

1 Running Head: Dispersal, competition, and isotopic niche breadth

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

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24 **Summary**

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

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

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

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

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

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

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

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63

64 **Introduction**

65 Among-individual variation in diet, also known as individual specialization, has important  
66 implications for population stability, the strength of intraspecific competition, and the rate of  
67 local adaptation (Bolnick et al., 2011; Bolnick et al., 2003; Violle et al., 2012). Accurate  
68 modeling of among-individual variation requires understanding the causes and consequences of  
69 this variation. The niche variation hypothesis and optimal foraging theory can provide a  
70 framework for understanding among-individual variation in diet and the resulting changes in  
71 niche breadth of populations (e.g., Bolnick et al., 2010; Svanbäck & Bolnick, 2005; Van Valen,  
72 1965).

73         The niche variation hypothesis proposes that populations have constrained niche breadth  
74 when exposed to strong interspecific competition, and have broad niche breadth when released  
75 from interspecific competition and are subject only to intraspecific competition (Bolnick et al.,  
76 2010; Van Valen, 1965). Increased diet niche breadth in a population can arise in two general  
77 ways: 1) all individuals in a population increase their diet niche breadth, or 2) variation in diet  
78 among individuals in the population increases. The second mechanism is proposed by the niche  
79 variation hypothesis and is often referred to as partitioning, as individuals partition resources  
80 among themselves. Early studies often found no support for the niche variation hypothesis (e.g.,  
81 Soulé & Stewart, 1970). However, the lack of support is generally thought to be a result of these  
82 studies using morphological variance as a proxy for diet variation (Bolnick et al., 2010). Recent  
83 studies using more direct measures of diet variation, such as gut content and stable isotope  
84 analyses, are generally supportive of the niche variation hypothesis (Araújo o et al., 2008;  
85 Bolnick et al., 2010; Bolnick et al., 2007; Codron et al., 2011; Costa et al., 2008; Jack & Wing,  
86 2011; Svanbäck & Bolnick, 2007).

87 Optimal foraging theory provides insight into potential mechanisms for among-individual  
88 variation. Optimal foraging theory states that an activity should be maintained as long as the  
89 gains from the activity are greater than the costs, including missed opportunity costs (MacArthur  
90 & Pianka, 1966). Other authors have expanded on the original tenets of optimal foraging theory  
91 by evaluating how individuals maximize the relationship  $E/(S+H)$ , with E being energy gain, S  
92 being time searching, and H being handling time (Stephens & Krebs, 1986; Svanbäck & Bolnick,  
93 2005). Local environmental factors (e.g., relative abundance of food sources, quality of food,  
94 predation risk) can affect handling time and search time, altering the energy income rate, and  
95 favoring alternate foraging strategies with varying local conditions (Schmitz et al., 1998;  
96 Staniland et al., 2010; Svanbäck & Bolnick, 2005; Tinker et al., 2009). These studies  
97 demonstrate that local environmental conditions can affect foraging strategy and, therefore, diet  
98 of individuals. Individual variation in efficiency of searching, capturing, or handling prey items,  
99 equates to intraspecific differences in energy acquisition (Ehlinger, 1990). These individual  
100 differences allow for variation in diet among individuals exposed to the same local conditions.

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

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

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

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

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

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

137

## 138 **Methods**

### 139 *Study System*

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

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

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

156

### 157 *Field Sampling Protocol*

158 Eastern mosquitofish were sampled following the procedure described in Sargeant et al.  
159 (2010) in November and December 2005, during the late wet season, when water levels begin to  
160 drop. Approximately 50 sites were sampled from a subset of randomly generated sites (Stevens  
161 & Olsen, 2003). All sites were located in wet prairie slough habitats. Of these sites, only 21  
162 yielded enough eastern mosquitofish to be included in this study ( $n \geq 17$ , Figure 2). Fish and  
163 large invertebrates were collected by throw-trap sampling as described in Jordan et al. (1997)  
164 and Sargeant et al. (2011). Three replicate samples were collected at each site. From each throw  
165 trap, all small fishes (<8 cm) and large invertebrates (>5mm) were collected. An MS-222  
166 (tricaine methanesulfonate) bath was used to euthanize all collected vertebrates following  
167 standard procedures (Nickum et al., 2003). Additional mosquitofish were collected for isotope  
168 analysis by 10 minutes of haphazard dip netting in the area. All collected organisms were placed  
169 on ice in the field and then frozen at  $-17.7^{\circ}\text{C}$  before sample processing. Three periphyton  
170 samples were collected. One periphyton sample was processed to determine total phosphorous  
171 for use as an indicator of nutrient enrichment (Gaiser et al., 2006). The second periphyton sample  
172 was processed to identify and categorize algal species. The combined relative abundance of the  
173 diatom and green algae categories was used as a measure of percent edible periphyton for  
174 analyses because these categories are thought to be more palatable to consumers (Geddes &  
175 Trexler, 2003). The final periphyton sample was collected for analysis of macroinvertebrate  
176 infauna (Liston & Trexler, 2005).



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

#### 185 *Laboratory Protocol*

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

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

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

208 In the lab, eastern mosquitofish samples were processed for isotope analysis following  
209 the protocol described in Sargeant et al. (2010). Muscle tissue was removed from the caudal  
210 region of each individual and the tissue was then rinsed in deionized water and dried at 55-60° C  
211 for at least 24 hours. After drying, the tissue was ground into fine powder and analyzed for  $\delta^{13}\text{C}$   
212 and  $\delta^{15}\text{N}$  using an isotope ratio mass spectrometer at the FIU Stable Isotope Laboratory. Pee Dee  
213 Belemnite was used for  $\delta^{13}\text{C}$  standard, and atmospheric  $\text{N}_2$  was used as  $\delta^{15}\text{N}$  standard. Tissues  
214 were not subject to lipid extraction prior to analysis because previous studies (Williams &  
215 Trexler, 2006) found little impact of lipid extraction on Everglades consumers. Also, eastern  
216 mosquitofish have a low C:N value, so lipid extraction is generally thought to be unnecessary  
217 (Post et al., 2007).

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

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

### 228 *Analytical Methods*

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

246 less among-individual variation in diet. Sample sizes were not equal across sites (range 17-54,  
247 mean 29.1, SD 10.7). However, linear regression showed that none of the isotope metrics were  
248 correlated with sample size (N Range  $R^2 = 0.069$ , C Range  $R^2 = 0.005$ , TA  $R^2 = 0.068$ , CD  $R^2 =$   
249  $0.00$ , and NND  $R^2 = 0.196$ ). Many of the isotope metrics were strongly correlated, so they were  
250 condensed into a single variable using varimax rotation in principal components analysis. Only  
251 one factor had an eigenvalue greater than 1.00, so only one factor was formed using factor  
252 scores. The factor score was used as a proxy for among-individual variation in analyses.

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

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

269 in the introduction (Muthén and Muthén, 2005). Structural equation modeling provides  
270 parameter estimates associated with specific paths, as well as measures of direct, indirect, and  
271 total effects. Another strength of SEM is that it provides fit indices that allow determination of  
272 which model (e.g., set of hypotheses) fits the data best (Browne & Cudeck, 1993; Hu & Bentler,  
273 1999). Model fit was determined using a Bollen-Stine Chi-Square Test of Model Fit; only  
274 models with  $p > 0.05$  were considered (Bollen & Stine, 1992). We used the Bollen-Stine (1992)  
275 bootstrapping approach for determining probability values because this simulation technique is  
276 appropriate for non-normal data. It creates multiple subsamples randomly with replacement from  
277 the original sample so that bias in the fit indices and parameter estimates can be evaluated  
278 (Bollen & Stine, 1992; Ievers-Landis et al., 2011). Concurrent with conducting the SEM analyses,  
279 we calculated Cook's D to determine the influence of each site on the model (Cook, 1977; Cook  
280 & Weisberg, 1982). No sites had overly high influence on the model, so all 21 sites were kept in  
281 the final model. Finally, Akaike information criterion (AIC) was compared among models to  
282 determine the best model(s).

283

## 284 **Results**

285 Eastern mosquitofish were divided into three classes: adult males, adult females, and  
286 juveniles. We used analysis of variance (ANOVA) on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to determine if all three  
287 classes differed systematically in isotopic values (SAS 9.2, SAS Institute Inc., Cary, NC, USA).  
288 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 =  
289  $-28.59(\text{male})$ ,  $-28.89(\text{female})$ ,  $-28.97(\text{juv})$ ,  $\text{SD} = 1.24(\text{m})$ ,  $1.32(\text{f})$ ,  $1.32(\text{j})$ ;  $\delta^{15}\text{N}$ :  $F_{2,609} = 1.03$   $p =$   
290  $0.36$ , mean =  $9.30(\text{m})$ ,  $9.11(\text{f})$ ,  $9.30(\text{j})$ ,  $\text{SD} = 1.66(\text{m})$ ,  $1.57(\text{f})$ ,  $1.38(\text{j})$ ) and pairwise comparisons  
291 demonstrated that males ( $N=82$ ) were responsible for this difference (juveniles and females were

292 not different, combined N=529). However, the sampled age/sex proportions are relatively stable  
293 across sites (Males: mean = 0.12, SD = 0.10, SE = 0.02; Females: mean = 0.39, SD = 0.17, SE =  
294 0.04; Juveniles: mean = 0.49, SD = 0.19, SE = 0.04) and match those predicted for the eastern  
295 mosquitofish because it is a rapidly growing population. Our samples are representative of the  
296 size and gender mix of eastern mosquitofish at each site, so we chose to pool all specimens from  
297 a site (juvenile, adult male, and adult female) for isotope metric calculations descriptive of the  
298 local populations.

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

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

315 and then the Dispersal model (618.5). Thus, all models provided similar model fit because the  
316 AIC values were within 3. Of the three models, the Combined model described the most  
317 variance in isotopic niche breadth ( $R^2$  for Combined = 0.606; Dispersal = 0.102; Partitioning =  
318 0.542). In the Combined model, all variables with direct links to isotopic niche breadth had  
319 similar effect sizes ( $\beta$  = 0.21 to 0.44). Detritivore density, omnivore density, and herbivore  
320 density negatively affected isotopic niche breadth, whereas carnivore density, percent edible  
321 periphyton, and DSD positively affected isotopic niche breadth (Figure 4). The indirect effects of  
322 heterospecific and conspecific fish densities on among-individual variation in diet were the  
323 greatest of the indirect effects ( $\beta$  = 0.18, 0.14 respectively).

324 Two more sets of models were run using the alternate measures of disturbance, depth and  
325 recession rate, and similar patterns were observed. For all models the Bollen-Stine  $\chi^2$  test  
326 indicated no lack-of-fit. For the models using depth, the Combined model had lowest AIC  
327 (709.4) and described the most variance in isotopic niche breadth ( $R^2$  Combined = 0.670;  
328 Dispersal = 0.103; Partitioning = 0.517). The Partitioning model (713.2) had slightly better fit  
329 than the Dispersal model (715.2). When using recession rate as the disturbance variable, the  
330 Partitioning model had the lowest AIC (599.1) followed by the Combined (601.0) and Dispersal  
331 (603.3) models. The  $R^2$  values for the Partitioning and Combined models were about equal  
332 (0.549 and 0.555, respectively), while the Dispersal model explained less variation ( $R^2$  = 0.003).

333

### 334 **Discussion**

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

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

344         The Partitioning hypothesis assumes that individual eastern mosquitofish use different  
345 foraging tactics and potentially eat only a subset of the available food sources. This niche  
346 partitioning is often attributed to increases in both intra- and interspecific competition as a way  
347 to ameliorate competitive effects (Chesson, 2000; Emmons, 1980; Langeland et al., 1991;  
348 Svanbäck & Bolnick, 2005; Wiens, 1977). In contrast to the niche variation hypothesis, that  
349 increased interspecific competition will decrease niche breadth, we found a positive relationship  
350 between both con- and hetero-specific fish densities and among-individual variation in diet,  
351 supporting general competition theory. The similar response to both inter- and intraspecific  
352 competition may be a result of similarities in diet among fish species in the Everglades (Loftus  
353 2000). The SEM did not allow direct effects of fish densities on isotopic niche breadth because  
354 their effects are thought to be mediated through their effects on food availability (Marks et al.,  
355 2000; Wootton & Power, 1993). The indirect effect of eastern mosquitofish density on among-  
356 individual variation in diet was slightly smaller than that of heterospecific fish, but both effect  
357 sizes were about half the strength of the direct effects of other parameters in the model,  
358 indicating that the level of both conspecific and heterospecific competition may influence eastern  
359 mosquitofish feeding strategies and increase niche partitioning. Also, the indirect effects of fish  
360 densities were greater than the indirect effects of DSD, supporting the Partitioning model and



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

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

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

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

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

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

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

423

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662

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

673 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    |

674

675 B)

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| 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 <sup>2</sup> ) | Heterospecific fish density (fish/m <sup>2</sup> ) | 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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680

681 **Figure Legends**

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

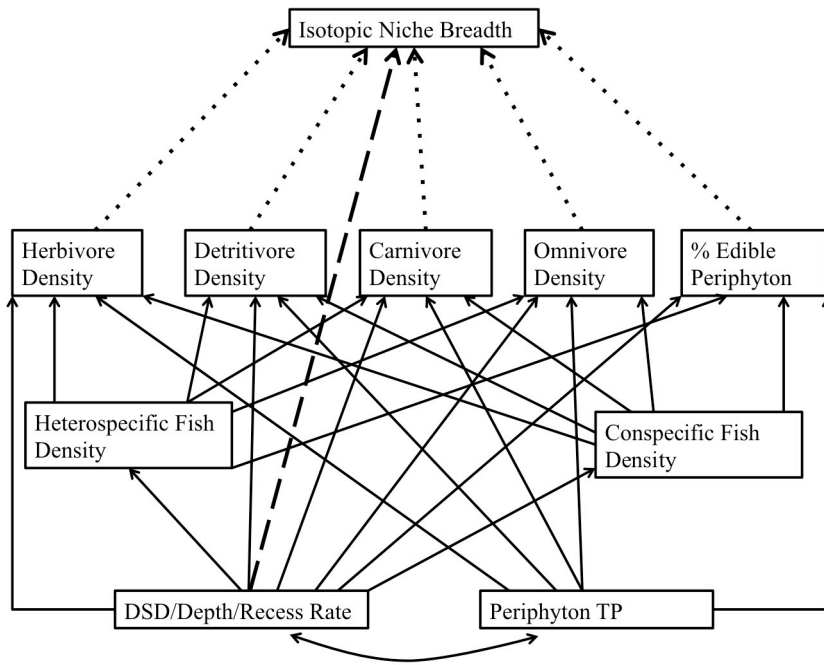
691 Figure 2. Map of the study area in the Florida Everglades. Sampling sites indicated by points.

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

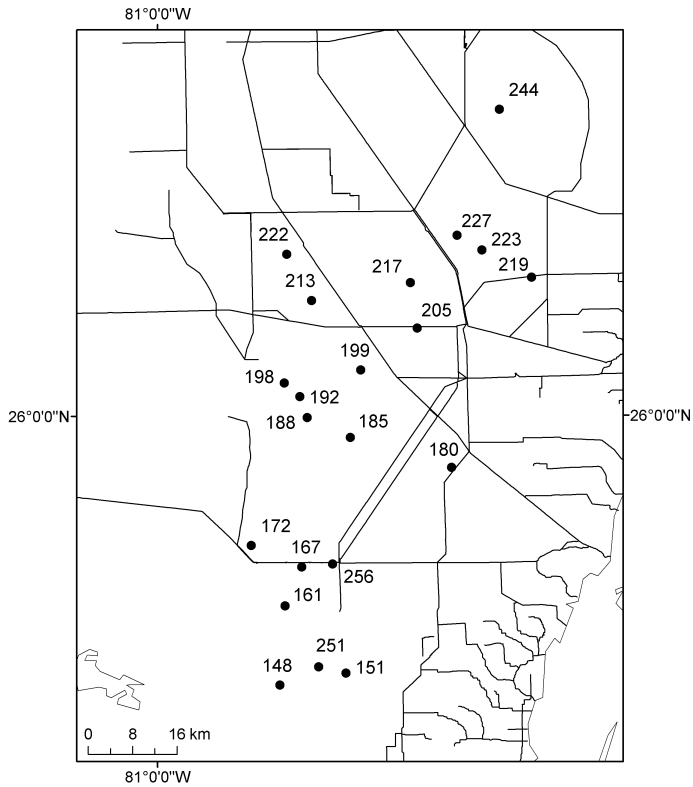
695 Figure 4. Results of Full model with day since dry (DSD) as the disturbance variable. Rectangles  
696 represent measured variables of interest and the  $R^2$  value is reported for each endogenous  
697 variable. Lines represent predicted effects, and point in direction of causation. Infauna are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

703

704 Figure 1.

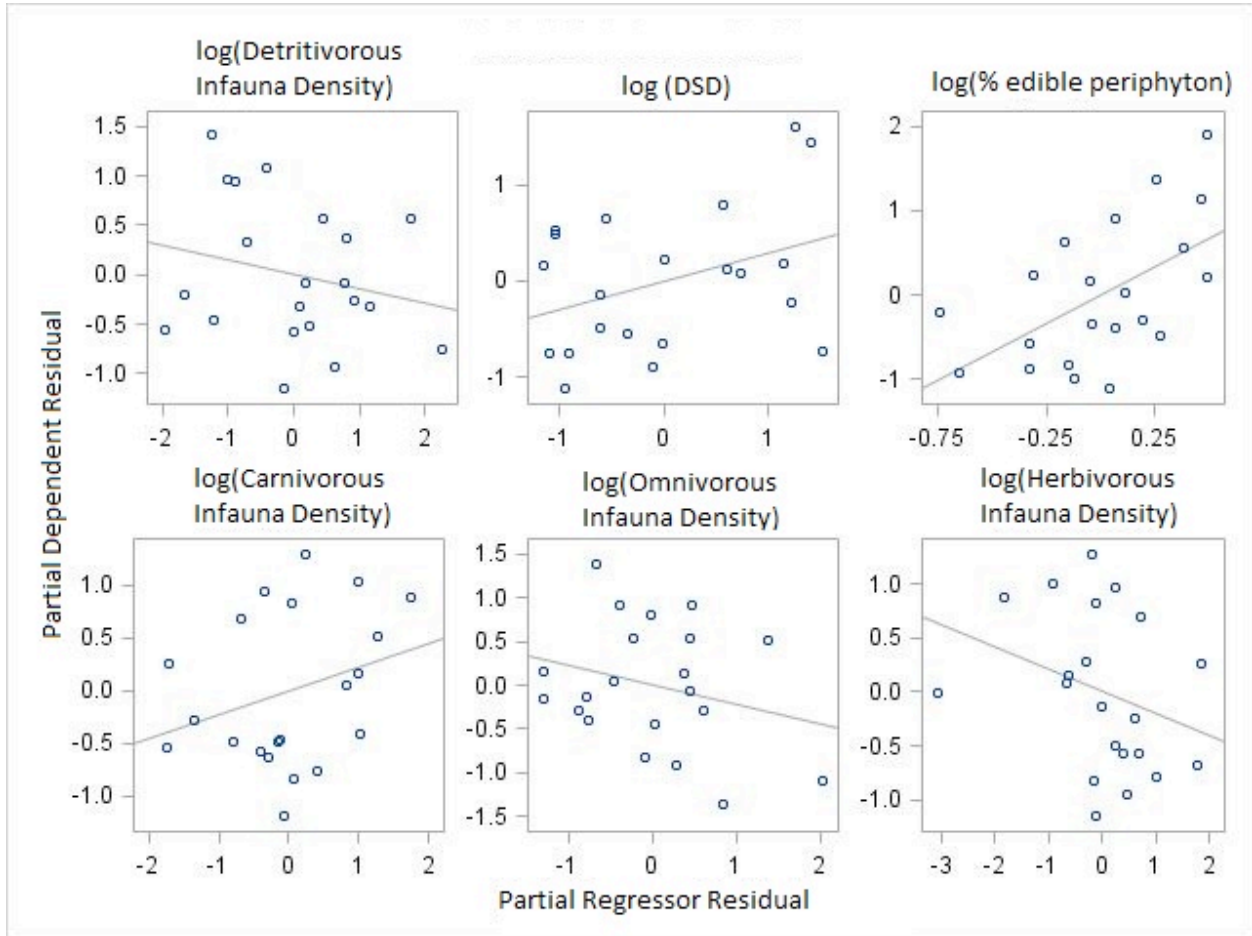


705  
706 Figure 2.



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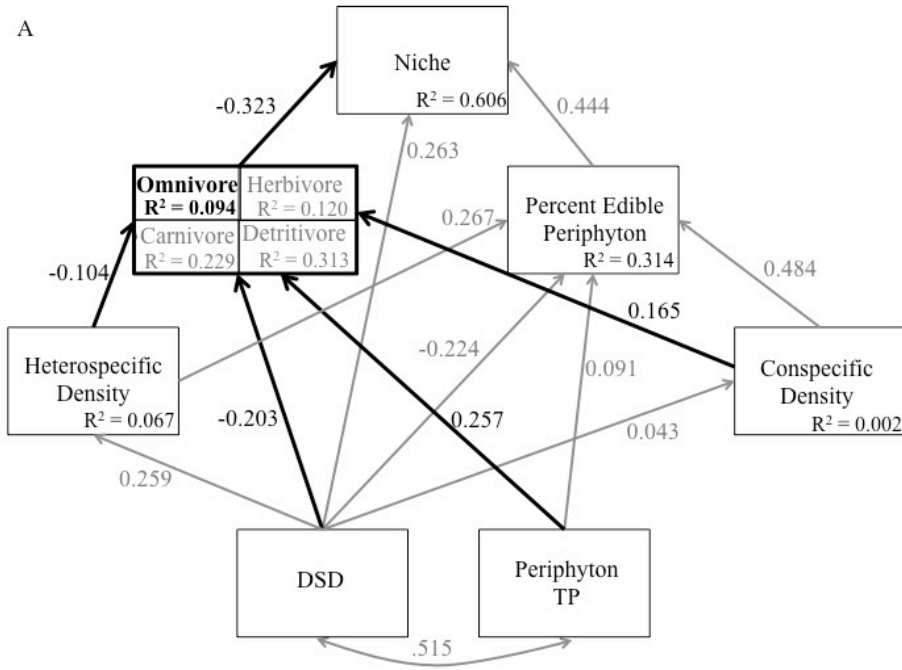
709 Figure 3.



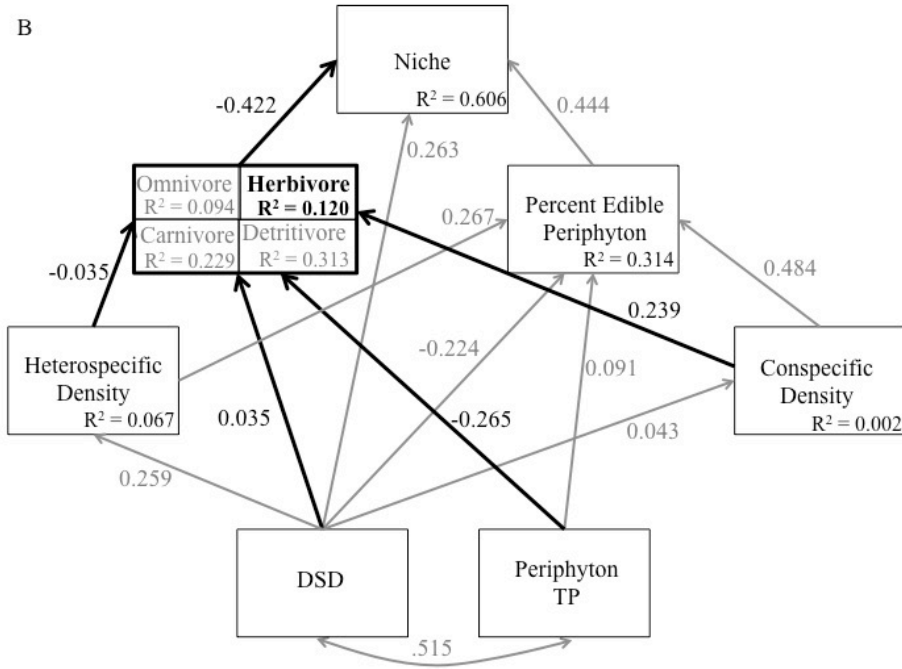
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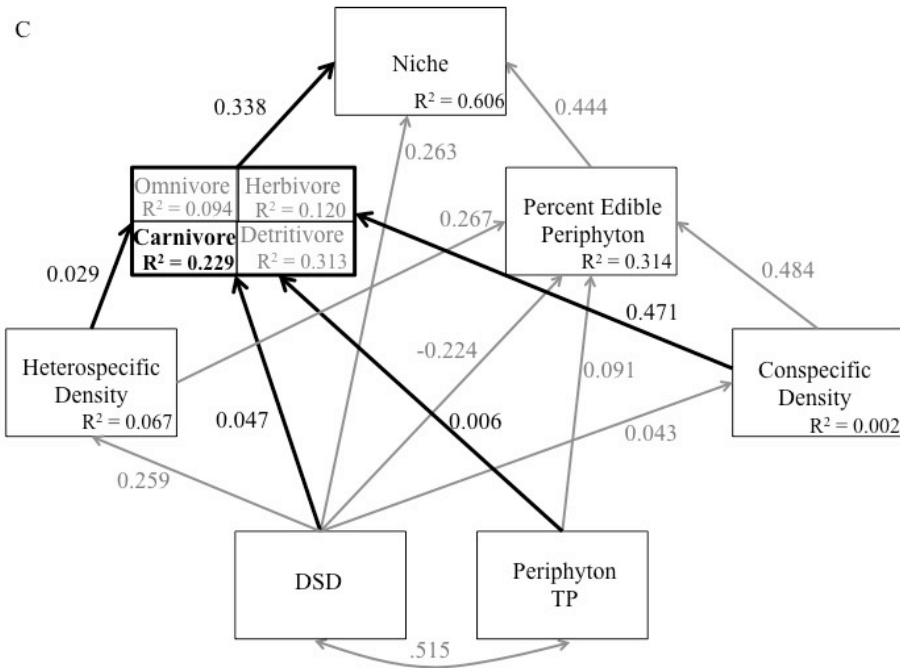
712 Figure 4.



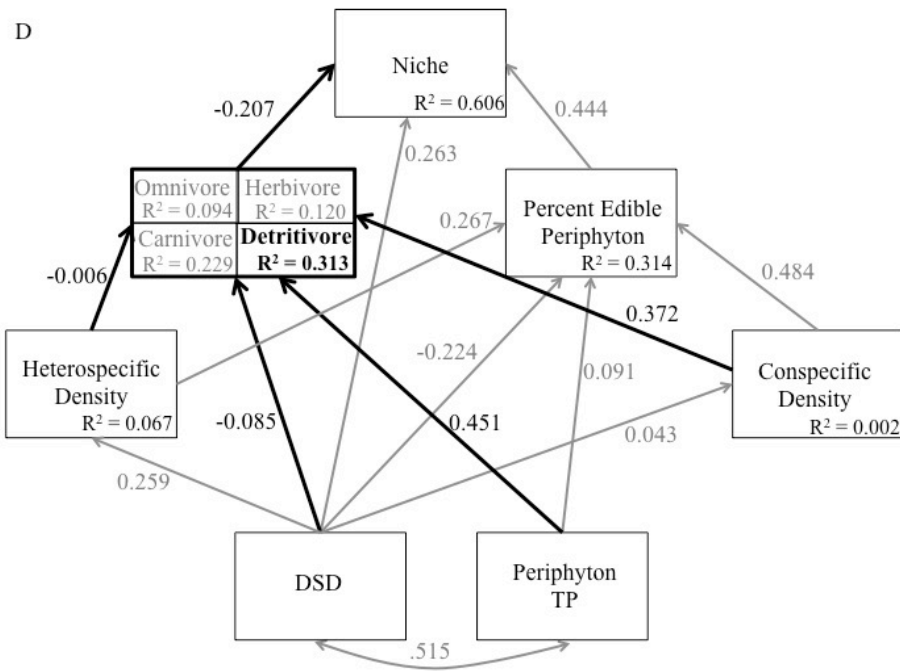
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722 Electronic Appendix

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

724

725 laymanmetrics(siteC, siteN)

726

727 Table A2. Untransformed stable isotope metrics for all sampling sites. n is the number of eastern

728 mosquitofish collected at each site and used for isotope analysis. N range is the range of  $\delta^{15}\text{N}$

729 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

730 hull polygon encompassing all individuals at the site. CD is the mean distance to centroid for the

731 site. NND is the mean nearest neighbor distance for the site.

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| 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 |

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