

Fishes in a seasonally pulsed wetland show spatiotemporal shifts in diet and trophic niche but not shifts in trophic position

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ABSTRACT

We examine temporal (seasonal) and spatial (habitat) effects on consumers' diet, trophic position, trophic niche, and food-web topology in a subtropical oligotrophic wetland to illustrate how consumers and food webs respond to hydrologic pulsing in a spatially complex ecosystem. We ask if the annual flood pulse causes fishes to undergo a trophic shift or if fishes maintain a constant diet, trophic position, and trophic niche all year and across habitats, as is often assumed. Furthermore, we ask if the flood pulse alters food-web topology in different habitats and if invasive fishes overlap in trophic niche with native fishes in this ecosystem. We found that trophic dispersion (shift in trophic-niche size) was common (66% and 71% of spatial and temporal comparisons respectively), trophic displacement (shift in trophic-niche location in niche space) was ubiquitous (spatial – 92%; temporal – 82%), and shifts in trophic position were relatively rare (spatial – 11%; temporal – 4%). Trophic dynamics were primarily driven by differing amounts of piscivory, detrital consumption, and diet plasticity across habitats and seasons. In the dry season, food-web topology indicated decreased complexity in all habitats (decreased number of links, link density, and connectance) and instability in ponds that may facilitate invasions. Both stomach contents and stable isotopes revealed trophic-niche overlap among native and invasive fishes, notably centrarchids and cichlids. Diverse, flexible trophic responses to seasonality across habitats may be pivotal to nutrient and energy cycling and in maintaining ecosystem stability and resilience, especially in regularly perturbed environments. Seasonal fluctuation typical of wetlands may require inter-habitat relocation, leading to the types of food-web changes we document. We conclude that spatiotemporal trophic plasticity is probably common and deserves additional study given its ability to influence food-web structure and function.

1. Introduction

Fluctuations in abiotic conditions such as precipitation, temperature, nutrients, and light drive variation in resource availability across habitats and seasons. It is widely assumed that this variation drives temporal and spatial dynamics of species composition, consumer-resource interactions, and emergent food-web properties (Winemiller, 1990). Seasonality is probably the most common temporal driver of food-web structure, yet little is known about how food webs respond to seasonal variation (McMeans et al., 2015; Paine, 1988). Elton (1927) noted the importance of seasonal dynamics to animal communities almost a century ago, and contemporary work demonstrates that spatial variation in food webs is a stabilizing force (McCann et al., 2005; Winemiller, 1990). Despite this recognition, most food webs have been treated as static

(Poisot et al., 2015). While empirical evidence on the influence of seasonality on food webs is lacking, some examples demonstrate its importance to trophic position and network structure (Carnicer et al., 2009; McMeans et al., 2019; Olesen et al., 2008; Winemiller, 1990). Recently, both terrestrial and aquatic ecologists have recognized the need to incorporate seasonality in food-web studies (CaraDonna et al., 2017; Hampton et al., 2017; McMeans et al., 2019).

Habitat heterogeneity influences food-web structure by creating resource asynchronies across the landscape. In response, many consumers exhibit flexible foraging among habitats, increasing food-web stability (McCann et al., 2005). Moreover, in the absence of spatially adaptive foragers, increased food-web complexity destabilizes community composition (Kondoh, 2003). This theory – that spatial heterogeneity weakens interaction strength and increases food-web stability –

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has garnered empirical support in below-ground food webs, streams, and river floodplains (Bellmore et al., 2015; Moore and de Ruiter, 1991; Thompson and Townsend, 2005). Much of that work implies that food webs are static.

Recent studies have demonstrated inter-annual or seasonal changes in trophic position and omnivory, often associated with shifts in habitat use (Akin and Winemiller, 2006; Heng et al., 2018; McMeans et al., 2019; Ruiz-Cooley et al., 2017). These trophic dynamics among habitats have been recognized as important for food-web structure and function (Cross et al., 2013; McCann et al., 2005; Thompson et al., 2007). Many fishes are adaptive foragers that undergo seasonal diet changes both within and among habitats (Jepsen et al., 1997; Lowe-McConnell, 1969; McMeans et al., 2019; Winemiller, 1989; Winemiller and Jepsen, 1998). Temporal shifts in diet, in which consumers adaptively track different resources (Kratina et al., 2012; Krivan and Diehl, 2005; Takimoto et al., 2002), may have consequences for ecosystems as important as those recognized for spatial diet shifts.

Aquatic ecosystems with marked wet and dry seasons governed by the flood pulse (Junk et al., 1989) offer excellent opportunities to evaluate impacts of seasonal variation on food webs. Rising waters during the wet season increase available habitat that supports primary and secondary production (Arias et al., 2013; DeAngelis and White, 1994; Junk et al., 1989; Trexler et al., 2005). Alternatively, drying concentrates fish and invertebrate biomass, leading to increased foraging efficiency for higher-level consumers (McConnell and Lowe-McConnell, 1987; Winemiller, 1989). Such resource pulses have been appreciated as driving forces in ecosystems for several decades (Odum, 1969; Odum et al., 1995) and may reverse ecosystem declines caused by disturbance and climate change (Kominoski et al., 2018). More recently, pulses of detritus have been found to be similarly important (Moore et al., 2004; Rooney and McCann, 2012; Yang et al., 2008). As a result, it is unsurprising that in pulsed, tropical systems both inter- and intra-specific dietary niche overlap reveal spatiotemporal shifts with mixed trends among studies (Costa-Pereira et al., 2017; Lowe-McConnell, 1964; Moyle and Senanayake, 1984; Zaret and Rand, 1971). Moyle and Senanayake (1984) and Payne (1986) both found dietary niche overlap to be greatest when resources were most abundant. Similarly, Quirino et al. (2017) showed the dietary niche for a population of small characids was larger in the wet season due to abundant allochthonous resources. Conversely, other studies have demonstrated that dietary niche overlap was highest during the dry season while resources were limiting (Lowe-McConnell, 1969; Power, 1983; Prejs and Prejs, 1987). Correa and Winemiller (2014) found no consistent seasonal trend for dietary niche among Amazonian fishes. Seasonal shifts in dietary niche are likely specific to feeding behavior (Azevedo et al., 2021) and may explain mixed trends among studies. Further research in additional ecosystems with temporal and spatial hydrological pulsing is needed to advance our understanding of the impact of seasonality on dietary niche.

We evaluate the impact of flood-pulse seasonality on food webs in the Everglades, USA, a subtropical, seasonally pulsed wetland. Basal resources of the Everglades food web are dominated by algal and detrital energy routes that drive spatiotemporal food-web dynamics (Belicka et al., 2012; Trexler et al., 2015; Williams and Trexler, 2006). We quantified temporal (seasonal) and spatial (among habitats) food-web dynamics in this oligotrophic wetland using stomach contents and stable isotopes of carbon and nitrogen. We calculated diet, niche breadth, and food-web structure both within and among populations and communities across habitats and seasons. We predicted that diets and niche breadths would follow similar trends within trophic guilds because of similar feeding behaviors among species (Azevedo et al., 2021), that omnivory should be common in both seasons based on previous studies in flood-pulsed ecosystems (Heng et al., 2018; McMeans et al., 2019), and that niche area and overlap among species size classes would increase during the dry season as habitats contract and resources become limited (Lowe-McConnell, 1969; McHugh et al., 2015; Power, 1983). Furthermore, we predicted that food-web complexity, measured as

connectance, would decrease during the dry season in shallow marsh habitats as species move to deep-water habitats in response to seasonal drying, and predicted the opposite for deep-water habitats where animals are concentrated in the dry season (donor control; Strong, 1992). We also investigated the relative importance of detrital energy routing across the same gradient and hypothesized that detritus will be consumed more in the dry season when alternate resources are limited, forcing species to use lower quality food. We report stable-isotope mixing models (SIMMs; Parnell et al., 2013) both with and without informative priors derived from stomach contents to test prey assimilation to complement prey-ingestion data from stomach contents. Finally, we discuss the implications of these results for ecosystem conservation and future work, particularly regarding species invasions that have occurred following the collection of our data.

2. Methods

2.1. Study area

The study site was a one-square kilometer area in north-central Shark River Slough, Everglades National Park (ENP), Florida, USA, at 25°38.090 N and 80°43.720 W, referred to in previous work as site Upper Slough (Loftus and Eklund, 1994), and site SRS 6 (Gatto et al., 2021; Gatto and Trexler, 2019; Ruetz et al., 2005; Trexler et al., 2002). The Everglades experiences wet (June through November; flood pulse) and dry (December through May; flood-pulse recession) seasonal rainfall resulting in water depths that are shallowest in late spring and deepest in late fall (Fig. A.1.1 and Table A.1.1, Loftus and Kushlan, 1987). The study area included three major aquatic habitats (Gunderson and Loftus, 1993): a slough/prairie system (hereafter “spikerush marsh” or “spikerush”) comprising about 35% of the wetland area, dominated by a relatively dense cover of *Eleocharis cellulosa*, *Panicum hemitomon*, and *Utricularia purpurea* and *U. foliosa*, a floating periphyton mat and some patches of white waterlily pads (*Nymphaea odorata*), with a peat substrate; sawgrass marshes, densely covered by *Cladium jamaicense* and comprising about 50% of the area (Davis et al., 1994); and alligator ponds, often surrounded by *Salix caroliniana*, *C. jamaicense*, *Pontedaria cordata*, and *Typha* spp., with open water over a peat or limestone bottom. The small areal coverage of ponds (< 0.1% of the area) is contrasted by their ecological significance. In most years, alligator ponds hold water through the dry season, acting both as refuges and sinks for various species of fishes (Loftus and Kushlan, 1987).

2.2. Field collections

Fishes and invertebrates analyzed for this project were collected between 1977 and 1994. Most specimens (> 90%) were collected between 1977 and 1981, but supplemental collections were taken from the same study area at the same time of year during the mid-1990s to increase sample sizes for less common species, mainly larger predators. Collections in the mid-1990s included non-native species that had colonized the Everglades (see Kline et al., 2014 for timeline), and all specimens for stable-isotope analysis. Wet-season samples were collected between January and early March, and dry-season samples in April. Most fishes were collected with 5% rotenone solution (Nox-Fish®), along with electrofishing, cast nets, dip nets, and angling. All fishes were preserved in 10% buffered formalin and transferred to 70% ethanol, except those captured for isotopic analysis, which were euthanized with MS-222 and frozen. In total, we collected 3509 individuals from thirty-two species, of which 600 had empty stomachs (see Arrington et al., 2002). We analyzed stomach contents for the remaining 2909 fishes, 83% of those collected. The target sample size was twenty-five individuals per species size class per habitat-season level and the average was sixteen (Table 1).

Table 1

Common and scientific names, species abbreviations, number of size classes, and sample size for each species across habitat-season levels (P = pond, Sr = spikerush, Sg = sawgrass). Species are abbreviated in other tables and figures as first letter of the genus, underscore, followed by first three letters of the species.

Common name	Species	Abbr.	Num. of size classes	Wet season			Dry season		
				P	Sr	Sg	P	Sr	Sg
Diamond Killifish	<i>Adinia xenica</i>	A_xen	1	0	0	0	0	2	0
Yellow Bullhead	<i>Ameiurus natalis</i>	A_nat	4	53	31	9	113	27	0
Bowfin	<i>Amia calva</i>	A_cal	1	0	1	0	18	0	0
Pike Killifish	<i>Belonesox belizanus</i>	B_bel	2	21	0	0	29	9	0
Black Acara	<i>Cichlasoma bimaculatum</i>	C_bim	1	2	1	0	1	0	0
Walking Catfish	<i>Clarias batrachus</i>	C_bat	1	17	0	0	14	0	0
Sheepshead Minnow	<i>Cyprinodon variegatus</i>	C_var	1	0	25	0	0	5	1
Everglades Pygmy Sunfish	<i>Elassoma evergladei</i>	E_ever	1	12	22	2	6	24	5
Bluespotted Sunfish	<i>Enneacanthus gloriosus</i>	E_glo	1	0	34	0	0	22	0
Lake Chubsucker	<i>Erimyzon sucetta</i>	E_suc	3	17	0	0	0	0	0
Swamp Darter	<i>Etheostoma fusiforme</i>	E_fus	1	5	2	0	0	0	0
Marsh Killifish	<i>Fundulus confluentus</i>	F_con	2	4	29	13	0	43	33
Golden Topminnow	<i>Fundulus chrysotus</i>	F_chr	2	21	72	62	8	68	76
Eastern Mosquitofish	<i>Gambusia holbrooki</i>	G_hol	2	50	51	51	49	48	43
Least Killifish	<i>Heterandria formosa</i>	H_for	2	14	50	36	14	48	44
Flagfish	<i>Jordanella floridae</i>	J_flo	2	17	50	20	0	31	31
Golden Silverside	<i>Labiesthes vanhyningi</i>	L_van	1	28	0	0	0	0	0
Florida Gar	<i>Lepisosteus platyrhincus</i>	L_pla	2	54	0	11	92	0	0
Warmouth	<i>Lepomis gulosus</i>	L_gul	4	84	4	4	40	6	1
Bluegill Sunfish	<i>Lepomis macrochirus</i>	L_mac	1	36	1	0	3	2	0
Dollar Sunfish	<i>Lepomis marginatus</i>	L_mar	1	22	42	14	7	57	1
Redear Sunfish	<i>Lepomis microlophus</i>	L_mic	2	17	11	0	2	1	0
Spotted Sunfish	<i>Lepomis punctatus</i>	L_pun	3	29	53	9	59	65	16
Bluefin Killifish	<i>Lucania goodei</i>	L_goo	2	43	86	60	0	79	70
Mayan Cichlid	<i>Mayaheros urophthalmus</i>	M_uro	2	16	0	0	0	0	0
Largemouth Bass	<i>Micropterus salmoides</i>	M_sal	1	24	0	0	0	0	0
Golden Shiner	<i>Notemigonus crysoleucas</i>	N_cry	1	4	0	0	0	0	0
Taillight Shiner	<i>Notropis maculatus</i>	N_mac	1	13	0	0	0	0	0
Coastal Shiner	<i>Notropis petersoni</i>	N_pet	1	26	0	0	0	0	0
Tadpole Madtom	<i>Noturus gyrinus</i>	N_gyr	1	3	20	4	6	8	1
Spotted Tilapia	<i>Pelmatolapia mariae</i>	P_mar	1	26	0	0	0	0	0
Sailfin Molly	<i>Poecilia latipinna</i>	P_lat	2	0	14	0	7	10	12

2.3. Laboratory analyses

We separated species into body-size groups based on length, termed species size classes (Table A.1.2), to examine the role of ontogeny in trophic resource partitioning within and among species, because most fishes undergo a change in diet with growth (Wainwright and Richard, 1995). The incorporation of ontogenetic changes (i.e. changes that occur as an organism grows and develops) in diet studies helps alleviate biases associated with niche-overlap and diet-breadth indices (Piet et al., 1999). We recorded the length and wet mass of each specimen before removing the stomach. In species without defined stomachs, we removed the digestive tract from the esophagus to the first bend in the tract. Each stomach was flushed of contents which were examined with a Wild®5A dissecting microscope and identified to the lowest-level taxon possible. Fragmented remains of insects, fishes, and crustaceans were termed “unidentifiable.” Insect taxa are larval forms, unless otherwise indicated. The number of individuals per prey type were recorded for individual consumers (Hyslop, 1980).

For stable-isotope samples, we dissected muscle from small fishes and invertebrates for drying at 50°C, then pulverized it (Fry, 2006). Samples of major primary producers were dried and powdered after being acid-washed in HCl before drying to remove carbonates. Three to five individuals were analyzed to produce a mean value per taxon. The samples were analyzed shortly thereafter in the mid-1990s at the University of Georgia Institute of Ecology isotope laboratory. The isotopic standards used for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were Pee Dee Belemnite (PDB) and air, respectively. Average isotopic error of replicate standards was $\delta^{15}\text{N} \leq 0.2\text{‰}$ and $\delta^{13}\text{C} \leq 0.1\text{‰}$.

2.4. Community dynamics in prey consumption

We analyzed changes in the numeric stomach-content diet matrix

across habitats and seasons. Spatiotemporal variation in prey consumption by the fish community was visualized with non-metric multidimensional scaling (NMDS, $k = 2$) using Morisita-Horn distances, which rely on relative abundance of taxa to avoid disproportionate influence of changes in absolute abundance when relative abundance remains the same (Jost et al., 2011). Visual differences among communities from different habitat-season levels were statistically assessed using permutational multivariate analysis of variance (PERMANOVA; 10,000 iterations). PERMANOVA can yield significant results for two reasons: differences in dispersion in multivariate space or differences in centroid location in multivariate space (Anderson and Walsh, 2013). We specifically tested for differences in multivariate dispersion (PERMDISP) by using the *betadisper* function and analyzing results using analysis of variance (ANOVA) followed by Tukey's HSD. Similarity percentages (SIMPER) were used to determine diet items contributing the most variance among habitat-season levels (Fig. 1). Analyses were done in R version 3.6.3 using the *vegan* package or base R (Oksanen et al., 2020; R Core Team, 2020). Additionally, we asked if the occurrence of detritus in diets of all consumers changed across habitats and seasons. To answer this question, we performed a one-way permuted ANOVA (10,000 iterations) to compare the amount of vascular detritus in stomachs among habitat-season levels followed by a pairwise permutation test (functionally like Tukey's HSD). These were conducted using *independence_test* and *pairwisePermutationTest* functions in *coin* and *rcompanion* packages respectively (Mangiafico, 2021; Zeileis et al., 2008). The relationship between these analyses and all subsequent analyses are summarized in Fig. 1.

2.5. Trophic position

Trophic position was calculated using both stomach-content and stable-isotope data. To estimate trophic positions of species size classes

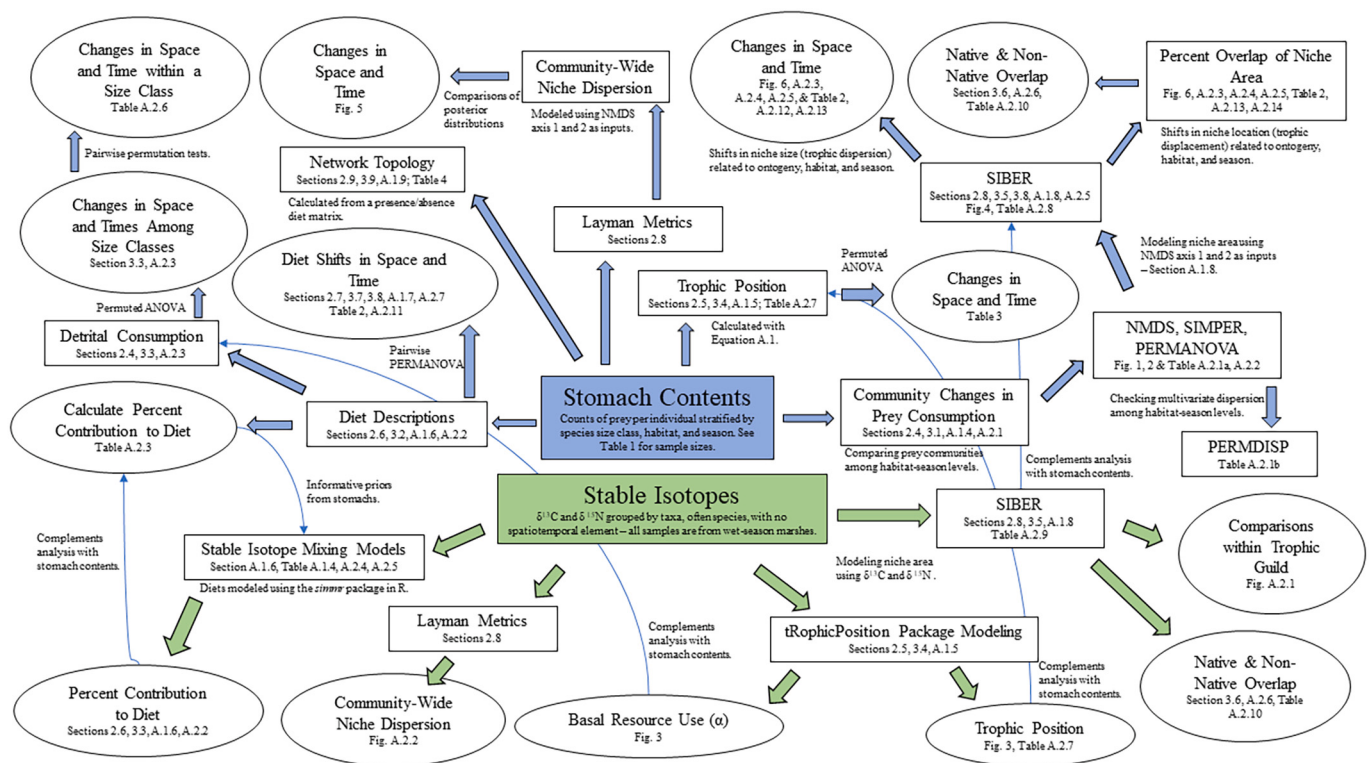


Fig. 1. Visual outline of the various statistical methods and corresponding data used (stomach contents in blue or stable isotopes in green) for those analyses. Thin blue arrows represent linkages between analyses performed on stomach-content and stable-isotope data. Emergent products that answer research questions or address hypotheses are in ellipses while the steps to arrive there are in boxes. Additional information (e.g., statistical test performed or where a method or result is described in the text) can be found next to the corresponding polygon or arrow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

based on stomach contents, we followed [Adams et al. \(1983\)](#), where trophic position of a predator is defined by the trophic levels of its prey (Appendix A.1.5, Eq. A.1, and Table A.1.3). Trophic position distributions for each species size class at each habitat-season level were tested for normality using Shapiro-Wilk tests. Differences among size classes and among habitat-season levels were assessed using permuted ANOVA (10,000 iterations) via the *aovp* function from the *lmPerm* package in R ([Wheeler and Torchiano, 2016](#)). Species size class, habitat-season level, and the interaction of the two were included as fixed effects.

Trophic position per species was modeled using stable isotopes of carbon and nitrogen in the *trophicPosition* package in R ([Quezada-Romegialli et al., 2018](#)). This Bayesian framework estimates posterior distributions for trophic position and a metric called alpha. Alpha is the proportion of $\delta^{15}\text{N}$ in a consumer's tissue derived from baseline one, which in this case was detritus. The Everglades aquatic food web has two baselines, green algae and detritus ([Williams and Trexler, 2006](#)). Therefore, alpha minus one is the proportion of $\delta^{15}\text{N}$ in a consumer's tissues derived from baseline two, green algae. We compared trophic position and alpha among species by calculating the probability one species had a trophic position or alpha less than or equal to the same metric for a different species for all possible pairwise comparisons (Fig. 1). We report the Gelman-Rubin diagnostic, values near one indicate convergence, for each model parameter ([Gelman and Rubin, 1992](#)).

2.6. Dietary proportions

The percent contribution of diet items to a consumer was calculated for individuals using numeric stomach contents and for species using stable isotopes when data permitted. Dietary proportions were calculated using the 8-group stomach-content matrix (prey groups are the functional groups from Table A.1.3) for each individual. Then, the mean

and standard deviation were calculated for each species size-class across habitats and seasons. Furthermore, we generated stable-isotope mixing models (SIMMs) using the *simmr* package in R to reconstruct the diet for each species as data permitted (Appendix A.1.6, [Parnell and Inger, 2016](#); [Parnell et al., 2010](#)) and following guidelines from [Phillips et al. \(2014\)](#). Whenever possible, SIMMs were generated both with and without informative priors based on stomach contents (Fig. 1, Appendix A.1.6 and Table A.1.4). Trophic enrichment factors used for each source group follow those from [McCutchan et al. \(2003\)](#) based on the type of source and source tissue.

2.7. Ontogenetic shifts in diet

Many species of fishes undergo ontogenetic shifts in diet that are likely influenced by environmental conditions. Differences among species size classes, habitat-season levels, and the interaction of those factors were examined using PERMANOVA via the *adonis* function from the *vegan* package in R ([Oksanen et al., 2020](#)). Afterwards, PERMANOVAs were performed for all possible pairwise comparisons using the *pairwise.perm.manova* function in the *RVAideMemoire* package in R ([Hervé, 2021](#)). We summarized ontogenetic shifts by size class for each habitat-season level and shifts among habitat-season levels for each species size class (Fig. 1). Size classes are denoted in text in parentheses after the species (e.g., *Gambusia holbrooki* (1)).

2.8. Dietary niche

Dietary-niche metrics were calculated for species size classes using stomach contents among habitat-season levels and for species using stable-isotope data. Trophic niches derived from stomach contents and stable isotopes may represent different aspects of the trophic niche, and

it is important to denote which is being discussed (Petta et al., 2020). We use the term niche, for the sake of brevity, referring exclusively to trophic niche, and specify whether it is derived from stomach contents or stable isotopes. There is no spatiotemporal component to the isotope dataset (isotope samples were collected only from wet-season spikerush), so all such trends in niche are referring to trophic niche derived from stomach contents (Fig. 1).

Stomach-content niche metrics and stable-isotope niche metrics were calculated separately using the *SIBER* package in R that generates niche areas as ellipses (standard ellipse area – SEA_b) in a Bayesian framework (Jackson et al., 2011). The *SIBER* package was designed with stable isotopes of carbon and nitrogen in mind. However, it can accommodate any appropriate two-dimensional data set. For our stomach-content data, we used NMDS axes one and two. Stable isotopes of carbon and nitrogen act as a two-dimensional ordination of diet that is found in nature. Therefore, axes from our ordination of stomach contents are an appropriate analog (Appendix A.1.8). We extracted modes and credible intervals from posterior distributions for all groups (species size-classes) within each community (habitat-season) using stomach contents and for each species using stable isotopes (Fig. 1).

Trophic niches can change in two ways: trophic dispersion (changing diet variability – SEA_b area) and trophic displacement (diet switching – SEA_b location in niche space; Cucherousset and Blanchet, 2012; Vander Zanden et al.; Wainright et al., 2021). Differences in trophic dispersion among groups were determined by calculating the probability that group A's SEA_b posterior distribution was less than group B's for ontogenetic and spatiotemporal pairwise comparisons (Appendix A.1). Trophic displacement was calculated as the proportion of overlapping SEA_b between groups. Proportion of overlap was defined as the area of overlap between groups ($A \cap B$) divided by the total combined area of both groups ($A \cup B$).

We described dispersion in two-dimensional space using the Layman metrics via the Bayesian framework within *SIBER* (Jackson et al., 2011; Layman et al., 2007). These metrics were also developed using stable-isotope data; however, they are equally applicable to describing niche space derived from our two-dimensional NMDS. Layman metrics were calculated using *extractPosteriorMeans* and *bayesianLayman* functions in *SIBER* (Jackson et al., 2011). Comparisons of Layman metrics among populations within a habitat-season level and among communities across habitat-season levels were calculated as the probability that one distribution was less than another in the same manner as SEA_b .

2.9. Network structure

Describing food-web topology can provide insight into food-web functioning (Kones et al., 2009). We sought to calculate topological attributes with well-understood biological meanings for food webs of each habitat-season level using the *foodweb* package in R (Perdomo et al., 2012). Diet information for taxa we did not directly study (e.g., invertebrates found in stomachs) were assembled using literature (Rader, 1994) and expert opinion (Loftus, Trexler), allowing us to create a symmetric presence/absence matrix for analysis. Some diet categories (e.g., Miscellaneous and Miscellaneous Insecta) were removed from the analysis because they are low-resolution trophic interactions already represented by more defined nodes. Afterwards, we filtered the dataset to isolate data from each habitat-season level into their own matrices. Then we used the *analyse.seq* function to calculate the following food-web network metrics: taxa richness, number of trophic links, link density, connectance, number of omnivores (defined as species feeding at multiple trophic levels), mean chain length, maximum chain length, number of basal taxa, number of intermediate taxa, number of top taxa, and prey to predator ratio (Perdomo et al., 2012).

3. Results

3.1. Community dynamics in prey consumption

We sought to understand spatiotemporal fluctuation in resource use by quantifying community-wide changes in relative consumption of different prey among habitats and seasons. Spatiotemporal variation in prey communities was driven by increased consumption of larger prey (*Palaemonetes paludosus* and fishes), particularly in dry-season ponds. NMDS ($k = 2$, stress = 0.17) separated consumers by trophic position and prey size (Fig. 2). MDS 1 was a gradient from small diet items (relatively small invertebrates such as zooplankton had lower values) to large diet items (dragonfly larvae, shrimp, crayfish, and fishes had larger values). Meanwhile, MDS 2 represented a gradient of fish size from first-order consumers to top predators. As a result, variation among habitats and seasons along MDS 1 is driven by changes in relative abundance of consumed prey, while variation on MDS 2 is the result of changes in relative abundance of consumers. For instance, in all habitats in the dry season, fishes consumed a wider range of prey (wider range on MDS 1; Fig. 2). PERMANOVA demonstrated spatiotemporal differences in communities of consumed prey ($F_2 = 15.3$, $p < 0.001$; Table A.2.1a), while comparisons of multivariate dispersion (PERMDISP) showed differences in three habitat-season comparisons ($p < 0.05$, Table A.2.1b) contributing to PERMANOVA results. In spikerush and sawgrass SIMPER found similarities in consumed prey within and between seasons, while ponds differed from other habitats and between seasons (Fig. 3 and Table A.2.2).

3.2. Diet descriptions

Our analyses revealed that consumers filled several functional feeding groups with omnivory being the most common, vascular plants were rarely consumed, and detritus played an important role for a variety of consumers (Table A.2.3). Based on stomach contents, most fishes collected in ponds were omnivores, but dry-season water recession often resulted in increased carnivory and detrital consumption. Omnivorous invertebrates, excluding decapods, were most often the diet group that constituted the largest proportion of an individual's stomach contents (Table A.2.3). These omnivorous invertebrates were the most important diet item in each habitat-season level, except for dry-season ponds where decapods and detritus played more important roles. SIMMs confirmed the relative importance of different functional groups to consumer diets with some exceptions (Table A.2.4). Relative to stomach contents, SIMMs suggested elevated consumption of larger prey items (i.e., decapods and fishes) and decreased consumption of detritus (Table A.2.5). Higher quality prey items (decapods, fishes) seem to be assimilated more readily than lower quality prey items (detritus) relative to amounts ingested.

3.3. Basal resource use

We predicted that the food web would be detritally based, and that detrital consumption would increase in the dry season as resources become more limited. Our stable-isotope analyses confirmed that first prediction, and stomach contents demonstrated spatiotemporal variation in detrital consumption. Alpha, the proportion of $\delta^{15}N$ from detritus, ranged from 0.079 in mayfly larvae to 0.997 in *Procambarus fallax* (Fig. 4). Alpha values indicated that the ecosystem was detritally based, having twenty-nine taxa (88%) with an alpha > 0.5 , including leafy bladderwort, *Utricularia foliosa*, a carnivorous vascular plant. Pond consumers consistently had more detritus in their gut contents than did consumers from spikerush and sawgrass habitats. One-way permuted ANOVA revealed a statistical difference in detrital consumption (maxT = 16.0, $p < 0.001$), and pairwise permutation tests revealed that 66% of species size classes shifted in detrital consumption among habitat-season levels (Table A.2.6). In the dry season, pond consumers ingested twice as

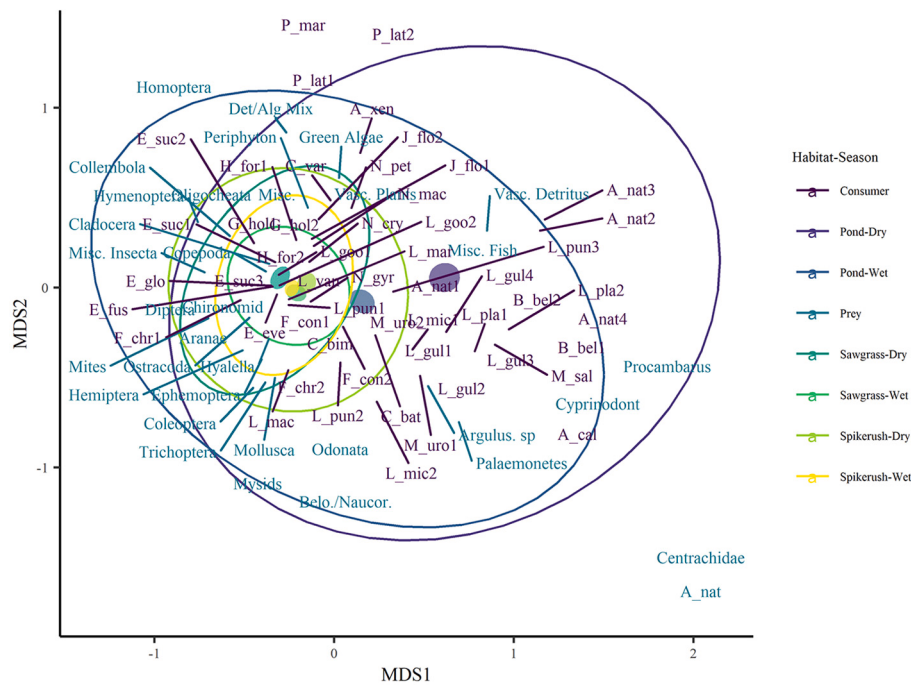


Fig. 2. NMDS plots of consumers and diet items (Prey). Labels represent the mean for that group among habitat-season levels. For some groups, lines extend from the label to their location in NMDS space to minimize overlap. MDS 1 is a directly related to prey size and MDS 2 is inversely related to consumer size and trophic position. Ellipses represent habitat-season levels. Filled ellipses are 95% confidence intervals and open ellipses are 95% data ellipses (they contain 95% of the data). Changes in ellipses size and location show spatiotemporal expansion or contraction of community-wide prey consumption. Prey that group near a given consumer are likely eaten by that consumer. Output from this NMDS is the basis for stomach-content niche modeling.

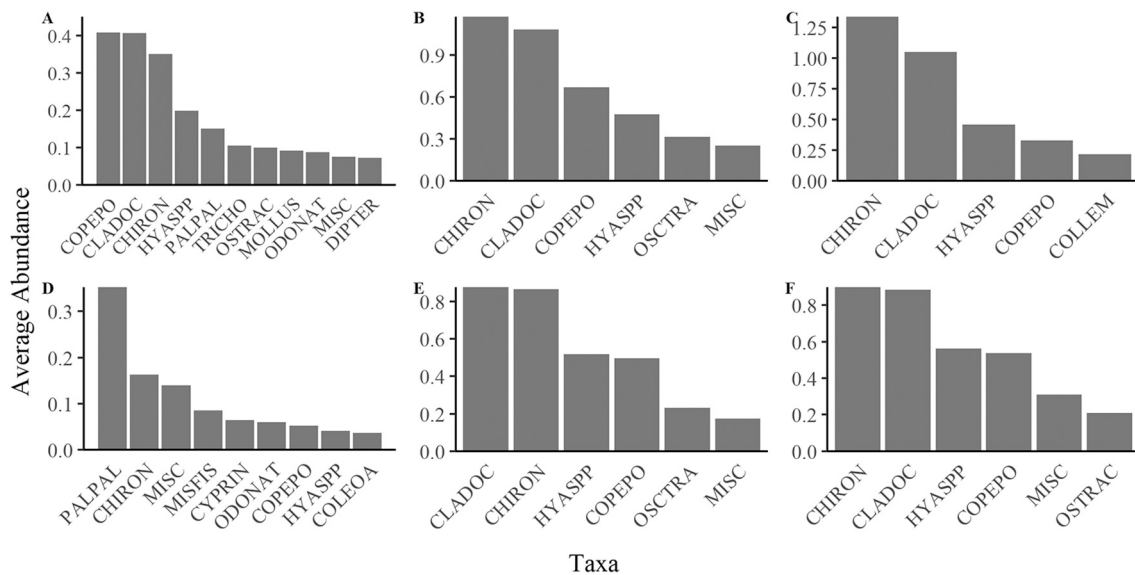


Fig. 3. Dominance-diversity curves for all habitat-season levels (A – Pond-Wet, B – Spikerush-Wet, C – Sawgrass-Wet, D – Pond-Dry, E – Spikerush-Dry, F – Sawgrass-Dry). Midge larvae (CHIRON) are the most important diet item across habitat-season levels. Only ponds see a notable shift in fish-diet communities between seasons. Prey item codes: CHIRON – Chironomidae larvae, CLADOC – Cladocera, HYASPP – *Hyalella* spp., COPEPO – Copepoda, COLLEM – Collembola, OSTRAC – Ostracoda, MISC – Miscellaneous, PALPAL – *Palaemonetes paludosus*, TRICHO – Trichoptera, MOLLUS – Mollusca, ODONAT – Odonata, DIPTER – Diptera, MISFIS – Miscellaneous fish, CYPRIN – Cyprinodontiformes.

much detritus as in the wet season. Spikerush and sawgrass marshes only differed in detrital consumption during the wet season when spikerush consumers had twice as much detritus in their guts on average.

3.4. Trophic position

Trophic positions derived from stomach contents had a narrower range than those from stable isotopes. Trophic positions among size classes of Everglades fishes for groups where $n \geq 5$ derived from stomach contents ranged from 1.94 for *Heterandria formosa* (1) in dry-season ponds ($n = 5$) to 3.11 for the invasive *Mayaheros urophthalmus* (1) in

wet-season spikerush ($n = 6$; Table A.2.7). Meanwhile, trophic positions modeled using stable isotopes ranged from 2.17 for larval *Caenis* spp. (Ephemeroptera) to 4.60 for *Micropterus salmoides* (Fig. 4). Unlike trophic positions calculated from stomach-content numeric data, several invertebrate taxa were included in the stable-isotope dataset. The range of trophic positions derived from stomach contents (1.17) was roughly half that of stable isotopes (2.43).

3.5. Niche breadth

We predicted that changes among habitats and seasons in trophic-

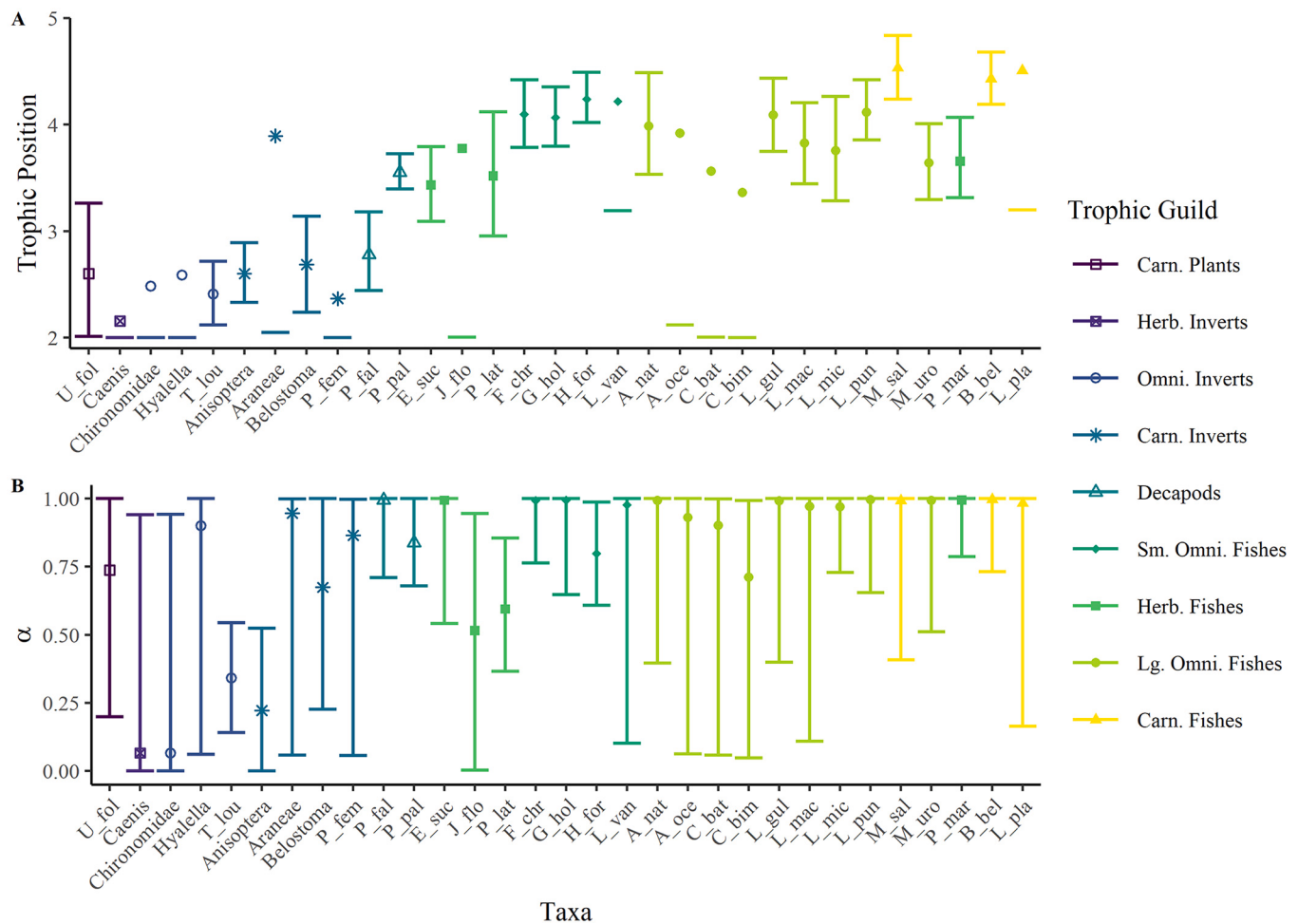


Fig. 4. A) Trophic position of consumers modeled using stable isotopes. B) Alpha, the proportion of $\delta^{15}\text{N}$ derived from detritus, of Everglades aquatic consumers. Colors and shapes correspond to trophic guilds from Table A.1, except for the carnivorous plant, *Utricularia foliosa*, which we placed in its own group “Carn. Plants”. Some consumers only have a lower bound of their 95% credibility interval on the plot denoted by a horizontal line because the upper limit of their trophic position extends off the plot.

niche areas would be similar within trophic guilds, that sawgrass and spikerush would have a higher frequency of larger niche areas than ponds, and that niche areas would increase in the dry season. Niche breadth (SEA_b) derived from stomach contents demonstrated spatiotemporal variation in frequency of niche size (relative generalization to specialization). For stomach contents, SEA_b varied from 6.31×10^{-4} for *Lepomis marginatus* in wet-season ponds to 2.55 for *L. punctatus* (1) in wet-season spikerush (Table A.2.8). Overall, modal SEA_b was more variable among species size classes during the wet season, and all trophic guilds demonstrated a range of niche areas with no clear spatiotemporal trends based on trophic guild (Fig. 5: (all) x Dry and (all) x Wet). Ponds had the highest frequency of small niche areas in the wet season while sawgrass had the lowest. However, dry-season ponds and sawgrass had similar frequencies of small niche areas among consumers. The range of niche areas more than doubled in sawgrass during the dry season relative to the wet season (Fig. 5). Meanwhile, SEA_b based on stable isotopes ranged from 0.03 for mysid shrimp (*Taphromysis louisianae*) to 7.38 for *U. foliosa* and showed differences among functional groups of consumers (Table A.2.9 and Figs. A.2.1 and A.2.2).

Community-wide trophic-niche area (i.e., Layman metrics) for habitats and seasons revealed spatiotemporal changes in trophic diversity (CD) and trophic redundancy (NND). We expected these to be highest in ponds (deeper habitats) and decrease in the dry season in all habitats. Range along MDS 1 (gradient of diet item size) was highest in ponds during both seasons and lowest in spikerush during both seasons and

dry-season sawgrass (Fig. 6). Conversely, all habitat-season levels had similar ranges along MDS 2 (gradient of consumer size). This suggests that among habitat-season levels differential prey consumption contributed more to trophic dynamics than differences in the relative abundance of consumers. Trophic diversity (TA) and mean trophic diversity (CD) were greatest in ponds with similar trends among habitat-season levels. Seasonal trends in spikerush were opposite those in ponds and sawgrass. In contrast, both trophic redundancy (NND) and evenness of trophic niches (SDNND) did not differ among habitat-season levels.

3.6. Non-native vs native niche overlap

We predicted that niche areas of non-native species would overlap with native species, especially non-native cichlids and native centrarchids. We found notable niche overlap between native and non-native species, particularly *M. urophthalmus* (Cichlidae). In total, we calculated the proportion of overlapping niche area for seventy-nine pairwise comparisons, forty-one from stomach contents and thirty-eight using stable isotopes (Table A.2.10). For stomach contents, proportional overlap ranged from 1.6% (*Clarias batrachus* vs. *A. natalis* (2), dry-season ponds) to 22.9% (*C. batrachus* vs. *L. punctatus* (3), dry-season ponds). In 10% of comparisons, proportional overlap exceeded 10% and most of these involved the native sunfish, *L. punctatus*. By contrast, stable isotopes revealed higher proportional overlap ranging from

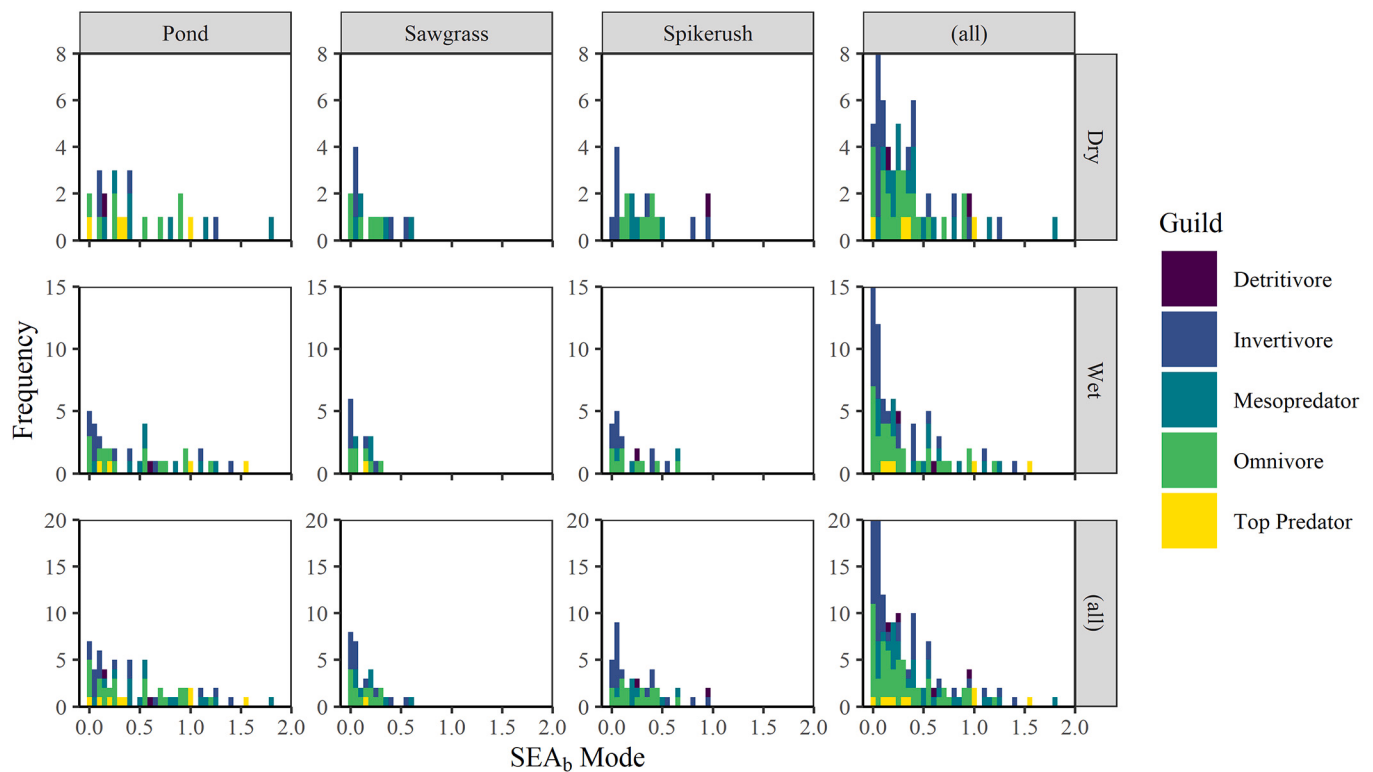


Fig. 5. SEA_b frequency distributions (colors correspond to trophic guild) for each habitat-season level, all wet-season consumers, all dry-season consumers, and all consumers. For all habitats, there was a higher frequency of larger niche sizes (increased generalization) in the dry season. Pond habitats had the highest frequency of smaller niche sizes (relative specialization) of any habitat for both seasons. Wet-season pond and dry-season pond both have a single outlier excluded from the plot.

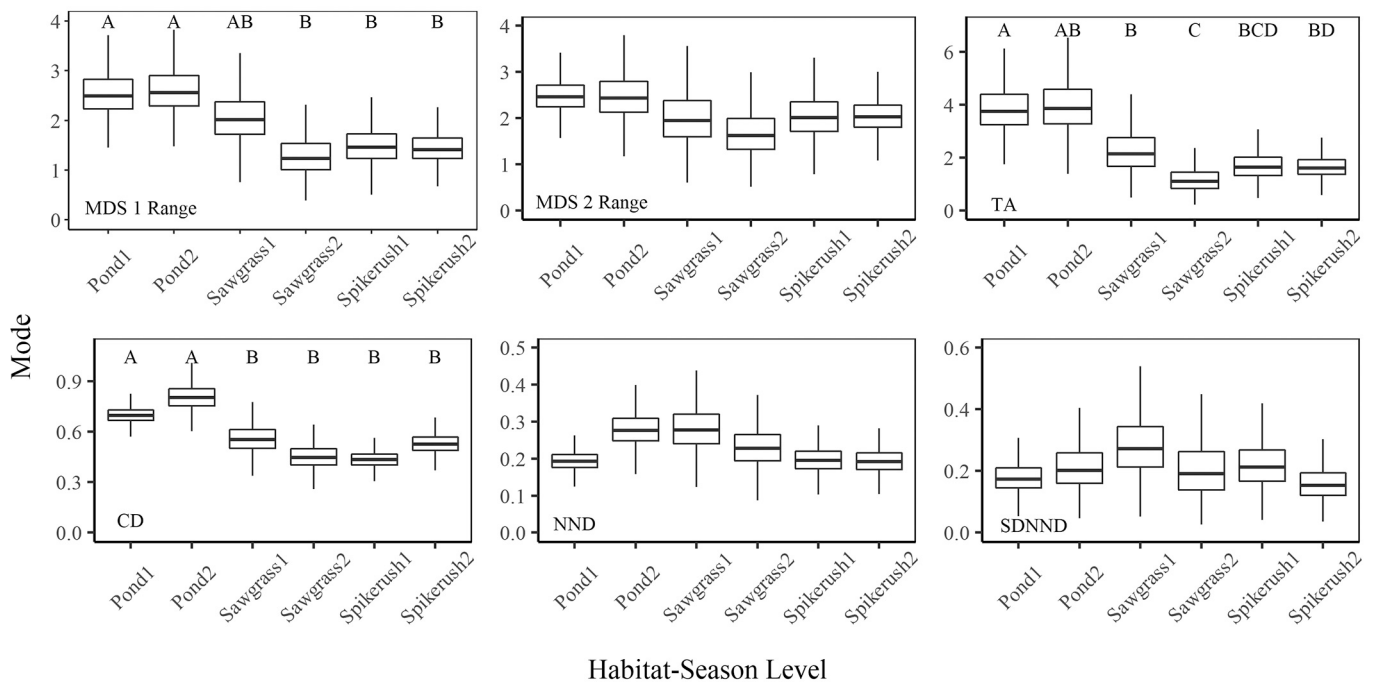


Fig. 6. Layman metrics derived from stomach contents across habitat-season levels (1 – Wet, 2 – Dry). Letters denote statistical differences at a 95% threshold. Layman metrics are MDS 1 (x-axis) range, MDS 2 (y-axis) range, TA – total area, CD – centroid distance, NND – nearest neighbor distance, SDNND – standard deviation of NND.

0.34% (*P. mariae* vs. *L. platyrhincus*) to 64.0% (*M. urophthalmus* vs. *L. macrochirus*), with 21% of comparisons exceeding 10% overlap (Table A.2.10).

3.7. Ontogenetic shifts in trophic dynamics

We predicted that most species would undergo ontogenetic diet shifts. There were thirty-eight instances of ontogenetic shifts in diet within a habitat-season level resulting from changes in carnivory (55% of observed ontogenetic shifts; often increased piscivory and decapod consumption with increasing size), diet plasticity (29%; similar mean contributions from prey categories between size classes, but different prey items within a category), herbivory (24%), and detritivory (21%). PERMANOVAs showed that eleven species (Table 2) underwent ontogenetic shifts (at least one size class's prey community differed, $p < 0.05$) in at least one habitat-season level (Table A.2.11). Ontogenetic shifts in diet were usually associated with trophic dispersion (90%) and

trophic displacement was common (57%) (Fig. A.2.3 and Tables 2 and A.2.12). A similar proportion of species underwent ontogenetic shifts in each habitat-season level.

3.8. Trophic dynamics in space and time

3.8.1. Spatial shifts in trophic dynamics

Spatial trophic shifts were ubiquitous and more common for trophic dispersion (66%) and displacement (92%) than trophic position (11%; Figs. 7 and A.2.4 and Tables 3, A.2.13, and A.2.14). Trophic dispersion and displacement among habitats were more common in the wet season than the dry season. Changes in trophic dispersion and displacement were driven by differing amounts of diet plasticity (68% of comparisons), carnivory (33%), piscivory (33%), and to a lesser extent detritivory (18%) and herbivory (13%) (Tables A.2.13 and A.2.14). Diet plasticity was defined as a consumer eating similar proportions of prey items from different functional groups (Table A.8), while having a shift

Table 2

Ontogenetic shifts in diet or trophic niche for species size classes within a habitat-season level. Pairwise PERMANOVA of stomach contents (p), probability of a change in niche breadth ($p(A < B)$), percent difference in SEA_b between groups A and B ($SEA_b\% \Delta$), percent niche overlap (Overlap), and driver for documented ontogenetic trophic dynamics. Driver abbreviations represent: H – herbivory, D – detritivory, DP – diet plasticity (a change in niche but not proportions of prey guilds), C – carnivory, and P – piscivory. Only species size classes with either a statistical difference in diet or SEA_b among size classes are included. See Table A.2.11 for full PERMANOVA results and Table A.2.12 for full ontogenetic SEA_b results.

Habitat-season level	Species	Size class A	Size class B	p	p (A < B)	$SEA_b\% \Delta$	Overlap	Driver
Pond – Wet	A_nat	1	2	0.018	0.810	31	7.34	C/P
		1	3	0.002	0.810	29	7.27	C/P
		1	4	0.002	0.300	–26	4.52	C/P
	E_suc	2	3	0.004	< 0.001	–99	0.03	DP
	F_chr	1	2	0.372	0.003	–85	1.13	H/D/P
	G_hol	1	2	0.002	1.000	656	12.90	H/D/P
	H_for	1	2	0.009	0.999	500	0.77	DP
	L_goo	1	2	0.004	0.945	67	0.99	H/DP
		1	2	0.663	0.133	–29	3.25	H/D/DP
		1	3	0.002	0.418	–4	4.11	H/D/DP
	L_gul	1	4	0.012	0.900	55	6.59	H/D/P
		2	3	0.012	0.848	35	4.23	DP
		2	4	0.067	0.991	118	6.70	P
	L_pun	1	2	0.029	0.988	160	9.72	P
		1	3	0.041	1.000	112	22.9	D
		1	2	0.020	< 0.001	–53	1.91	D/C/P
Pond – Dry	A_nat	1	3	0.230	0.844	26	5.33	P
		1	4	0.050	0.948	72	9.28	P
		2	3	0.130	1.000	168	5.36	P
		2	4	0.020	1.000	264	9.37	P
		1	2	0.141	1.000	1013	6.36	H/D/P
		1	2	0.049	1.000	4233	2.76	D
	L_gul	1	3	1.000	0.006	–69	4.11	DP
		3	4	0.241	1.000	225	6.65	P
		1	2	0.010	1.000	167	7.27	P
	L_pun	2	3	0.050	0.999	120	12.9	H/D/C/P
	A_nat	1	2	0.004	0.226	–48	3.55	H/D/C
	F_chr	1	2	0.002	0.433	–7	2.95	P
Spikerush – Wet	G_hol	1	2	0.002	1.00	4233	2.68	P
	L_goo	1	2	0.002	< 0.001	–67	0.42	DP
	L_pun	1	2	0.002	1.000	220	5.20	C/P
	F_chr	1	2	0.002	1.000	159	7.36	C/P
	F_con	1	2	0.026	0.492	0	2.03	C/P
	G_hol	1	2	0.018	0.999	154	3.09	H/P
Spikerush – Dry	H_for	1	2	0.010	0.161	–23	1.16	DP
	L_goo	1	2	0.009	0.990	100	1.22	DP
	L_pun	1	2	0.002	0.999	122	4.06	C/P
	F_chr	1	2	0.007	0.994	92	2.73	DP
	G_hol	1	2	0.004	< 0.001	–67	0.77	H/DP/P
	H_for	1	2	0.131	0.000	–92	0.17	H/DP
Sawgrass – Wet	L_goo	1	2	0.004	< 0.001	–60	0.38	DP
	L_pun	2	3	0.025	0.544	5	1.89	C/P
	F_chr	1	2	0.007	0.893	34	4.52	C/P
	F_con	1	2	0.085	1.000	325	3.45	C/P
	G_hol	1	2	0.013	0.671	13	2.47	H/P
	H_for	1	2	0.242	1.000	350	1.56	H/DP
Sawgrass – Dry	J_flo	1	2	0.037	< 0.001	–94	0.22	H/C
	L_goo	1	2	0.002	0.537	25	1.17	DP
	L_pun	1	2	0.002	1.000	589	6.68	C/P

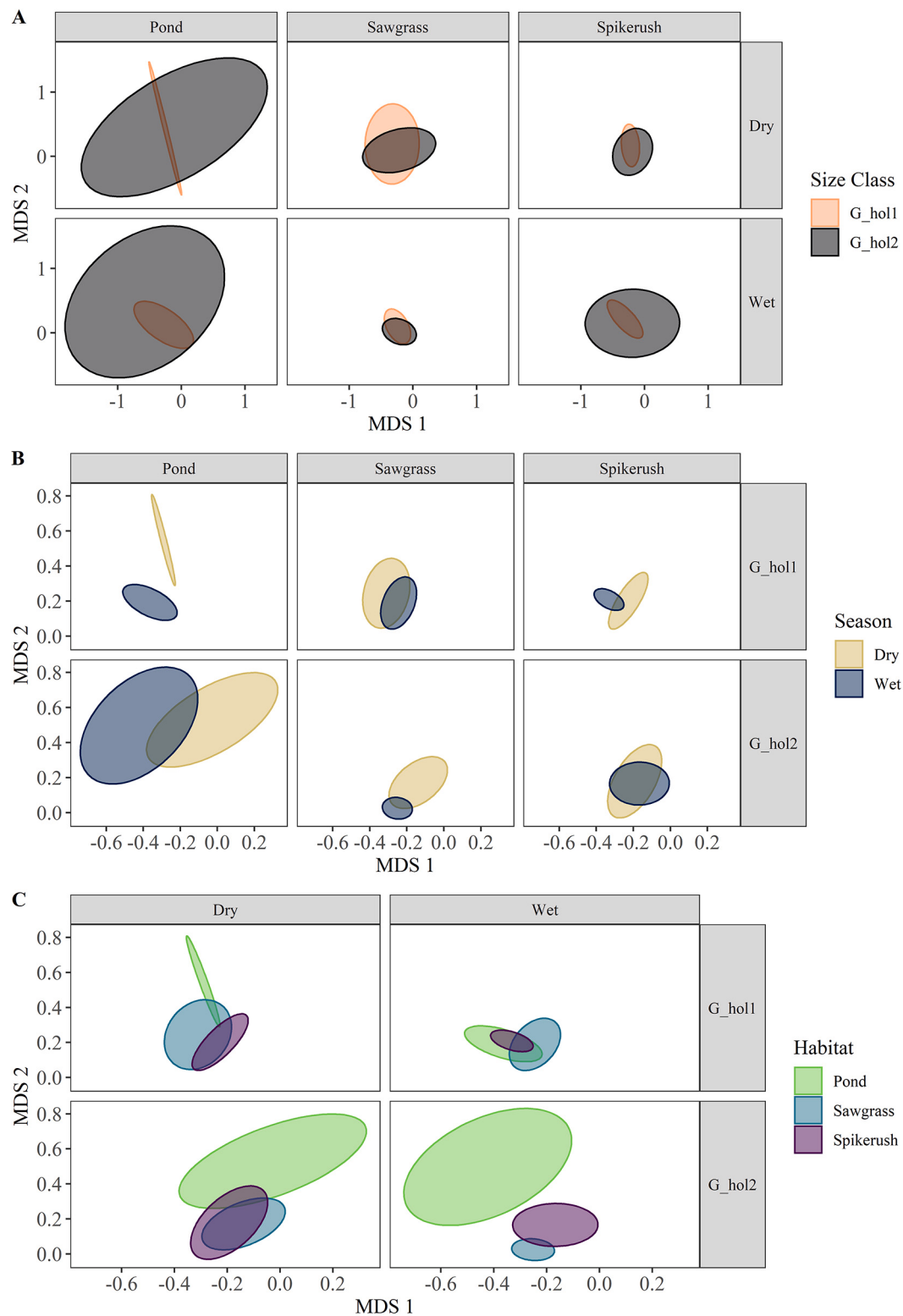


Fig. 7. Trophic-niche ellipses ($SEAs$) based on stomach contents in NMDS space for *G. holbrooki* across ontogeny (A), seasons (B), and habitats (C). Plots for other species are in Fig. A.2.4 and A.2.5. Note that the scale for each axis varies across plots to optimize each visualization. This results in the same ellipse looking slightly different among plots.

in trophic position and/or trophic niche. This indicated consumption of different prey items from the same functional group between habitats. Multiple drivers may be responsible for a given comparison, so percentages do not sum to one. There were only six species size classes that had statistically different trophic positions between habitats (Table 3).

Carnivory (66%), piscivory (50%), and diet plasticity (50%) were the most important drivers of shifts in trophic position. Detritivory contributed to one spatial shift in trophic position while herbivory contributed to none.

Table 3

Permuted ANOVA for trophic positions among species size classes across habitat-season levels derived from stomach contents. Only comparisons with statistical differences are reported here, complete results are reported in Appendix A (Table A.2.7). Species names are abbreviated as first letter of the genus, underscore, first three letters of the species, followed by size class. Group A is from the first habitat-season level in the Habitat-Season Comparison column, and Group B is from the latter habitat-season level. Season 1 = Wet; season 2 = Dry. Driver abbreviations represent: H – herbivory, D – detritivory, DP – diet plasticity (a change in niche but not proportions of prey guilds), C – carnivory, and P – piscivory.

Ontogenetic shifts						
Group A	Group B	Habitat-season comparison	F	p-value	%Δ	Driver
A_nat1	A_nat4	Pond1 – Pond1	–2.48	0.01	25.5	C/P
L_gul2	L_gul3	Pond1 – Pond1	–2.40	0.02	17.1	DP
J_flo1	J_flo2	Spikerush1 – Pond1	–2.37	0.02	19.8	D/C
A_nat1	A_nat2	Pond1 – Pond1	–2.20	0.03	19.8	C/P
L_pun2	L_pun3	Sawgrass1 – Pond2	–2.20	0.03	14.1	H/D
A_nat1	A_nat4	Pond1 – Pond2	–2.15	0.03	27.4	C/P
F_chr1	F_chr2	Sawgrass2 – Pond1	–2.09	0.04	16.3	C/P
L_pun1	L_pun3	Sawgrass2 – Pond2	–2.06	0.04	11.3	H/D
A_nat1	A_nat4	Sawgrass1 – Pond1	–2.00	0.05	27.3	C/P
H_for1	H_for2	Pond2 – Spikerush1	–1.99	0.05	26.3	DP
H_for1	H_for2	Pond2 – Sawgrass1	–1.97	0.05	25.8	H/DP
Habitat-season shifts						
Group A	Group B	Habitat-Season Comparison	F	p-value	%Δ	Driver
F_con1	F_con1	Sawgrass2 – Spikerush1	2.73	0.01	–13.1	C/P
A_nat1	A_nat1	Spikerush2 – Pond1	2.43	0.01	–15.9	D/C/P
A_nat1	A_nat1	Spikerush1 – Pond1	2.40	0.02	–14.9	D/C/P
L_gul3	L_gul3	Pond1 – Pond2	2.26	0.02	–18.9	DP
F_chr2	F_chr2	Sawgrass1 – Pond1	–2.19	0.03	16.8	C
H_for1	H_for1	Spikerush1 – Pond2	2.18	0.03	–23.6	DP
F_con1	F_con1	Sawgrass2 – Spikerush2	2.15	0.03	–9.9	DP/C
L_mar	L_mar	Spikerush1 – Pond2	2.10	0.04	–16.3	D/DP/C
L_pun2	L_pun2	Sawgrass1 – Sawgrass2	–2.05	0.04	28.1	P
F_chr2	F_chr2	Sawgrass2 – Pond1	–2.01	0.04	14.1	C/P
J_flo2	J_flo2	Sawgrass1 – Pond1	–1.99	0.05	17.4	DP
J_flo2	J_flo2	Spikerush2 – Pond1	–1.97	0.05	16.9	H/D/C
L_pun2	L_pun2	Sawgrass1 – Pond1	–1.97	0.05	11.6	C/P
G_hol1	G_hol1	Sawgrass1 – Spikerush1	–1.96	0.05	12.0	DP/P

3.8.2. Temporal shifts in trophic dynamics

Temporal trophic shifts were commonplace and more likely for trophic dispersion (71%) and displacement (82%) than trophic position (4%; Figs. 7 and A.2.5 and Tables 3, A.2.13 and A.2.14). Seasonal trophic displacement was more common than trophic dispersion in spikerush (89% vs 63% of comparisons) and sawgrass (100% vs 83%), while trophic displacement (65%) and dispersion (71%) occurred at a similar frequency in ponds. Temporal shifts in trophic dispersion and displacement were driven by changes in relative amounts of piscivory (56%), diet plasticity (48%), carnivory (37%), detritivory (23%), and herbivory (13%). There were only two seasonal changes in trophic position driven by diet plasticity and piscivory respectively.

3.9. Network structure

We predicted that during the dry season, food-web complexity would

Table 4

Food-web network metrics for each habitat-season level (Prop. Omni. – proportion of omnivores, Prop. Cann. – proportion of cannibalism, Num. trophic positions – number of trophic positions, Prop. Basal – proportion of basal taxa, Prop. Intermediate – proportion of intermediate consumers, Prop. Top – proportion of top consumers, Prop. Herb. – proportion of herbivores, Prey:Predator – prey to predator ratio).

Network metric	Pond		Spikerush		Sawgrass	
	Wet	Dry	Wet	Dry	Wet	Dry
Species richness	40	37	34	35	33	32
Total # Links	298	225	209	197	188	169
Connectance	0.186	0.164	0.181	0.161	0.173	0.165
Link density	7.450	6.081	6.147	5.629	5.697	5.281
Proportion of omnivores	0.600	0.541	0.471	0.457	0.515	0.469
Proportion of cannibalism	0.400	0.378	0.294	0.257	0.242	0.281
Total number of trophic positions	9	8	9	9	9	9
Proportion of basal resources	0.125	0.135	0.147	0.200	0.152	0.188
Proportion intermediate consumers	0.675	0.757	0.824	0.771	0.818	0.781
Proportion top consumers	0.200	0.108	0.029	0.029	0.030	0.031
Proportion herbivores	0.275	0.297	0.324	0.314	0.333	0.344
Prey:Predator	0.914	1.031	1.138	1.214	1.143	1.192

decrease in marshes and increase in ponds as aquatic species respond to water recession. Network topology differed among habitat-season levels with variable magnitudes and directions (Table 4). Taxon richness was highest in wet-season ponds and lowest in dry-season sawgrass. During the dry season, all habitats displayed a decrease in total number of links, link density, connectance, and proportion of omnivores and an increase in proportion of basal resources and prey-to-predator ratio. We observed mixed seasonal trends among habitats for proportion of herbivores that increased in ponds and sawgrass during the dry season yet decreased in spikerush. Similarly, proportion of cannibalism, intermediate consumers, and top consumers all showed mixed seasonal trends among habitats. Cannibalism (defined here as a consumer feeding within its own trophic guild, Perdomo et al., 2012) increased in sawgrass and decreased in ponds and spikerush during the dry season. In the dry season, intermediate consumers increased in ponds but decreased in spikerush and sawgrass. Proportion of top consumers roughly halved in ponds during the dry season, with spikerush and sawgrass showing no seasonal change.

4. Discussion

Spatial variation in resource profitability is important for ecosystem resilience and dynamic stability of fluctuating ecosystems (Leigh et al., 2010; Pettit et al., 2017). Our results that include many food-web metrics from a seasonally flood-pulsed ecosystem support the hypothesis that food webs are highly variable in space and time and that this variability is likely an underappreciated aspect of maintaining energy and material flows in dynamic ecosystems (McMeans et al., 2019). We found that spatiotemporal food-web dynamics of the Everglades aquatic biota were characterized by varying degrees of piscivory, detritivory, and diet plasticity. For a given species size class, changes in trophic position were uncommon. However, even when trophic position remained constant, spatiotemporal shifts in diet and trophic niche were common. Trophic dispersion decreased for many taxa in the dry season compared to the wet season, often accompanied by trophic displacement. Previous work in hydrologically pulsing systems found either a dry-season increase or no seasonal change in number of trophic links, link density, and connectance (Winemiller, 1990). Differences between this study and others in tropical, flood-pulsed ecosystems are likely the result of the temperate origin of native fauna that have had relatively little time to adapt (~ 6000 years) to the hydrologic regime and radiate to take advantage of the available resource pools (Loftus and Kushlan,

1987; Turner et al., 1999). In this study, all habitats displayed a dry-season decrease in total number of trophic links, link density, connectance, and proportion of omnivores. In contrast, proportion of basal resources and prey-to-predator ratio increased during water recession. In addition to variability in food quantity (proportion of omnivores, prey-to-predator ratio) and quality (proportion of basal resources), consumer foraging behavior, habitat structure, and other ecological factors drive resource profitability (de Almeida et al., 1997; Winemiller and Kelso-Winemiller, 1994).

Prey consumption varied across habitat-season levels. This was driven by differences in relative abundance of consumers collected in the field and could be driven by different relative abundances of prey items in time and space. For example, Everglades studies have documented spatiotemporal variation in periphyton, invertebrate, and fish communities that reveal dynamic resource pools (Gaiser et al., 2012; Gunderson and Loftus, 1993; Loftus and Kushlan, 1987; Rader, 1994; Trexler et al., 2005; Trexler and Loftus, 2016). Consumers may track specific prey or switch prey based on availability. As a result, increased consumption of a given prey in a certain habitat or season does not necessarily mean that prey is more abundant in that habitat or season. For instance, as drying progresses, fishes move from shallow wetlands to become concentrated in ponds, especially large-bodied predators like *L. platyrhincus*, *L. gulosus*, and *A. natalis* (Loftus and Kushlan, 1987; Parkos et al., 2011). During both seasons, omnivorous cyprinodontoids dominated spikerush and sawgrass habitats (Loftus and Kushlan, 1987). This dominance explains in part the shift towards larger prey (i.e., decapods and fishes) in pond-fish stomachs relative to marsh-fish stomachs, particularly in the dry season.

Primary producers were more common in diets in spikerush and sawgrass food webs than in ponds, although the food web was primarily detrital across all habitats and both seasons. This was consistent with previous findings (Belicka et al., 2012; Williams and Trexler, 2006). The largest heterotrophic pathway in this food web may be through *Utricularia* spp. Carnivorous bladders create a mutualism between *Utricularia* spp. and a community of algae and zooplankton that in the Everglades is dominated by rotifers (Richards, 2001). Based on our results, the extensive mats of *Utricularia* spp. are deriving their energy from detrital sources, likely assimilating microbes from decaying organisms in their bladders. Given their prevalence across the landscape (Davis et al., 1994), this may represent the greatest heterotrophic food-web pathway in terms of biomass.

McMeans et al. (2019) found that flexible omnivory permitted seasonal fluctuations in trophic position. While shifts in trophic position were uncommon in the Everglades habitats in this study, for the rare trophic position shifts that did occur, they were associated with three aspects of flexible omnivory – variable amounts of piscivory, detritivory, and diet plasticity. Differences in foraging tactics combined with spatial differences in invertebrate communities (food availability) may explain mixed direction (i.e., piscivory, detritivory, or diet plasticity) and magnitude of trophic shifts among taxa. For example, dry-season *G. holbrooki* demonstrated elevated piscivory. While stomach contents often could not identify prey to species, mixing models showed that most *G. holbrooki* piscivory was cannibalism. Cannibalism in *G. holbrooki* may be a mechanism to continually consume high-quality prey as other resource bases fluctuate in time and space. Meanwhile, trophic shifts in *F. chrysotus* were related to diet plasticity in the amount of non-aquatic invertebrates (e.g., Hymenoptera, Araneae) in their diets that could potentially increase (Araneae) or decrease (Hymenoptera) their trophic position. Additionally, ponds are phosphorus-enriched relative to adjacent marshes (Kushlan and Hunt, 1979). The impact of nutrient status on structuring freshwater invertebrate communities is well documented (Sterner and Elser, 2002; Trexler and Loftus, 2016). Species-specific foraging tactics that facilitate differential access to spatially variable prey (e.g., nutrient-enriched ponds versus more oligotrophic marshes) may contribute to shifts in trophic position. Species size classes that underwent spatiotemporal shifts in trophic position included some of

the most abundant fishes in the freshwater Everglades, such as *G. holbrooki*, *H. formosa*, and *F. chrysotus* (Loftus and Eklund, 1994; Loftus and Kushlan, 1987; Trexler et al., 2005). The trophic flexibility of these species contributes to their success in a dynamic ecosystem.

The prevalence of shifts in trophic dispersion and displacement, while trophic position remained constant, indicates that most species forage on different yet trophically similar prey as resources fluctuate in space and time. Niche overlap among habitat-season levels for a given species size class never exceeded 12.5% and for most comparisons was <5%. Like shifts in trophic position, these changes were most often driven by changes in piscivory, detritivory, and diet plasticity, all of which are thought to increase food-web stability. For example, diet plasticity, such as facultative omnivory, where an organism consumes more prey from lower trophic levels as ideal prey become scarce, as documented in this study, is thought to increase food-web stability relative to fixed omnivory (Křivan and Diehl, 2005). Furthermore, spatial and temporal trophic shifts among spatiotemporally asynchronized prey items (e.g., dynamic invertebrate assemblages) also work to stabilize food webs by providing a consistent resource base (Takimoto et al., 2002). Detritivory also increases ecosystem stability and species persistence with positive effects on trophic structure and biodiversity (Moore et al., 2004; Rooney and McCann, 2012). In fact, the habitat in which fishes consumed the most detritus – ponds – had the most diverse communities in both seasons. Trophic flexibility within food webs, such as facultative omnivory and detritivory, which facilitates exploitation of asynchronized resource availability (e.g., detritus and prey communities), may be necessary for stability in nonequilibrium ecosystems (Kratina et al., 2012; McCann and Rooney, 2009).

Topology revealed that food-web complexity decreased in the dry season in all habitats. This finding aligned with our prediction for shallow-water habitats (spikerush and sawgrass) but was the opposite of our prediction for deep-water habitats (ponds). Our prediction was based on the idea that, as consumers became concentrated in ponds during the dry season, additional trophic interactions would materialize and increase food-web complexity. However, we observed reduced food-web complexity represented by decreases in total number of links, connectance, and link density during the dry season in all habitats. Decreased food-web complexity corresponded with an increase in the proportion of empty stomachs. There was evidence of fishes concentrating in ponds during the dry season in the form of increased proportions of herbivores and intermediate consumers along with a decreased proportion of top consumers. Given the seasonal decrease in species richness in ponds and decreased complexity, the concentration of fishes in ponds may not have created additional trophic interactions during the dry season but instead strengthened links already present. If a preponderance of weak interactions leads to stability (McCann et al., 1998; Rooney and McCann, 2012), then fewer, stronger interactions in dry-season ponds may be relatively unstable. Interestingly, wet-season ponds were the only habitat-season level with a prey-predator ratio less than one. Practically, this means that there are more predatory taxa than prey taxa, which indicates food-web instability (Perdomo et al., 2012). Ponds are donor-controlled habitats (Strong, 1992) that can sustain a high predator-to-prey ratio for a relatively short period of time, until the next wet season when they are reconnected to the adjacent marsh. In the absence of re-flooding, pond food webs would probably collapse to a relatively small community. Solution hole communities, which provide temporary drought refuges in short-hydroperiod areas of the Everglades like alligator ponds in longer hydroperiod regions, have declining species richness and functional diversity after they become isolated from surface aquatic connections and water quality deteriorates as the dry season progresses (Kobza et al., 2004; Rehage et al., 2014).

Food webs play a pivotal role in understanding the consequences of biological invasions (David et al., 2017). Trophic impacts from invasive species at the top and bottom of food webs are well studied and can be dramatic (Capps et al., 2015; Sharpe et al., 2017; Simon and Townsend, 2003; Tait et al., 2015; Wahl et al., 2011; Zaret and Paine, 1973).

Meanwhile, mid-level consumers (e.g., many of the cichlids in this ecosystem) are underrepresented in the literature, and their location in the food web facilitates multidirectional effects that may be difficult to interpret without taking a network approach (Flood et al., 2020). Our study system, Everglades National Park, is home to seventeen non-native fish species (Kline et al., 2014). This study was conducted prior to the invasion of many of these, most notably the African Jewfish (*Hemichromis letourneuxi*) and Asian Swamp Eel (*Monopterus albus javanensis*). Therefore, the data reported here constitute a “vanishingly rare” description of a pre-invasion baseline (Strayer, 2012). This baseline food web accounts for spatial and temporal variation that could otherwise obscure effects of invasions. Furthermore, we can use results from analyses here to predict that native sunfishes, particularly *L. punctatus*, will decrease in abundance as a result of trophic overlap with invasive *M. urophthalmus*, and that trophic overlap between native taxa and another invasive cichlid, *H. letourneuxi*, will be similar.

Spatiotemporal shifts in trophic position, trophic niche, and diet are well documented in a variety of taxa and ecosystems, including stream macroinvertebrates (Hellmann et al., 2013), temperate forest birds and rodents (Nakano and Murakami, 2001; Stephens et al., 2019), tropical forest bats (Salinas-Ramos et al., 2015), and mammals from arid shrubland, desert, and temperate forests (Balestrieri et al., 2019; Dawson and Ellis, 1996; Soykan and Sabo, 2009). Conversely, these metrics, particularly trophic position, can remain static through space and time in some cases, as observed in stream fishes (Rybczynski et al., 2008), tropical floodplain fishes (Correa and Winemiller, 2014), black swamp snakes (Willson et al., 2010), and certain taxa in this study. Thus, spatiotemporally flexible omnivory seems variable in its direction and magnitude and more likely to result in a change in diet and niche breadth than trophic position. Questions remain about how spatiotemporal dynamics of flexible omnivory are influenced by individual specialization within a species (Bolnick et al., 2011; Matich et al., 2021) or species size class, and how spatiotemporal dynamics of omnivory change across ecosystems, particularly at higher latitudes (Hampton et al., 2017; McMeans et al., 2015).

5. Conclusions

Spatiotemporal variability in flexible omnivory is a critical food-web attribute that helps maintain energy and nutrient cycling, facilitates species coexistence, and influences ecosystem stability (McMeans et al., 2019; Post and Takimoto, 2007; Wootton, 2017). Our results indicate that fishes in a subtropical, seasonally pulsed wetland show spatiotemporal shifts in trophic niche (i.e. trophic dispersion and trophic displacement) that are not associated with shifts in trophic position. Throughout the flood pulse, most species are tracking variable, yet trophically similar, prey. Trophic dynamics were driven by varying levels of piscivory, detrital consumption, and diet plasticity. Variability across time and space at both habitat and ecosystem scales likely facilitates divergent resource pools and foraging tactics. Spatiotemporal food-web dynamics are not confined to fishes in subtropical ecosystems, and further knowledge of how organisms adapt their foraging strategies across time and space is important for understanding potential impacts of climate change, hydrologic alterations, and invasive species. Spatiotemporal trophic plasticity seems to play an important role in maintaining ecosystem stability and resilience particularly in ecosystems with regular perturbations.

CRedit authorship contribution statement

Peter J. Flood: Data curation, Formal analysis, Methodology, Software, Visualization, Writing – original draft. **William F. Loftus:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Resources, Writing – review & editing. **Joel C. Trexler:** Conceptualization, Funding acquisition, Methodology, Resources, Writing – review & editing, Supervision, Project administration.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

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