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Running Head: Dispersal, competition, and isotopic niche breadth

Relative Role of Dispersal Dynamics and Competition in Determining Isotopic Niche Breadth

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Summary

1. The niche variation hypothesis predicts that among-individual variation in niche use will increase in the presence of intraspecific competition and decrease in the presence of interspecific competition. We sought to determine if local isotopic niche breadth of fish inhabiting a wetland was best explained by competition for resources and the niche variation hypothesis, by dispersal of individuals from locations with different prey resources, or a combination of the two. We analyzed stable isotopes of carbon and nitrogen as indices of feeding niche and compared metrics of within-site spread to characterize site-level isotopic niche breadth. We then evaluated the explanatory power of competing models of the direct and indirect effects of several environmental variables spanning gradients of disturbance, competition strength, and food availability on among-individual variation of the eastern mosquitofish (*Gambusia holbrooki*).

2. The Dispersal model posits that only the direct effect of disturbance, changes in water level known to induce fish movement, influences among-individual variation in isotopic niche. The Partitioning model allows for only direct effects of local food availability on among-individual variation. The Combined model allows for both hypotheses by including the direct effects of disturbance and food availability.

3. A linear regression of the Combined model described more variance than models limited to the variables of either the Dispersal or Partitioning models. Of the independent variables considered, the food availability variable describing the percent edible periphyton explained the most variation in isotopic niche breadth, followed closely by the disturbance variable, day since last drying event.

4. Structural equation modeling provided further evidence that the Combined model was best supported by the data, with the Partitioning and the Dispersal models only modestly less

informative. Again, the percent edible periphyton was the variable with the largest direct effect on niche variability, with other food availability variables and the disturbance variable only slightly less important. Indirect effects of heterospecific and conspecific competitor densities were also important, through their effects on prey density.

5. Our results support the Combined hypotheses, though partitioning mechanisms appear to explain the most diet variation among individuals in the eastern mosquitofish. Further work examining these relationships in the dry season is needed to determine if the same variables are predictors of among-individual isotopic variation throughout the year. Examining niche breadth of other wetland species and assesement by metrics other than stable isotopes would also help determine the generality of these results.

6. Our results support some predictions of the niche variation hypothesis, though both conspecific and interspecific competition appeared to increase isotopic niche breadth in contrast to predictions that interspecific competition would decrease it. We propose that this resulted because of high diet overlap of co-occurring species, most of which consume similar macroinvertebrates.

Introduction

Among-individual variation in diet, also known as individual specialization, has important implications for population stability, the strength of intraspecific competition, and the rate of local adaptation (Bolnick et al., 2011; Bolnick et al., 2003; Violle et al., 2012). Accurate modeling of among-individual variation requires understanding the causes and consequences of this variation. The niche variation hypothesis and optimal foraging theory can provide a framework for understanding among-individual variation in diet and the resulting changes in niche breadth of populations (e.g., Bolnick et al., 2010; Svanbäck & Bolnick, 2005; Van Valen, 1965).

The niche variation hypothesis proposes that populations have constrained niche breadth when exposed to strong interspecific competition, and have broad niche breadth when released from interspecific competition and are subject only to intraspecific competition (Bolnick et al., 2010; Van Valen, 1965). Increased diet niche breadth in a population can arise in two general ways: 1) all individuals in a population increase their diet niche breadth, or 2) variation in diet among individuals in the population increases. The second mechanism is proposed by the niche variation hypothesis and is often referred to as partitioning, as individuals partition resources among themselves. Early studies often found no support for the niche variation hypothesis (e.g., Soulé & Stewart, 1970). However, the lack of support is generally thought to be a result of these studies using morphological variance as a proxy for diet variation (Bolnick et al., 2010). Recent studies using more direct measures of diet variation, such as gut content and stable isotope analyses, are generally supportive of the niche variation hypothesis (Araújo et al., 2008; Bolnick et al., 2010; Bolnick et al., 2007; Codron et al., 2011; Costa et al., 2008; Jack & Wing, 2011; Svanbäck & Bolnick, 2007).

Optimal foraging theory provides insight into potential mechanisms for among-individual variation. Optimal foraging theory states that an activity should be maintained as long as the gains from the activity are greater than the costs, including missed opportunity costs (MacArthur & Pianka, 1966). Other authors have expanded on the original tenets of optimal foraging theory by evaluating how individuals maximize the relationship $E/(S+H)$, with E being energy gain, S being time searching, and H being handling time (Stephens & Krebs, 1986; Svanbäck & Bolnick, 2005). Local environmental factors (e.g., relative abundance of food sources, quality of food, predation risk) can affect handling time and search time, altering the energy income rate, and favoring alternate foraging strategies with varying local conditions (Schmitz et al., 1998; Staniland et al., 2010; Svanbäck & Bolnick, 2005; Tinker et al., 2009). These studies demonstrate that local environmental conditions can affect foraging strategy and, therefore, diet of individuals. Individual variation in efficiency of searching, capturing, or handling prey items, equates to intraspecific differences in energy acquisition (Ehlinger, 1990). These individual differences allow for variation in diet among individuals exposed to the same local conditions.

Niche-use theories assume that past conditions at a site affect current conditions, and are the basis for predicting future actions of individuals (Beckerman et al., 2002; Ehrlén, 2000; Helle et al., 2012; Tanner et al., 1996; Tanner et al., 2011). However, among mobile species inhabiting patchy landscapes, a simple alternative explanation for among-individual variation is that diet resources differed in the environments from which they dispersed (Tilman, 1994). Many species move between microhabitats that can vary substantially in the abundance and types of food available (Heithaus et al., 2006; Polis et al., 1997; Sargeant et al., 2007; Tilman, 1994). Therefore, for mobile animals, dispersal can affect niche breadth of a population (Thompson et al., 2012). Consequently, models of contemporary population niche breadth need to account for

dispersal patterns of individuals and the variation among individuals exposed to different prior conditions. Use of tools like stable isotopes to assess niche breadth, which provide a cumulative measure of diet breadth dependent on the turn-over time of the tissue sampled, may exacerbate this issue (Thomson et al. 2012).

We evaluated two hypothesized mechanisms determining among-individual variation of a freshwater fish species, eastern mosquitofish (*Gambusia holbrooki*), in an environment characterized by seasonal disturbance events. The first hypothesis, Dispersal, assumes that all individuals forage optimally in proportion to prey availability and that dietary variation among individuals is caused by spatial differences in local prey availability (Figure 1). Therefore, sites with large among-individual variation should contain individuals from disparate areas that had different prey resources. This occurs as a result of seasonal flooding and drying events that induce movement in fish, and is expected to be most strong in areas with long hydroperiod that receive dispersers from areas that dry annually, as well as supporting a resident population (McElroy et al., 2011). Also key to this hypothesis is the assumption that there is no relationship between eastern mosquitofish isotopic niche breadth and food availability at the collection site, since fish have recently moved from other areas and therefore have not yet incorporated enough of the local foods into their diets to affect their isotopic signature.

The second hypothesis, Partitioning, stems from the niche variation hypothesis and assumes that among-individual variation is determined by intraspecific competition pressure; therefore, the observed variation in isotopic value of eastern mosquitofish is a result of partitioning of food resources (Figure 1). Thus, in contrast to the Dispersal hypothesis, the Partitioning hypothesis predicts that fish densities and food sources have direct effects on

among-individual variation and the disturbance effects only have indirect effects via effects on food availability and competitor density.

A third model, Combined (Figure 1), evaluates the hypothesis that both previously described mechanisms are working in conjunction; that direct and indirect effects of disturbance and food availability causes variation among individuals.

Methods

Study System

Our study encompassed sites spanning a range of disturbance (water depth, DSD, recession rate), nutrient (periphyton total phosphorous), food availability (invertebrate density and edible periphyton) and potential competition (fish density) (Table 1). These sites were located across the Everglades in a number of water management units (Figure 2). Sites included areas that range from yearly drying and flooding cycles (hydroperiod length less than 360 days) to areas that have been inundated continuously for over 5 years. Sites also vary greatly in nutrient content as a result of their proximity to nutrient input. These wide ranges in environmental parameters allow for great variation in the biological variables at a site.

The eastern mosquitofish is a meso-consumer known for having a diverse and variable diet (Blanco et al., 2004; Geddes & Trexler, 2003; Loftus, 2000; Pyke, 2005; Specziár, 2004). Having a broad potential feeding niche means that there is an opportunity for among-individual variation in diet. Eastern mosquitofish are found across the Everglades in relatively high numbers, allowing for analysis at a number of sites across environmental gradients in the Everglades. Finally, eastern mosquitofish are known to disperse and colonize newly flooded

areas (Alemadi & Jenkins, 2008; Obaza et al., 2011; Trexler et al., 2001), possibly driven by changing food availability (DeAngelis et al., 2010).

Field Sampling Protocol

Eastern mosquitofish were sampled following the procedure described in Sargeant et al. (2010) in November and December 2005, during the late wet season, when water levels begin to drop. Approximately 50 sites were sampled from a subset of randomly generated sites (Stevens & Olsen, 2003). All sites were located in wet prairie slough habitats. Of these sites, only 21 yielded enough eastern mosquitofish to be included in this study ($n \geq 17$, Figure 2). Fish and large invertebrates were collected by throw-trap sampling as described in Jordan et al. (1997) and Sargeant et al. (2011). Three replicate samples were collected at each site. From each throw trap, all small fishes (<8 cm) and large invertebrates (>5 mm) were collected. An MS-222 (tricaine methanesulfonate) bath was used to euthanize all collected vertebrates following standard procedures (Nickum et al., 2003). Additional mosquitofish were collected for isotope analysis by 10 minutes of haphazard dip netting in the area. All collected organisms were placed on ice in the field and then frozen at -17.7°C before sample processing. Three periphyton samples were collected. One periphyton sample was processed to determine total phosphorous for use as an indicator of nutrient enrichment (Gaiser et al., 2006). The second periphyton sample was processed to identify and categorize algal species. The combined relative abundance of the diatom and green algae categories was used as a measure of percent edible periphyton for analyses because these categories are thought to be more palatable to consumers (Geddes & Trexler, 2003). The final periphyton sample was collected for analysis of macroinvertebrate infauna (Liston & Trexler, 2005).

Depth, recession rate, and the number of days since the site was dry (DSD) were used as measures of hydrological disturbance. Average depth was measured to the nearest centimeter for each throw trap at the time of sampling. The Everglades Depth Estimation Network (EDEN; <http://sofia.usgs.gov/eden/>) stores daily depth data across the Everglades for many years, and these data were used to determine recession rate and DSD. The DSD variable is defined as the number of days since the area was first reflooded (water level > 5cm) after the most recent drying event (water depth < 5 cm). The recession rate is the absolute value of the difference in water level at the sampling date and 30 days prior.

Laboratory Protocol

Stable isotope data are often used to determine variation in diet and are appropriate for this type of study because they provide information on long-term integrated diet, as opposed to gut contents that provide snap-shot information (Bearhop et al., 2004; Tieszen et al., 1983; Weidel et al., 2011). For the eastern mosquitofish, stable isotope data reflect approximately 50 days, or one-third of an individual's lifespan (Green, 2007). Thus, stable isotope data are able to answer questions regarding long-term among-individual variation in diet.

Previous studies have shown that the range of prey species' isotopic values is potentially a confounding factor with niche breadth of consumers (Matthews & Mazumder, 2004). Because of the scale and complexity of the Everglades, all sites were accessed by helicopter in order to complete sampling within the same season, which limited sampling time per site. Thus, we were not able to obtain the large number of small prey necessary for isotopic analysis at each site (e.g., we have found that at least 20 amphipods are required to have enough tissue mass to obtain one pair of carbon and nitrogen isotope values). Previous work in the Everglades using a two end-member model with *Planorbella duryi* (grazer) and *Hyallela azteca* (detritivore) has shown that

there is very low variance in the range of prey isotopic values among sites separated at a similar scale to those sampled for this study (Williams & Trexler, 2006). These two end members bracket the $\delta^{13}\text{C}$ range in the Everglades: *P. duryi* have carbon isotopic values similar to green algae and diatoms and represent the algae based food pathway, while *H. azteca* have carbon isotopic values representative of the detritus based food pathway (Williams & Trexler, 2006; Belicka et al., 2012). Thus, we assumed that prey availability and diet, not spatial variation in the isotopic value of specific prey types, is the primary source of eastern mosquitofish isotopic variation.

In the lab, eastern mosquitofish samples were processed for isotope analysis following the protocol described in Sargeant et al. (2010). Muscle tissue was removed from the caudal region of each individual and the tissue was then rinsed in deionized water and dried at 55-60° C for at least 24 hours. After drying, the tissue was ground into fine powder and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using an isotope ratio mass spectrometer at the FIU Stable Isotope Laboratory. Pee Dee Belemnite was used for $\delta^{13}\text{C}$ standard, and atmospheric N_2 was used as $\delta^{15}\text{N}$ standard. Tissues were not subject to lipid extraction prior to analysis because previous studies (Williams & Trexler, 2006) found little impact of lipid extraction on Everglades consumers. Also, eastern mosquitofish have a low C:N value, so lipid extraction is generally thought to be unnecessary (Post et al., 2007).

In order to analyze food availability, periphyton cores were processed for macroinvertebrates following the protocol described in Sargeant et al. (2011). Periphyton cores were thawed and all macroinvertebrates were removed, identified, and counted using a light microscope. After identification, all individuals were classified into dietary functional groups (herbivores, carnivores, detritivores, and omnivores) on the basis of previous studies (Belicka et

al., 2012; Loftus, 2000; Thorp & Covich, 2001). After the macroinvertebrates were removed, the remaining periphyton was dried at 80°C for 48 hours, then incinerated at 500°C for 3 hours to determine ash free dry mass (AFDM) of the sample (Liston, 2006). Infauna density was determined for each functional group by calculating the number of macroinvertebrates of the group in the sample divided by the AFDM of the sample.

Analytical Methods

We used the SIAR package in R to calculate the niche parameters for each site (R Development Core Team, 2012, Appendix 1). Metrics calculated for each site are: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ range, mean nearest neighbor distance (NND), mean distance to centroid (CD) and total area (TA) (Electronic Supplement, Table A2). The metric “Total Area” was reported as a measure of total niche breadth and the metrics NND and CD were indicative of similarity between individuals in isotopic signatures. If a site had a relatively large value for total area and a relatively large value for either NND or CD, then the large niche breadth is likely a result of increased among-individual variation. However, if the same site with a large total area has a relatively small value for average NND or CD, it suggests that some fish were outliers and that in general the site has low among-individual variation. For the range calculations, the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value at each site was subtracted from the highest value. Nearest neighbor distance was calculated by taking the mean of the Euclidean distances between each individual and its nearest neighbor (the next closest individual in the isotope bi-plot space). The centroid is calculated for each site separately, and its coordinates are the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the individuals at the site. Mean distance to centroid was calculated by taking the mean of the Euclidean distances between each individual and the centroid. Total area was calculated using the convex hull method (Cornwell et al., 2006). For all measured isotope metrics, shorter/smaller values indicate

less among-individual variation in diet. Sample sizes were not equal across sites (range 17-54, mean 29.1, SD 10.7). However, linear regression showed that none of the isotope metrics were correlated with sample size (N Range $R^2 = 0.069$, C Range $R^2 = 0.005$, TA $R^2 = 0.068$, CD $R^2 = 0.00$, and NND $R^2 = 0.196$). Many of the isotope metrics were strongly correlated, so they were condensed into a single variable using varimax rotation in principal components analysis. Only one factor had an eigenvalue greater than 1.00, so only one factor was formed using factor scores. The factor score was used as a proxy for among-individual variation in analyses.

We used bivariate Pearson product moment correlations and linear regressions to explore the patterns of relationships among the variables. Bivariate correlations were run to determine basic relationships between each pair of variables without considering shared variance with other variables. Linear regression were also run to examine simultaneous direct effects of the measured variables on among-individual variation in diet (Berk, 2010). Many of the variables were skewed and were therefore $\ln + 1$ transformed (Tabachnick & Fidell, 2007). After transformation, only DSD remained skewed and did not meet normality assumptions.

Finally, we used structural equation modeling (SEM) to compare hypotheses. SEM allows examination of hypotheses that involve a network of interrelated variables and analysis of both direct and indirect effects, as opposed to traditional regression models that only allow analysis of direct effects (Arhonditsis et al., 2006; Austin, 2007; Grace & Pugeseck, 1998; Sargeant et al., 2011). Indirect effects are essential for a full understanding of isotopic niche dynamics. For example, disturbance variables can directly affect among individual variation in diet, but can also indirectly affect this variation via effects on food availability and quality. Consequently, SEM is a powerful analytic technique for evaluating the intricacies of these hypotheses. We used SEM in Mplus version 6.11 to compare the alternate hypotheses described

in the introduction (Muthén and Muthén, 2005). Structural equation modeling provides parameter estimates associated with specific paths, as well as measures of direct, indirect, and total effects. Another strength of SEM is that it provides fit indices that allow determination of which model (e.g., set of hypotheses) fits the data best (Browne & Cudeck, 1993; Hu & Bentler, 1999). Model fit was determined using a Bollen-Stine Chi-Square Test of Model Fit; only models with $p > 0.05$ were considered (Bollen & Stine, 1992). We used the Bollen-Stine (1992) bootstrapping approach for determining probability values because this simulation technique is appropriate for non-normal data. It creates multiple subsamples randomly with replacement from the original sample so that bias in the fit indices and parameter estimates can be evaluated (Bollen & Stine, 1992; Ievers-Landis et al., 2011). Concurrent with conducting the SEM analyses, we calculated Cook's D to determine the influence of each site on the model (Cook, 1977; Cook & Weisberg, 1982). No sites had overly high influence on the model, so all 21 sites were kept in the final model. Finally, Akaike information criterion (AIC) was compared among models to determine the best model(s).

Results

Eastern mosquitofish were divided into three classes: adult males, adult females, and juveniles. We used analysis of variance (ANOVA) on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to determine if all three classes differed systematically in isotopic values (SAS 9.2, SAS Institute Inc., Cary, NC, USA). The $\delta^{13}\text{C}$ values of individuals did differ by sex/age group ($\delta^{13}\text{C}$: $F_{2,609} = 2.81$, $p = 0.06$, mean = -28.59(male), -28.89(female), -28.97(juv), SD = 1.24(m), 1.32(f), 1.32(j); $\delta^{15}\text{N}$: $F_{2,609} = 1.03$ $p = 0.36$, mean = 9.30(m), 9.11(f), 9.30(j), SD = 1.66(m), 1.57(f), 1.38(j)) and pairwise comparisons demonstrated that males (N=82) were responsible for this difference (juveniles and females were

not different, combined N=529). However, the sampled age/sex proportions are relatively stable across sites (Males: mean = 0.12, SD = 0.10, SE = 0.02; Females: mean = 0.39, SD = 0.17, SE = 0.04; Juveniles: mean = 0.49, SD = 0.19, SE = 0.04) and match those predicted for the eastern mosquitofish because it is a rapidly growing population. Our samples are representative of the size and gender mix of eastern mosquitofish at each site, so we chose to pool all specimens from a site (juvenile, adult male, and adult female) for isotope metric calculations descriptive of the local populations.

We evaluated the direct effects from the Combined model using linear regression. DSD, percent edible periphyton, and density of infauna groups described the most variance in isotopic niche breadth ($F_{6,14} = 2.5$, $p = 0.07$, $R^2 = 0.52$). Dropping groups of independent variables consistent with the Dispersal model (dropping diet variables) and, separately, the Partitioning model (dropping hydrological variables) diminished model fit. Of the independent variables considered for the Combined model, the percent edible periphyton contributed the most support (Figure 3). Isotopic niche breadth increased with increasing percent edible periphyton, increasing DSD, and carnivorous infauna density. Isotopic niche breadth decreased with omnivorous, herbivorous, and detritivorous infauna densities. Regressions using depth or recession rate instead of DSD as the disturbance variable gave similar results: the Combined model described the most variance in isotopic niche breadth. However, in the Combined model with either depth or recession rate, the disturbance variables had the smallest effect size of the variables, but in the model using DSD, it had the second largest effect size.

All three models were compared using SEM to include indirect effects. Using DSD as an indicator of disturbance, the Bollen-Stine χ^2 test indicated no lack-of-fit ($p \geq 0.23$). The Combined model provided the lowest AIC (615.5), followed by the Partitioning model (616.5)

and then the Dispersal model (618.5). Thus, all models provided similar model fit because the AIC values were within 3. Of the three models, the Combined model described the most variance in isotopic niche breadth (R^2 for Combined = 0.606; Dispersal = 0.102; Partitioning = 0.542). In the Combined model, all variables with direct links to isotopic niche breadth had similar effect sizes (β = 0.21 to 0.44). Detritivore density, omnivore density, and herbivore density negatively affected isotopic niche breadth, whereas carnivore density, percent edible periphyton, and DSD positively affected isotopic niche breadth (Figure 4). The indirect effects of heterospecific and conspecific fish densities on among-individual variation in diet were the greatest of the indirect effects (β = 0.18, 0.14 respectively).

Two more sets of models were run using the alternate measures of disturbance, depth and recession rate, and similar patterns were observed. For all models the Bollen-Stine χ^2 test indicated no lack-of-fit. For the models using depth, the Combined model had lowest AIC (709.4) and described the most variance in isotopic niche breadth (R^2 Combined = 0.670; Dispersal = 0.103; Partitioning = 0.517). The Partitioning model (713.2) had slightly better fit than the Dispersal model (715.2). When using recession rate as the disturbance variable, the Partitioning model had the lowest AIC (599.1) followed by the Combined (601.0) and Dispersal (603.3) models. The R^2 values for the Partitioning and Combined models were about equal (0.549 and 0.555, respectively), while the Dispersal model explained less variation (R^2 = 0.003).

Discussion

Our study evaluated dispersal and competition as two hypothetical explanations for among-individual variation in diet of eastern mosquitofish in an environment with seasonal fluctuation in hydrology. We found that the Combined and Partitioning models fit better than the

Dispersal model. Since the Combined model is less parsimonious and had a very similar AIC value to the Partitioning model, we conclude that the Partitioning hypothesis is a viable explanation for among-individual variation in diet in eastern mosquitofish in the Everglades, though we cannot eliminate a supporting role for dispersal. Given the long turn-over time for isotopic signatures relative to the life span of eastern mosquitofish and the hydrology-driven dispersal known for these fish (McElroy et al. 2011), some role for dispersal is not surprising.

The Partitioning hypothesis assumes that individual eastern mosquitofish use different foraging tactics and potentially eat only a subset of the available food sources. This niche partitioning is often attributed to increases in both intra- and interspecific competition as a way to ameliorate competitive effects (Chesson, 2000; Emmons, 1980; Langeland et al., 1991; Svanbäck & Bolnick, 2005; Wiens, 1977). In contrast to the niche variation hypothesis, that increased interspecific competition will decrease niche breadth, we found a positive relationship between both con- and hetero-specific fish densities and among-individual variation in diet, supporting general competition theory. The similar response to both inter- and intraspecific competition may be a result of similarities in diet among fish species in the Everglades (Loftus 2000). The SEM did not allow direct effects of fish densities on isotopic niche breadth because their effects are thought to be mediated through their effects on food availability (Marks et al., 2000; Wootton & Power, 1993). The indirect effect of eastern mosquitofish density on among-individual variation in diet was slightly smaller than that of heterospecific fish, but both effect sizes were about half the strength of the direct effects of other parameters in the model, indicating that the level of both conspecific and heterospecific competition may influence eastern mosquitofish feeding strategies and increase niche partitioning. Also, the indirect effects of fish densities were greater than the indirect effects of DSD, supporting the Partitioning model and

indicating that food availability is more important than disturbance in predicting isotopic niche breadth in this study.

The Partitioning hypothesis also predicts that the indirect effects of hydroperiod on among-individual variation in diet via increased fish density and food sources are more important than the direct effects. The results did not support this assumption. The food availability variables were not strongly correlated with DSD, depth, or recession rate, indicating little possibility for indirect effects of disturbance on isotopic niche breadth. Also, the SEM showed a weak indirect effect of disturbance on isotopic niche breadth and a strong direct effect. In the linear regression model DSD explained approximately 8% of the variance in niche breadth and had the second largest effect size of the parameters in the model, indicating potentially strong direct effects of DSD and disturbance on among-individual variation in diet. Even though all of the indirect effects of DSD were small, the effects via food availability were approximately an order of magnitude greater than the others, suggesting that DSD influences isotopic niche breadth by affecting food availability, not fish densities. The results support previous work showing that hydroperiod length and/or water depth are positively correlated with increased infauna densities (Leeper & Taylor, 1998; Liston, 2006; Murkin & Kadlec, 1986) and edible periphyton (Gottlieb et al., 2006). These food availability measures are, in turn, correlated with hetero- and conspecific fish densities. Therefore, DSD appears to influence among-individual variation in diet by affecting food availability, which alters the strength of competition and resource partitioning.

We noted some heterogeneity in the effect of prey functional groups on isotopic niche breadth. Omnivorous, herbivorous, and detritivorous macroinvertebrate density were all negatively correlated with niche breadth, while carnivorous macroinvertebrates were positively

correlated. Aquatic mites comprised 67% of the carnivorous macroinvertebrates and are often avoided by aquatic predators, and may be chemically defended (Kerfoot 1982). However, excluding them did not change the sign of the impact of this group on isotopic niche breadth. Tanypodinae (predatory midge larvae) and calinoid copepods were the other members of the carnivorous group, and it seems unlikely that eastern mosquitofish avoids these as prey. Combining the prey groups and dropping carnivorous macroinvertebrates decreased model fit. Periphyton edibility was also positively correlated with isotopic niche breadth, indicating that a higher frequency of edible algal taxa corresponded to greater niche breadth. We believe that these results suggest some prey selection by eastern mosquitofish that warrants further research.

This study had some limitations that influence the generality of the findings. First, data were collected late in the Everglades wet season. We chose to sample during the wet season to have sites that spanned a larger gradient in hydroperiod and water depth; many of these sites would have been dry in the dry season. However, the high-water conditions associated with wet season sampling may have diminished the effects of dispersal dynamics on niche partitioning. Evidence for dispersal effects should be stronger in the dry season when fish are condensed in a few refuge areas (Kushlan, 1974; Lake, 2003; McElroy et al., 2011; Parkos et al., 2011; Perry & Bond, 2009; Ruetz et al., 2005) or just after marsh re-flooding, when individuals from the refuges are still moving through the marsh. Therefore, the current study may have been conducted at a time when dispersal effects are weakest. However, the dry season is accompanied by high densities of fish in local refuge habitats that may strengthen competitive interactions and niche partitioning. Further examination of these relationships in the dry season is needed to determine if the same drivers of among-individual variation in diet are important throughout the year. Furthermore, replication of these findings in other wetland ecosystems with other species

would increase confidence that our support of the Partitioning hypothesis are not unique to the Everglades or eastern mosquitofish.

Eastern mosquitofish are used as an indicator species for mercury contamination in the Everglades food web because of their ubiquitous distribution and ease of sampling (Scheidt and Kalla, 2007). Mercury ‘hot spots’ have been documented in eastern mosquitofish, though recent surveys have found generally lower levels of contamination (Rumbold et al., 2008). Two competing hypotheses exist for the origins of patchy levels mercury contamination and hot spots, either they reflect local areas of intense mercury methylation from biogeochemical processes (Bates et al., 2002) or they reflect local areas of greater food-chain length leading to eastern mosquitofish, resulting in greater biomagnification. This study suggests that local food availability and niche partitioning are present in eastern mosquitofish in the wet season. Thus, the conditions for spatial variation in food chain length and local biomagnification are present. We do not know if inter-individual variation in mercury burden is present, but this study suggests it may be. Further work on food-web complexity using molecular methods such as stable isotope analysis may improve our understanding of ecological relationships with implications for ecosystem management (Fry and Chumchall, 2012).

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662

Table 1. A) Descriptive statistics for measured parameters included in structural equation models. DSD is the number of days since the site was last dry. Depth is depth of water in centimeters at time of sampling. Recess rate is the change in depth between sampling date and 30 days prior. Herbivore density through detritivore density are the densities of each infauna functional group (number of individuals per g AFDM of periphyton). Periphyton TP is the total phosphorus in the periphyton at each site, reported as $\mu\text{g/g}$ dry mass. Percent edible periphyton is the percent of the periphyton that is diatom and green algae, found to be most palatable to consumers (Geddes & Trexler, 2003). Conspecific fish density is the density of eastern mosquitofish at the collection site ($\#$ individuals/ m^2). Heterospecific fish density is the density of all other fish species at the site ($\#$ individuals/ m^2). B) Untransformed data for each site.

A)

Variables	Minimum Value	Maximum Value	Mean $\pm$ SE
DSD	160	2200	760 $\pm$ 160
Depth	30	93	59 $\pm$ 3
Recess Rate	2	41	13 $\pm$ 2
Omnivorous Infauna Density	3	990	250 $\pm$ 72
Carnivorous Infauna Density	0	580	67 $\pm$ 28
Herbivorous Infauna Density	0	740	120 $\pm$ 47
Detritivorous Infauna Density	0	170	28 $\pm$ 9
Periphyton total phosphorus ($\mu\text{g g dry}^{-1}$)	59	760	310 $\pm$ 46
% Edible Periphyton	16	88	45 $\pm$ 3
Conspecific fish density	0	38	9 $\pm$ 2
Heterospecific fish density	0	92	14 $\pm$ 4

675 B)

Site	Longitude	Latitude	Management Area	Depth	DSD	Recess Rate	Periphyton TP	% Edible Periphyton
148	522064	2827223	ENP	42	178	7	279.2	47
151	533946	2829412	ENP	38	174	6	58.9	16
161	523007	2841503	ENP	50	179	10	93.8	40
167	525989	2848534	ENP	61	160	5	243.3	48
172	516901	2852383	WCA3A	93	2164	5	617.1	16
180	552930	2866473	WCA3A	67	1653	11	495.9	59
185	534712	2871878	WCA3A	62	1656	13	366.4	54
188	526958	2875445	WCA3A	60	1655	12	134.8	48
192	525654	2879218	WCA3A	51	212	14	267.1	54
198	522838	2881704	WCA3A	55	274	14	187.4	37
199	536594	2884041	WCA3A	64	1653	14	351.8	46
205	546747	2891594	WCA3A	78	1657	18	690.4	26
213	527780	2896559	WCA3A	51	267	19	92.2	45
217	545499	2899782	WCA3A	59	212	15	372.8	59
219	567320	2900755	WCA3A	47	510	41	425.4	31
222	523268	2904903	WCA3A	30	183	22	133.1	58
223	558362	2905685	WCA2A	80	266	4	158.0	34
227	553918	2908303	WCA2A	79	183	16	132.2	46
244	561491	2931042	LOX	50	1652	2	549.8	51
251	529024	2830516	ENP	58	181	5	100.7	35
256	531525	2849087	ENP	71	249	10	760.0	89

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Site	Conspecific fish density (fish/m ²)	Heterospecific fish density (fish/m ²)	Omni- vorous Infauna Density	Carni- vorous Infauna Density	Herbi- vorous Infauna Density	Detriti- vorous Infauna Density
148	2	2	472.4	94	283	39
151	1	2	40.4	20	19	0
161	3	0	74.6	13	141	3
167	15	15	592.0	27	56	8
172	4	12	6.9	9	0	3
180	15	7	340.0	49	109	24
185	25	22	68.4	166	76	61
188	7	22	40.5	20	34	8
192	6	15	990.6	139	233	70
198	1	4	829.0	24	705	21
199	9	15	3.2	2	0	0
205	0	4	35.6	0	0	14
213	4	12	65.7	15	30	0
217	4	20	39.1	0	0	13
219	5	1	140.7	10	0	6
222	5	4	47.3	6	24	0
223	12	8	30.7	15	10	46
227	22	9	214.3	24	64	73
244	10	29	986.0	580	742	31
251	4	5	6.3	1	1	1
256	38	92	191.6	189	16	166

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Figure Legends

Figure 1. Full model of predicted factors influencing isotopic niche breadth. Rectangles represent measured variables of interest. The bottom left box represents the disturbance variable, for the different model types one of the three listed variables (DSD, depth, or recess rate) were used. Lines represent predicted effects and point in direction of causation. Infauna are broken into functional groups. For ease of view, in the other figures only one square is used for all infauna variables and one set of lines. For the Dispersal model, the betas for the dotted lines are set at 0 (allowing for no direct effect of food availability on niche, and therefore no indirect effects of disturbance on niche). For the Partitioning model, the beta for the dashed line is set at 0 (allowing for no direct effect of disturbance on niche).

Figure 2. Map of the study area in the Florida Everglades. Sampling sites indicated by points.

Figure 3. Partial regression plots of direct effects on isotopic niche breadth included in the Full model. Axes are the residuals of each axis and are reported in units of standard deviations from the grand mean for each variable labelled.

Figure 4. Results of Full model with day since dry (DSD) as the disturbance variable. Rectangles represent measured variables of interest and the R^2 value is reported for each endogenous variable. Lines represent predicted effects, and point in direction of causation. Infauna are divided into functional groups but for ease of view single lines are used and each figure A-D highlights a single infauna functional group. Reported numbers next to lines are standardized betas. A) shows the omnivorous infauna betas, B) shows the herbivorous infauna betas, C) shows the carnivorous infauna betas, and D) shows the detritivorous infauna betas.

704 Figure 1.

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706 Figure 2.

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709 Figure 3.

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712 Figure 4.

Electronic Appendix

Appendix 1. R code for stable isotope analysis. Run using SIAR loaded package.

laymanmetrics(siteC, siteN)

Table A2. Untransformed stable isotope metrics for all sampling sites. n is the number of eastern mosquitofish collected at each site and used for isotope analysis. N range is the range of $\delta^{15}\text{N}$ values at the site. C range is the range of $\delta^{13}\text{C}$ values at the site. TA is total area of the convex hull polygon encompassing all individuals at the site. CD is the mean distance to centroid for the site. NND is the mean nearest neighbor distance for the site.

Site	n	N Range	C Range	TA	CD	NND
148	17	1.16	0.83	0.60	0.38	0.13
151	17	1.87	4.27	3.05	0.87	0.35
161	23	1.50	1.51	1.60	0.50	0.21
167	40	1.73	1.91	1.91	0.47	0.13
172	36	1.56	2.29	2.54	0.61	0.18
180	28	1.17	4.32	4.26	0.86	0.24
185	45	1.27	2.53	2.31	0.61	0.14
188	32	1.42	2.21	1.97	0.51	0.18
192	20	2.11	1.44	1.70	0.52	0.24
198	17	1.96	2.10	2.15	0.62	0.25
199	33	1.60	9.13	7.94	0.84	0.38
205	25	1.22	2.26	2.17	0.60	0.24
213	20	1.20	1.90	1.20	0.42	0.20
217	34	2.20	2.44	2.86	0.59	0.19
219	20	1.49	2.22	1.67	0.61	0.20
222	27	2.12	2.23	2.95	0.64	0.22
223	33	1.29	1.22	1.10	0.44	0.11
227	54	2.00	1.62	2.34	0.57	0.11
244	17	0.95	2.49	1.51	0.53	0.21
251	28	1.46	1.96	1.56	0.48	0.16
256	46	1.99	3.04	3.55	0.55	0.18