Δ), and effect size (±95% confidence intervals) of the change in trophic position (calculated as mean wet − mean dry trophic position) for 26 fish species from the Tonle Sap.

						n		CV	
Species	Functional group	Length (mm)	Seasonal Δ TP	Effect size	95% CI	Dry	Wet	Dry	Wet
Trichopodus trichopterus	omnivore	79	0.09	0.27	0.80	10	15	0.13	0.14
Rasbora aurotaenia	omnivore	93	0.16	0.65	0.93	8	11	0.06	0.10
Pristolepis fasciata	invertivore	99	0.13	0.44	0.63	16	27	0.06	0.11
Trichopodus microlepis	**omnivore**	**101**	**0.54**	**2.66**	**1.24**	**9**	**10**	**0.06**	**0.09**
Paralaubuca typus	invertivore	103	0.16	0.59	0.94	5	37	0.10	0.09
Anabas testudineus	**piscivore**	**108**	**−0.30**	**−1.02**	**0.94**	**11**	**9**	**0.09**	**0.13**
Henicorhynchus siamensis	**herbivore**	**111**	**0.28**	**0.76**	**0.73**	**9**	**48**	**0.11**	**0.15**
Thynnichthys thynnoides	**omnivore**	**112**	**−0.31**	**−1.34**	**0.77**	**9**	**39**	**0.13**	**0.09**
Labiobarbus leptocheila	omnivore	124	−0.27	−0.82	0.84	8	22	0.11	0.14
Parambassis wolffii	piscivore	124	0.00	0.00	0.72	16	14	0.04	0.09
Barbonymus gonionotus	**omnivore**	**151**	**0.23**	**0.66**	**0.64**	**12**	**50**	**0.08**	**0.13**
Mystus albolineatus	piscivore	155	0.12	0.57	0.76	13	15	0.08	0.05
Osteochilus melanopleura	**omnivore**	**157**	**−0.52**	**−2.09**	**1.10**	**8**	**12**	**0.06**	**0.11**
Puntioplites proctozysron	omnivore	164	0.09	0.23	0.82	16	9	0.10	0.17
Ompok bimaculatus	piscivore	166	0.14	0.51	0.99	12	6	0.09	0.07
Hemibagrus spilopterus	invertivore	185	−0.03	−0.09	0.66	12	35	0.04	0.11
Macrognathus siamensis	invertivore	200	−0.10	−0.28	0.90	12	8	0.10	0.18
Notopterus notopterus	piscivore	212	−0.03	−0.10	0.81	14	10	0.11	0.11
Kryptopterus apogon	**piscivore**	**216**	**−0.51**	**−1.89**	**1.02**	**13**	**9**	**0.09**	**0.06**
Clarias microcephalus	piscivore	220	−0.15	−0.57	1.03	15	5	0.09	0.11
Cyclocheilichthys enoplos	**omnivore**	**230**	**0.37**	**1.04**	**0.72**	**15**	**19**	**0.10**	**0.13**
Labeo chrysophekadion	herbivore	231	0.01	0.02	0.80	11	13	0.11	0.12
Channa striata	piscivore	290	−0.30	−0.55	0.83	16	9	0.20	0.09
Pangasius larnaudii	omnivore	305	0.09	0.31	0.86	7	20	0.10	0.09
Boesemania microlepis	**piscivore**	**311**	**0.43**	**1.47**	**0.93**	**13**	**10**	**0.06**	**0.09**
Channa micropeltes	piscivore	353	0.25	0.66	0.96	16	6	0.08	0.21

Notes: Species with values in boldface type had effect sizes ± 95% CI that did not bound zero. Sample size (*n*), coefficient of variation (CV) for each season, and the putative functional group for each species are also provided.

where $\delta^{15}N_{baseline}$ is the mean $\delta^{15}N$ of primary consumer baselines in each season (5.92‰ in the wet season, 6.15‰ in the dry season; see Appendix S1: Table S1 for details), and $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value for an individual fish. A constant TDF (trophic discrimination factor, the increase in $\delta^{15}N$ between a predator and prey) of 3.4‰ was applied (Post 2002). We also calculated trophic position using a scaled TDF to explore the influence of potentially decreasing TDF values with increasing trophic positions, but the two approaches produced the same results (see Appendix S1 for details). We therefore applied a constant TDF value for comparisons of trophic positions. The seasonal shift in mean trophic position was calculated for each of the 26 species as mean wet minus mean dry trophic position. Negative values supported our prediction of lower trophic positions in the wet season. For a given element, the stable isotope composition of a consumer's tissue is determined by its diet composition and tissue turnover time, isotopic differences among sources, the element's TDF, and other factors (Dalerum and Angerbjorn 2005, Fink et al. 2012, Woodland et al. 2012, Yeakel et al. 2016). Muscle tissue turnover time of Tonle Sap fishes should be sufficiently fast to reflect major dietary shifts between the wet and dry season (see Appendix S1 for details), an assumption supported by findings from a recent study that documented shifts in isotopic ratios of fishes in the Lower Mekong and tributary rivers in eastern Cambodia (Ou and Winemiller 2016). Effect sizes with pooled standard deviations and 95% confidence intervals (Coe 2002) were calculated to explore variation around mean values for trophic position shifts, and quadratic regression was used to explore how the seasonal shift in trophic position related to mean body size and functional group across the 26 species.

RESULTS

Dietary data

Diets of the four Tonle Sap piscivores were dominated by fish and invertebrates with minor fractions of plant material (Table 2). Zero-inflated beta regression revealed that the probability of invertebrates being eaten increased during the wet season and decreased with fish length. This is indicated by the parameter $b0_{wet}$ (Appendix S1: Table S2), which shows a significant negative effect on the probability of zero (i.e., nothing is eaten), whereas length had a negative effect on mean invertebrate consumption ($b_{\text{bodylength}}$ in Appendix S1: Table S2). Thus, smaller piscivores (i.e., *A. testudineus* and *N. notopterus*) consumed significantly more invertebrates than larger piscivores (i.e., *Channa* spp.), and the probability of invertebrates being eaten was significantly higher during the wet season (Fig. 2A). Season did not have a significant effect on the probability of plants or fish being eaten (Appendix S1: Table S2).

Out of the 34 evidence items obtained from the literature review, seasonal diet information was provided for 33 cases and δ^{15}N values were provided for 1 case (Table 3). Twelve evidence items supported the hypothesis of increased plant or invertebrate consumption by piscivores during the wet season, which should lower trophic positions (Table 3). Twelve other cases revealed increased piscivory during the wet season (the opposite of our prediction). The remaining 10 cases reported consistent diets comprised of either diverse prey (n = 1) or fish exclusively throughout the year (n = 9, Table 3). While variable, maximum body size of species reported in the literature (used here because actual body lengths of fish sampled in each study were not always provided) was smaller for species that had lower trophic positions during the wet season (mean body length ± SD = 28.6 ± 21.2 cm) compared to species that had consistent diets (55.0 ± 18.7 cm) or higher trophic positions during the wet season (62.9 ± 62.3 cm).

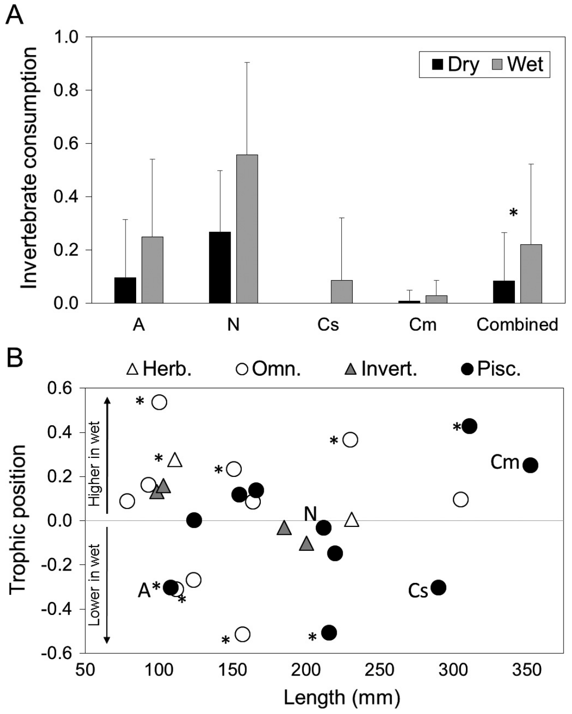

FIG. 2. (A) Proportional consumption of invertebrates (by mass; mean and SD) by four Tonle Sap fish species and by the four species combined for the dry and wet seasons. A significant seasonal effect ($P \le 0.05$) was identified for the combined data (indicated by *). (B) Shifts in mean trophic position between seasons (mean wet − mean dry) for 26 Tonle Sap fishes. Significant seasonal shifts in trophic position (i.e., effect sizes whose 95% CI did not bound zero, Table 2) are indicated by "*". Species with both stable isotope and stomach contents data are abbreviated as follows: A, *Anabas testudineus*; N, *Notopterus notopterus*; Cs, *Channa striata*; Cm, *Channa micropeltes.*

Stable isotope analysis

For the broader Tonle Sap fish community comprised of 26 common species, seasonal trophic position shifts (mean wet − mean dry) ranged from −0.52 to 0.54 and revealed a parabolic relationship with mean body length (Fig. 2B), which was not significant based on quadratic regression (P = 0.09). Inclusion of functional group as a categorical variable in this regression also yielded a nonsignificant relationship (all $P > 0.10$). Functional group, alone (without body size), also did not explain variation in seasonal trophic position shifts (ANOVA, P = 0.83). Instead, the direction and magnitude of trophic position shifts were variable in all functional groups and ranged from 0.01 to 0.28 in herbivores (n = 2 species), −0.10 to 0.16 in invertivores (n = 4 species), −0.52 to 0.54 in omnivores (n = 10 species), and −0.51 to 0.43 in piscivores (n = 10). With the exception of invertivores that all maintained seasonally consistent trophic positions, each functional group contained multiple directional responses to the flood pulse (Fig. 2B).

Among piscivores, species that reduced their trophic position in the wet season were smaller bodied compared to those that increased their trophic position or maintained similar trophic positions (Fig. 2B), which agrees with the pattern derived from the broader literature (Table 3). Aquatic (Appendix S1: Table S1) and terrestrial invertebrates (e.g., beetles and spiders, data not shown) had lower δ^{15}N values than the 26 fish species from the Tonle Sap (Appendix S1: Table S3), confirming that greater consumption of herbivorous or carnivorous invertebrates would reduce trophic position of piscivores in this system. However, only 2 out of 10 piscivores showed significant shifts toward lower wet season trophic positions in support of our prediction (i.e., had 95% CI that did not bound zero, *Anabas testudineus*, *Kryptopterus apogon*; Table 2). One piscivore had a higher trophic positions during the wet season (*Boesemania microlepis*) and the others did not significantly shift their trophic position seasonally based on 95% CI that bounded zero (n = 7, Fig. 2B, Table 2).

DISCUSSION

The major finding of our study is that fishes have diverse trophic responses to the seasonal hydrology of tropical floodplain systems. Analysis of combined dietary and δ^{15}N data revealed that small piscivores tended to have lower trophic positions during the wet season, caused by increased consumption of invertebrates and/or plant material, as predicted. However, variation in

TABLE 3. Data extracted from a literature review performed to explore seasonal diet changes in tropical floodplain piscivorous food chain omnivores.

Species	Maximum length	Dry season diet	Wet season diet	TP in wet season	Source
Fish community	NA	significantly higher δ^{15}N by 1.45‰	lower δ^{15}N	lower	1
Fish community	NA	5% aquatic inverts, 20% fish	18% aquatic invertebrates, 10% fish	lower	2
Fish community	NA	fish prey dominate	plant and invertebrate prey dominate	lower	3
Serrasalminae sp.	NA	fish	terrestrial plant matter and fish	lower	5
Hemigrammus marginatus	4.5	73% fish, 24% plant, 0.2% invertebrates	0% fish, 20% plant, 60% invertebrates	lower	6
Moenkhausia collettii	5	invertebrates and fish	invertebrates	lower	5
Aphyocharax dentatus	7.2	33% invertebrates, 16% fish	5% invertebrates, 87% fish	higher	6
Hypselecara coryphaenoides	16	fish	invertebrates	lower	5
Pimelodella gracilis	18	21% plants, 15% fish, 14% invertebrates	2% plant, 67% fish, 26% invertebrates	higher	6
Pimelodus argenteus	25	39% plant, 18% invertebrates, 10% fish	36% plant, 11% invertebrates, 38% fish	higher	6
Serrasalmus marginatus	27	99% fish, 1% detritus	93% fish, 7% invertebrates	lower	6
Acestrorhynchus lacustris	27	100% fish (*Steindachnerina insculpta*)	100% fish (*Astyanax bimaculatus*, *S. insculpta*)	similar	8
Acestrorhynchus lacustris	27	100% fish (*S. insculpta*)	100% fish (*Leporinus obtusidens*)	similar	8
Serrasalmus gouldingi	28	64% fish, 12% fruits/seeds, 10% arthropods	45% fish, 40% fruits/seeds, 8% arthropods	lower	7
Serrasalmus elongatus	30	78% fish, 12% plant, invertebrates, 6% eggs and scales	89% fish, 8% plant and invertebrates, 4% eggs and scales	higher	4
Hoplarchus psittacus	32	fish	aquatic invertebrates and fish	lower	5
Acestrorhynchus pantaneiro	35	100% fish	100% fish	similar	6
Plagioscion ternetzi	39	100% fish	97% fish	similar	6
Acestrorhynchus falcirostirs	40	77% fish, 23% shrimp	100% fish	higher	4
Hepsetus odoe	44	100% fish (*Haplochromine* cichlids, Mormyrids)	100% fish (*Haplochromine* cichlids)	similar	9
Pygocentrus nattereri	50	100% fish	99% fish, 1% plant	similar	6
Pygocentrus nattereri	50	48% fish, 28% plant, 20% invertebrates	69% fish, 16% plant, 9% invertebrates	higher	4
Pimelodus maculatus	51	50% fish, 25% plants	32% fish, 57% plants	lower	6
Hoplias malabaricus	65	100% fish (*Hoplias malabaricus*)	100% fish (*Prochilodus lineatus*)	similar	8
Hoplias malabaricus	65	100% fish (*Acestrorhynchus lacustris*)	100% fish (*Serrapinnus notomelas*)	similar	8
Hoplias malabaricus	65	100% fish (*L. obtusidens*)	100% fish (*H. malabaricus*)	similar	8
Hoplias malabaricus	65	93% fish, 3% shrimp	86% fish, 7% shrimp, 7% eggs and scales	lower	4
Cichla monoculus	70	93% fish, 7% plant	100% fish	higher	10
Cichla monoculus	70	57% fish, 43% shrimp	100% fish	higher	4
Hydrocynus forskahlii	78	100% fish (*Synodontis* spp.)	100% fish (*Hepsetus odoe*, cichlids)	similar	9
Rhaphiodon vulpinus	80	100% fish	100% fish	similar	6
Pellona castelnaeana	80	71% fish, 18% shrimp	79% fish, 21% shrimp	similar	4
Salminus Brasiliensis	100	95% fish, 5% invertebrates	100% fish	higher	6
Wallago attu	240	10% fish, 30% prawn (during January)	30% fish, 0% prawn (during July)	higher	11

Notes: Reported maximum total body length (NA, not applicable when multiple species were combined), dominant prey items, and quantitative contribution to diet, when provided, are reported for each study, as is whether diet composition suggests a higher, lower, or similar trophic positions during the wet season (compared to the dry season).

Sources: 1, Wantzen et al. (2002), Pantanal wetland, Brazil; 2, Winemiller (1989), Venezuelan Llanos; 3, Peterson (1997), Venezuelan Llanos; 4, de-Mérona and Rankin-de-Mérona (2004), lago de Rei, Amazon; 5, Goulding et al. (1988), Rio Negro, Amazon; 6, Novakowski et al. (2008), Pantanal wetland, Brazil; 7, Prudente et al. (2016), Anapu River, Brazil; 8, Almeida et al. (1997), Pantanal wetland, Brazil; 9, Winemiller and Kelso-Winemiller (1994), Upper Zambezi, Zambia; 10, Oliveira et al. (2006), Amazon River; 11, Islam et al. (2006), Bangladesh.

trophic responses across the fish assemblage was large, and not all species followed this trend. Instead, seasonal diet shifts revealed little consistency among species within functional groups. The direction and magnitude of trophic shifts among species were not associated with body size or functional group, but might be explained by other ecological factors (e.g., foraging tactics). Importantly, the wide distributions and high mobility of fishes, throughout a heterogeneous habitat and resource landscape, likely underpin the divergence of seasonal feeding patterns observed here. Fish assemblages of tropical river–floodplain systems are known to contain diverse trophic niches and foraging strategies (Winemiller 1989, Wantzen et al. 2002, Correa and Winemiller 2014, Bellmore et al. 2015). Foraging across distinct habitats is considered important for the "dynamic stability" (Leigh et al. 2010) and resiliency of these complex systems (Pettit et al. 2017). Our findings additionally suggest that flexible, yet diverse, trophic interactions could play a currently underappreciated role in sustaining energy and material flow in fluctuating ecosystems.

The largest seasonal shifts in trophic position were observed in piscivores and omnivores, consistent with previous findings in tropical floodplains (Wantzen et al. 2002). Based on the literature review, lower wet season trophic positions in piscivores could be explained by increased plant or invertebrate consumption (as predicted), compared to other species that shifted toward greater invertivory during the dry season (contrary to our prediction). The two snakeheads (*Channa* spp.) from the Tonle Sap predominantly consumed fish during both seasons (based on dietary data), but some individuals could still have shifted their diet seasonally between different types of fish prey. This behavior was revealed by several other species in our literature review (e.g., sources 8 and 9 in Table 3) and could explain the high intraspecific variation and large, but statistically non-significant, seasonal trophic position shifts observed in the *Channa* spp. from the Tonle Sap (Table 2). However, several other Tonle Sap piscivores also had similar δ^{15}N-based trophic positions during the two seasons, and some piscivores in our literature review consumed the same prey type, or a similar makeup of diverse prey, all year, suggesting a consistent trophic position can be maintained throughout the seasonal flood pulse.

Among omnivores, trophic position could be higher during the wet season, as in *Hemigrammus* spp. and other small tetras (Neotropical Characidae), if more invertebrates and less plant material (e.g., algae) were consumed during the flood pulse (Goulding et al. 1988, Peterson 1997). Conversely, lower trophic positions have been reported during the flood pulse for larger tetras that exploit fruits and seeds in flooded forests, and switch to insects during the dry season (e.g., *Brycon* spp.), whereas a fairly consistent diet of plants and insects can also produce similar trophic positions during various phases of the flood pulse (e.g., *Pristobrycon* sp.; Correa and Winemiller 2014). These different foraging strategies likely explain the varied trophic responses observed among Tonle Sap omnivores. Fishes classified as herbivores that exploit different plants or plant parts (e.g., periphyton; aquatic macrophytes; terrestrial plant leaves, flowers, fruits, and seeds; vegetative detritus) could introduce variation in δ^{15}N values (Wantzen et al. 2002) and explain the 0.2 increase in wet season trophic position observed for one of the two Tonle Sap herbivores. Invertivores have been previously reported to undergo seasonal shifts in trophic position (Wantzen et al. 2002), but a consistent diet of aquatic or terrestrial invertebrates (e.g., *Copella nattereri*; Goulding et al. 1988) is suggested by our findings for the four invertivores from the Tonle Sap.

Variation in seasonal foraging strategies among species was not explained by body size or functional group in our study, but could relate to physiological, behavioral, or other ecological traits not examined here. Many fishes are capable of exploiting multiple food resources, but may track the most profitable food types when these are abundant during certain periods or within certain habitats (Winemiller 1989, Correa and Winemiller 2014). Food profitability depends on its quality and quantity, but also consumer foraging tactics, habitat features and other ecological factors (Winemiller and Kelso-Winemiller 1994, Almeida et al. 1997). For example, piscivores that employ a sit-and-wait foraging tactic can efficiently exploit abundant juvenile fishes during the wet season by using vegetation as cover, whereas stalk-and-chase predators may be more efficient predators as water levels fall and prey encounter rates peak (Peterson 1997). Species that maintain a fairly constant trophic position could possess morphological and behavioral traits that enable them to feed efficiently on one or a few food types, while compromising foraging efficiency for other food resources (Almeida et al. 1997). The capacity to forage across spatially complex habitats has also been linked to cognitive capacity (brain size) both within and among freshwater fish species (Edmunds et al. 2016), suggesting there could be physiological limits on the types of habitats and resources used by fish. Additional data for foraging behavior, habitat, mobility and physiology of Tonle Sap species would help address these ideas, but body size (Ou et al. 2017) and seasonal feeding strategies are known to vary widely within fish functional groups from other tropical floodplains (Novakowski et al. 2008). While difficult to predict, the variable nature of seasonal foraging strategies therefore appear characteristic of fishes inhabiting these systems.

High spatiotemporal variation in habitats and resources is also characteristic of tropical floodplain ecosystems (Junk et al. 1989, Pettit et al. 2017). Our prediction of lower trophic positions during the wet season was based on the idea that fish have greater access to plant and invertebrate prey during the flood pulse. The fact that many species deviated from this prediction, either by exploiting these food resources during the dry season or maintaining consistent trophic positions during both seasons, could reflect habitat and resource tracking at smaller scales (Arias et al. 2013, Pettit et al. 2017). While we lack resource abundance data to test this idea, an intriguing possibility is that gradual expansion and recession of floodwaters into different habitats could cause resource abundance to peak asynchronously across the landscape (Fig. 1), such as arises during a resource wave (Humphries et al. 2014, Armstrong et al. 2016). Floodplain-derived resources might be relatively ephemeral at any given location (e.g., rice field; Fig. 1), but widely available for a mobile consumer capable of "surfing" these peaks across the landscape (Armstrong et al. 2016). Even brief access to floodplain resources is known to support fish production (Jardine et al. 2012). This high spatiotemporal resource variation at multiple scales, coupled with high mobility and wide distribution of fishes across the Tonle Sap (Kong et al. 2017), could provide the opportunity for fishes to adopt a wide variety of behavioral responses to the flood pulse. Variable conditions across systems could also explain why the same species exhibited different strategies in different tropical floodplains (e.g., *Hoplias malabaricus*; Table 3). Based on these combined findings, it appears that fishes perceive seasonal fluctuations in the abundance of alternative food resources differently and respond by flexibly altering their diet and trophic position, or by maintaining a consistent trophic position throughout the flood pulse (possibly by tracking similar resource types across the spatiotemporally variable landscape).

The magnitude of seasonal omnivory reported here (plus or minus approximately one-half of a trophic level) is comparable to previous studies in tropical floodplains (Wantzen et al. 2002) and reflects changes in fish foraging behavior that have potentially large consequences for food web structure, as well as individual fitness. For example, a shift from eating 100% fish to eating 50% fish and 50% invertebrates (i.e., a reduction in trophic position of ~0.5) would likely change the number and strength of species interactions in the food web as well as the activity costs and growth of individual fish (Sherwood et al. 2002). Such temporally dynamic omnivory could also have consequences for stability. Theory argues that "adaptive" omnivory, whereby consumers incorporate prey from lower trophic levels into their diet when preferred prey become rare, slightly increases stability relative to the case of fixed omnivory (Křivan and Diehl 2005). Seasonal diet shifts between temporally asynchronized prey also stabilize consumer dynamics by providing access to a consistent resource base (Takimoto et al. 2002). Prey refugia, prey defense, stage-structured cannibalism, and adaptive foraging are all mechanisms that are thought to prevent strong and destabilizing omnivory (Kratina et al. 2012). Although not well considered theoretically, flexible food web properties, such as omnivory, that capitalize on asynchronized prey dynamics, could be extremely important for stability in nonequilibrium or periodically forced systems (McCann and Rooney 2009, Kratina et al. 2012).

Even less well considered theoretically is how diverse consumer–resource interactions across seasonally changing conditions could influence food web stability. At a community level, diet diversity within and among species is widely considered important for dampening competition and promoting coexistence of fishes in tropical floodplains (Winemiller and Pianka 1990, Pool et al. 2017, Costa-Pereira et al. 2017). From a whole food web perspective, preventing extinction is inarguably a component of stability. However, there could be additional conditions when species adopting different foraging strategies could strongly stabilize the food web. In systems where consumer abundance is high, and potentially inflated due to high mobility and subsidized foraging across large spatial areas, all consumers converging on a single, seasonally abundant, resource pool could suppress that prey type to very low densities. Such situations could possibly arise in tropical flood plains during dry years when the system is spatially compressed. A usually abundant prey type falling to low densities might drive species to diversify in their foraging strategies. Diverse foraging strategies that weaken consumptive pressure on a low-density prey would promote stability (Wootton 2017), and possibly ecosystem resiliency, by decreasing the risk of widespread collapse in the fish community. More theoretical and empirical work that tests the relationship between structure and stability (e.g., Cross et al. 2013) is currently needed to explore these ideas.

Temporally changing trophic positions also arise in other taxa and ecosystems, including stream macroinvertebrates (Hellmann et al. 2013), birds (Nakano and Murakami 2001), and desert mammals (Soykan and Sabo 2009). Consumer trophic positions can also remain static through time (e.g., in stream fish; Rybczynski et al. 2008). Temporal omnivory therefore appears variable in its direction and magnitude of change based on existing literature, consistent with our findings from tropical floodplains. Remaining questions include how the extent of temporal omnivory changes among individuals within a single species depending on body size (e.g., during ontogeny; Winemiller 1989) or morphotype (e.g., Smith and Skúlason 1996), and how the capacity for seasonal omnivory differs among ecosystem types, including between summer and winter in temperate and arctic systems (e.g., McMeans et al. 2015).

CONCLUSIONS

Vertical trophic position and the related concept of food-chain omnivory are key food web attributes that are known to vary spatially and influence ecosystem stability (Post and Takimoto 2007). Based on our findings, tropical floodplain fishes are capable of flexibly switching between prey occupying different trophic positions seasonally, or of tracking prey at a similar trophic position throughout the flood pulse. Spatiotemporal variability at both large and small scales likely provides the conditions that promote these diverse seasonal foraging strategies. More research is needed to explain why different species respond differently to the flood pulse, which undoubtedly involves physiological and behavioral traits not examined here. Regardless, seasonal shifts in trophic position are not unique to tropical fishes inhabiting floodplains and knowledge about how species and ecosystems respond to seasonality is crucial for anticipating the consequences of climate change and hydrological alterations. Maintenance of species assemblages encompassing diverse foraging strategies and trophic responses to seasonal cycles could be critical for food web stability and in buffering ecosystems from perturbations.

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