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Seasonal fish dispersal in ephemeral wetlands of the Florida Everglades

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Draft

Abstract

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We hypothesized that fishes in short-hydroperiod wetlands display pulses in activity tied to seasonal flooding and drying, with relatively low activity during intervening periods. To evaluate this hypothesis, sampling devices that funnel fish into traps (drift fences) were used to investigate fish movement across the Everglades, U.S.A. Samples were collected at six sites in the Rocky Glades, a seasonally flooded karstic habitat located on the southeastern edge of the Everglades. Four species that display distinct recovery patterns following drought in long-hydroperiod wetlands were studied: eastern mosquitofish (*Gambusia holbrooki*) and flagfish (*Jordanella floridae*) (rapid recovery); and bluefin killifish (*Lucania goodei*) and least killifish (*Heterandria formosa*) (slow recovery). Consistent with our hypothesized conceptual model, fishes increased movement soon after flooding (immigration period) and just before drying (emigration period), but decreased activity in the intervening foraging period. We also found that eastern mosquitofish and flagfish arrived earlier and showed stronger responses to hydrological variation than either least killifish or bluefin killifish. We concluded that these fishes actively colonize and escape ephemeral wetlands in response to flooding and drying, and display species-specific differences related to flooding and drying that reflect differences in dispersal ability. These results have important implications for Everglades fish metacommunity dynamics.

42 Changes in habitat use, activity level, and movement strategies of animals may be
43 adaptive responses to environmental fluctuation (Armsworth and Roughgarden 2005, Nams
44 2006). For example, as habitat patch quality deteriorates, optimal foraging theory suggests
45 individuals should increase exploratory behavior and the frequency of long-distance
46 displacements to gain better information about other habitat patches. These behavioral changes
47 can decrease the odds of time wasted in low-quality sites and reduce the risk of being stranded in
48 a dangerous site (Fretwell and Lucas 1970, Fretwell 1972). In aquatic ecosystems, fluctuations
49 in habitat quality favoring dispersal include changes in oxygen availability, predation risk and
50 water depth and temperature (Cucherousset et al. 2007, Correa et al. 2008, Rayner et al. 2008,
51 Mosepele et al. 2009, Schofield et al. 2009), as well as food availability and sites for
52 reproduction (Lowe-McConnell 1987). In wetlands, floodplains, arid-zone rivers, and littoral
53 zones, seasonal fluctuations in water depth may be so severe as to strand aquatic animals
54 (Chapman et al. 1991, Perry and Bond 2009). Environmental fluctuation also may provide
55 temporary access to previously unavailable high-quality habitats that provide food resources and
56 reproductive sites free from predators for species able to colonize transient environments. In
57 such variable environments, behaviors sensitive to the changing risk of stranding by habitat loss
58 and that enable exploitation of newly available habitat should be favored (Resetarits 2001, Segev
59 et al. 2011).

60 Though ecologists have always been aware of the limitations of assuming closed
61 populations and communities, increased attention during the past two decades has been paid to
62 spatial ecology, and metapopulation and metacommunity dynamics. Much of metapopulation
63 and metacommunity ecology has been spatially implicit, but recently efforts have focused on
64 using behavioral rules of movement to integrate spatial dynamics into theory (Jacobson and

65 Peres-Neto 2010). Fisher (1937) and Skellam (1951) proposed ecological analysis of movement
66 by establishing a null model of diffusion based on three behaviors: movement speed, time
67 dispersing in a direction, and turning angle. The speed, time moving in a particular direction,
68 and turning angle determine individual displacement and, collectively, population spread across
69 a landscape. Despite their historical significance, simple diffusion models tend to predict
70 spreading that is too slow to respond to environmental fluctuation (DeAngelis et al. 2010 and
71 citations therein). Thus, bias in turning angle and speed that affect directedness of spread may be
72 common. At the population level, changes in the speed and directionality of movement in
73 response to cues of habitat change determine the ability of a species to persist in a spatially
74 complex and temporally fluctuating environment (Armsworth and Roughgarden 2005, Abrams et
75 al. 2007, Jacobson and Peres-Neto 2010). In aquatic systems, change in water chemistry,
76 presence of desiccated conspecifics, and elevated intra and interspecific density may act as cues
77 that indicate changing habitat quality (Magoulick and Kobza 2003, Davey and Kelly 2007,
78 Sadeh et al. 2011). Spatial complexity and temporal fluctuation are ubiquitous features of
79 wetlands, and fish movement dynamics in these systems likely play an important role in
80 metapopulation and metacommunity persistence.

81 The Florida Everglades is a large landscape of hydrologically dynamic, shallow wetlands,
82 where hydrologic connectivity among permanent and ephemeral habitats facilitates fish
83 persistence throughout this system. Aquatic habitat size of the Everglades fluctuates seasonally,
84 with the spatial extent of drying varying annually in roughly decadal cycles of drought severity
85 (Childers et al. 2006; Gaiser et al. 2012). Annual fluctuation in the spatial area of flooding leads
86 to local variation in the time between drying events. Local drying forces fishes to move to areas
87 that remain inundated; those individuals that fail to respond appropriately die from desiccation or

88 predation. Regional drying can limit fish communities and drive transitions in community
89 composition as the time since a regional drying event increases (Trexler et al. 2005, Ruetz et al.
90 2005). Three life-history strategies related to recovery following drought have been identified
91 within the Everglades fish assemblage: rapid recovery and sustained high density (eastern
92 mosquitofish - *Gambusia holbrooki*); rapid recovery followed by decline in density as time since
93 re-flooding increases (flagfish - *Jordanella floridae*); and slow recovery over a number of years
94 to an asymptotic density (bluefin killifish - *Lucania goodei* and least killifish - *Heterandria*
95 *formosa*) (Trexler et al. 2005, DeAngelis et al. 2005). The relative contributions of immigration
96 and local reproduction in supporting those recovery patterns are not well understood, but
97 reproduction alone cannot explain the first two patterns, as all age classes appear in samples soon
98 after re-flooding (unpublished data). Furthermore, the magnitude of fish emigration from
99 wetlands prior to drying is uncertain, as is its effect on population and community responses to
100 drought in the Everglades landscape.

101 In this study, we sought to characterize patterns of fish activity in response to hydrologic
102 variation in the Florida Everglades (Figure 1). To investigate fish immigration and emigration in
103 response to annual flooding and drying, we focused on short-hydroperiod wetlands that dry
104 completely every year. Eastern mosquitofish, flagfish, least killifish and bluefin killifish were
105 monitored because of their documented differences in recovery following hydrologic disturbance
106 (Trexler et al. 2005, DeAngelis et al. 2005). Our primary objectives were to determine whether
107 fish-activity patterns change in predictable ways in response to flooding and drying and whether
108 there are interspecific differences in response to flooding and drying. We hypothesized that
109 there are three distinct periods of fish activity that correspond to hydrologic conditions: 1)
110 immigration period, a response to flooding, 2) emigration period, a response to drying, and 3) an

111 intervening foraging period (Figure 2). The duration of these periods is expected to be shortest
112 when fish activity is elevated (immigration and emigration periods) and longest when fish
113 activity is depressed (foraging period). We also hypothesized that eastern mosquitofish and
114 flagfish arrive sooner, have stronger responses to both flooding and drying, and are generally
115 more dominant numerically than either least killifish or bluefin killifish.

116 **Methods**

117 *Study Area and Sampling Method*

118 From 2000 to 2004 fishes were sampled in the Rockland Ridge, aka Rocky Glades, a
119 karstic short-hydroperiod wetland in the eastern portion of the Everglades National Park (ENP)
120 (Fig. 1). Here the water table drops below the ground surface for extended periods of time and
121 supports a substrate of mainly limestone and marl instead of peat (a long-hydroperiod Everglades
122 soil). Vegetation in the Rocky Glades is characterized by semi-aquatic gramminoids and upland
123 shrubs, with bayheads and tree islands on topographic highs and aquatic plants in solution holes
124 (Craighead 1971).

125 Fishes were sampled by constructing six drift-fences in the Rocky Glades (Loftus et al.
126 2001). To determine population dynamics and successional patterns in the wetlands, we sampled
127 from 2000 to 2004 at four sites (sites 1-4) located along the ENP main road, and from 2001 to
128 2004 at two sites (sites 5 and 6) located north of the road (Figure 1). Park policies and logistics
129 limited work to sites that could be reached on foot. The X-shaped structures had 12-m wings of
130 black plastic agricultural ground cloth to direct animals into metal minnow traps (3-mm mesh) at
131 the center (see Obaza et al. 2011). To capture fishes moving across the landscape at sites 1
132 through 4 the traps faced three directions (N, E, W), while sites 5 and 6 had traps facing all four
133 cardinal directions (N, S, E, W). The minnow traps were set overnight and fishes were removed

134 after approximately 24 hours to yield fish catch-per-unit-effort (CPUE). Following wetland
135 flooding, samples were taken daily for the first two weeks, twice weekly for the next two weeks,
136 and finally weekly for the rest of the wet season until all wetlands dried. We saw no evidence
137 that repeated visits to the sites affected the local habitat because the hard karst limestone
138 substrate and the sparse emergent/submerged vegetation resisted trampling. Therefore, site visits
139 likely resulted in little to no consistent effects on our data.

140 Our data, as well as other studies (e.g., Obaza et al. 2011), indicate that CPUE obtained
141 from drift-fence minnow traps are indicative of fish activity rates. In cases where both drift-
142 fence CPUE and throw-trap samples of fish density are available, little or no correlation has been
143 found (Hoch et al., unpublished manuscript). Following Obaza et al. (2011), we use the term
144 "encounter rate" to refer to drift-fence CPUE because the traps are stationary and fish must
145 encounter and enter the trap to be captured, implying fish are moving; stationary fish will not be
146 caught.

147 Depth measurements obtained at permanent staff gauges at each drift fence were adjusted
148 to reflect local variation in elevation. Measurements were taken frequently to capture
149 hydrological variation [on average approx. every 11 days; less frequently when the wetland was
150 dry (depth = 0) and more frequently when the wetland was wet (depth > 0)]. To estimate
151 hydrologic parameters, we interpolated data among days by retaining the previous measurement
152 until the next recorded measurement. The hydrologic parameters we estimated from the data
153 were: 1) Hydroperiod - the number of days the wetland was flooded (depth > 0) within a given
154 water year; 2) Flooding Event - the intervening time between dry periods when the wetland is
155 inundated with water; 3) Days Since Flooding (DSF) – at the time of sampling, the number of
156 continuous days that a marsh has been flooded (this value resets each time the water depth

157 reaches zero). Because the study sites are only inundated for a portion of each year and rainfall
158 that floods them is variable annually, we defined a “water year” to correspond to a period that
159 begins near the onset of the rainy season (April) and ends at the termination of the dry season the
160 following year (March). In instances when there was an early pulse of rain indicating the onset
161 of the wet season, we pushed back the date to include March; we also pushed up the date of the
162 beginning of the water year if a site dried later.

163 *Data Analysis*

164 The response variable in our analysis was the mean number of fishes caught in all
165 minnow traps at each drift fence (3-4 traps/fence). When one or more of the traps was
166 compromised (e.g., fell out of drift fence), or if the wetland was dry, the sample was treated as
167 missing. In some instances, traps were set in anticipation of flooding to capture fish immediately
168 after they moved into a wetland. This sometimes resulted in heterogeneity among traps (i.e.,
169 some traps were submerged longer than others) and less than 24 hours of total "soak time".
170 Because those samples were important to capture pulses of movement, we included them in the
171 analyses and treated them as equal to periods when all traps are completely submerged for the
172 entire 24-h period.

173 To capture variation in fish movement throughout the year, we used a change-point
174 analysis (reviewed in Andersen et al. 2009). In the present study the purpose of using a change-
175 point analysis was to determine where there are statistically detectable shifts in fish encounter
176 rate as a flooding event progresses. Fish encounter-rate data were analyzed using the
177 changepoint package (Killick and Eckly 2012) in R (R Core Team 2012), which can be used to
178 identify breaks in a time series based on changes in the mean and variance. We used the
179 Schwartz Information Criterion (SIC) and the binary segmentation search algorithm to detect

180 changes in the mean and variance of fish encounter rate within a given flooding event (assuming
181 a normal distribution). In this analysis, the number of change points is determined by the fit
182 statistics (e.g., SIC) and by specifying a maximum number of change points to be fit. The
183 maximum number of change points was set to three (to yield at most four temporal segments),
184 which enabled us to capture variation in the data related to our conceptual model of three discrete
185 periods (Figure 2), and to accommodate "extra" periods of movement such as if there was low
186 fish movement prior to an immigration pulse (for an example of an extra period see least killifish
187 graph in Figure 5). We were interested in flooding events where enough samples were collected
188 to be able to detect at least one transition between periods (e.g., immigration to foraging period).
189 Because a minimum of four observations are needed to obtain two separate estimates for the
190 mean and variance, we did not analyze flooding events where less than four samples were
191 collected. Although the change-point analysis assumes equally spaced data points, we found that
192 it adequately detected trends in our unequally spaced observations. As an estimate of model fit,
193 we calculated a mean r^2 value across sites and years using estimates from change-point models
194 with the equation: $r^2 = 1 - (\text{residual sums of squares}/\text{total sums of squares})$.

195 Within a flooding event, we defined the immigration period as the first pulse (i.e.,
196 elevated mean estimate relative to adjacent temporal segments) in movement after flooding of a
197 wetland (1 per flooding event); the emigration corresponded to the last pulse in movement prior
198 to wetland drying (1 per flooding event). If the first pulse in movement continued until the end
199 of the time series, we defined it as the emigration period. All other periods were defined as the
200 foraging period, and as a result there were some flooding events with more than one foraging-
201 period estimate (see Figures 2 and 5 for examples of different periods).

202 After we determined the different temporal segments from the change-point analysis, we
203 estimated 95% confidence intervals for the means of three different response variables during
204 each period for each species to characterize responses to hydrologic variation: 1) timing of each
205 period (the time point at which one segment changed to another, or the end of a flooding event);
206 2) the duration of each period; and, 3) the fish encounter-rate estimates for each period. The
207 timing and duration of each period was estimated by calculating proportion DSF variables that
208 measure when a particular period ended relative to the duration of the entire flooding event
209 (period timing = maximum DSF within a period/maximum DSF for entire flooding event) and
210 the total duration of a period relative to the duration of the entire flooding event (period duration
211 = total # of days within a period/maximum DSF for entire flooding event). These variables
212 provide a comparable measure of response among flooding events of varying duration. Because
213 of variation movement patterns among flooding events (e.g., an event with an immigration, but
214 no emigration period), we detected unequal numbers of movement periods over the course of the
215 study: 35, 28, 24, 26 immigration periods were detected for eastern mosquitofish, flagfish, least
216 killifish and bluefin killifish, respectively; 19, 19, 15, 18 emigration periods; and 58, 59, 43, and
217 51 foraging periods. Data from each period were aggregated by estimating the mean within
218 water years and then among water years to yield one mean estimate for each of the three
219 response variables (timing, duration and encounter rate) at each site, and these mean estimates
220 were used to generate period specific 95% confidence interval estimates for each response
221 variable (six total observations for each confidence interval estimate). Only five observations
222 were used for the least killifish emigration pulse estimate because this species did not exhibit an
223 emigration pulse at Site 2. Although aggregating the data across years within sites homogenizes
224 some of the variation in the data, we were interested in extracting general patterns that were

225 detectable regardless of site-level idiosyncrasies. In some instances there was more than one
226 estimate for the foraging period within a flooding event; in those instances we estimated the
227 mean encounter rate within a flooding event and then aggregated the data as we did the other
228 periods. For these analyses we focused on the effects, given that there was at least one change
229 point observed within a given flooding event. Therefore, if there were no change points for a
230 given event (i.e., a constant value was fit for the entire time series) then it was not used to
231 estimate confidence intervals. We interpreted mean estimates as different (i.e., significant) if the
232 95% confidence intervals did not overlap.

233 **Results**

234 *Site Hydrology*

235 Though our study sites encompassed a range of hydroperiods, all sites completely dried
236 during each year of the study (Figure 3). Sites 1 and 2 had the shortest mean hydroperiod
237 estimates (96.8 and 97.5 days, respectively), followed by sites 3 and 6 (178 and 168.7 days,
238 respectively), with sites 4 and 5 having the longest mean hydroperiod estimates (273 and 238.3
239 days, respectively). The mean and maximum number of days since flooding were positively
240 related to hydroperiod, with means ranging from approximately 6 to 104 days and 76 to 332 days
241 for the maximum (Table 1). The total number of flooding events ranged from 6 events at Site 4
242 to 19 events at Site 2, with all other estimates in between (Table 1). Although there were
243 exceptions, sites generally flooded (depth > 0) between May and August and dried (depth = 0)
244 between November and March, with longer hydroperiod sites flooding earlier and drying out
245 later than the shorter hydroperiod sites (Figure 3).

246 *Fish Summary Statistics*

247 Fish encounter-rate estimates showed marked differences among species. Over this four-
248 year study we collected 95,236 fish at the six study sites. Eastern mosquitofish (76.1% of total
249 catch) had a mean encounter rate of 80.2 fish/day, flagfish (19.1%) a mean encounter rate of 20.1
250 fish/day, least killifish (3.4%) a mean encounter rate of 3.6 fish/day, and bluefin killifish (1.4%)
251 had a mean encounter rate of 1.4 fish/day. This overall ranking of species encounter rates was
252 consistent across sites (Table 2). Eastern mosquitofish had the highest maximum number of
253 individuals captured during a single sampling event at all sites, and flagfish had the second
254 highest single-day capture of individuals at four of the six sites (Table 2). There were also
255 differences among species in the order in which they arrived in the wetland. The confidence
256 interval estimates of the rank order of fish arrival indicated that flagfish and eastern mosquitofish
257 were generally the first to arrive, while least killifish and bluefin killifish took longer to colonize
258 (Figure 4).

259 *Change-point Analyses*

260 Our change-point analyses indicated considerable variability in model fits and movement
261 dynamics among species. Overall, we fit 164 models (41 flooding events for each species over
262 all years and sites) with a mean of approximately 21 observations per model and a range of 4 to
263 64 per model. The mean r^2 values across sites and years were higher for eastern mosquitofish
264 and flagfish than for least killifish and bluefin killifish (Table 3). However, regardless of
265 species, the models were able to explain a substantial amount of variation in the data, with
266 maximum r^2 values ranging from 0.65 to 0.94. All species exhibited pulses in activity more
267 frequently when immigrating into a wetland (range of 26 to 36 segments) than when leaving a
268 wetland (range of 13 to 18 segments), with eastern mosquitofish and flagfish having greater
269 numbers of immigration and emigration segments than either least killifish or bluefin killifish.

270 For all species, the number of flooding events during which fishes responded to both flooding
271 and drying of wetlands was similar to the number of emigration segments, indicating that in
272 periods when fish emigrated in response to drying, they also had immigrated in response to
273 wetland flooding earlier in the event (Table 3). All species exhibited pulses in greater than 60%
274 of the models with eastern mosquitofish having the highest percentage, followed by flagfish and
275 bluefin killifish, and least killifish had the lowest percentage. The total number of change points
276 estimated for both eastern mosquitofish and flagfish was higher than for the other two species
277 (Table 3).

278 Of the flooding events that exhibited detectable variation in encounter rate through time
279 (i.e., at least one change point), the change-point analyses indicated that all species exhibited
280 distinct periods of movement (Figure 5). The confidence interval estimates of the timing for each
281 period (immigration, emigration and foraging as measured in proportion DSF) indicated that the
282 study species moved during similar time periods. For all species the immigration period
283 occurred earlier than the emigration and foraging periods, and two of the four species had later
284 emigration periods than foraging periods (Figure 6). Within each period there were no
285 detectable differences in the timing of movement among species. Our estimates of period
286 duration showed that for two of the four species the immigration period was shorter than the
287 foraging period (Figure 7). We found no detectable species-specific differences in duration
288 among any of the other periods. However, when we aggregated the species duration estimates
289 within periods there was a slight trend of lower mean duration for both the immigration and
290 emigration periods relative to the foraging period (see dotted lines on Figure 7). As with the
291 timing of the periods, duration estimates were indistinguishable among species.

292 In contrast to similarities in the timing and duration of fish activity, the change-point
293 analyses revealed marked differences in the encounter-rate estimates among species. Our
294 estimates of mean encounter rate in each period showed that eastern mosquitofish had higher
295 encounter rates in the immigration and emigration periods than in the foraging period (Figure 8).
296 Flagfish mean encounter rates in both the foraging and emigration periods were lower than the
297 immigration period. The encounter rate in the immigration period for least killifish was higher
298 than the foraging period (difference in means was < 4 fish/day), but there were no differences
299 among the foraging and emigration period estimates. There were no detectable differences in
300 mean encounter rates among any of the periods for bluefin killifish. Eastern mosquitofish and
301 flagfish had higher encounter rate estimates than least killifish and bluefin killifish in both the
302 immigration period and the foraging period. Eastern mosquitofish had the highest emigration-
303 period estimate of any species, while flagfish had a higher emigration estimate than least
304 killifish, but not bluefin killifish (Figure 8).

305 **Discussion**

306 Consistent with our conceptual model of fish movement, our results indicate that fish
307 alter their activity rates in response to hydrological variation. Pulses in movement soon after
308 flooding and just prior to drying suggest that fish are actively moving into and out of short-
309 hydroperiod wetlands in response to seasonal hydrological fluctuations. Further, there was
310 evidence of species-specific differences in activity levels that correspond to patterns of recovery
311 following disturbance in long-hydroperiod wetlands (Trexler et al. 2005, DeAngelis et al. 2005).
312 Our results are consistent with theoretical work on the importance of behavioral differences in
313 movement for structuring communities (Armsworth and Roughgarden 2005, Abrams et al.

314 2007), and suggest that the interaction between dispersal and the environment is a key process
315 driving metacommunity dynamics in the Everglades landscape.

316 Results from this study suggest that eastern mosquitofish and flagfish can move in large
317 groups into short-hydroperiod wetlands, and are generally more abundant in ephemeral aquatic
318 habitats than either least killifish or bluefin killifish. These data add to a growing body of
319 evidence that recovery from hydrological disturbance is a primary driver of fish-community
320 structure in the Everglades. Several studies have illustrated the importance of hydrological
321 disturbance driving successional dynamics of fish communities in long-hydroperiod
322 environments (Trexler et al. 2005, Ruetz et al. 2005, McElroy et al. 2011). The current study
323 expands our inference to include environments that are disturbed annually and border the long-
324 hydroperiod sites where past work has focused.

325 Our analysis of change-point results corroborated the hypothesis that fish can exhibit
326 three distinct movement periods in ephemeral wetlands. Fish exhibited pulses in activity soon
327 after flooding or prior to drying in the majority of flooding events we analyzed: eastern
328 mosquitofish exhibited pulsed activity in almost ninety percent of the models, flagfish and
329 bluefin killifish in about three quarters of the models, and least killifish in greater than sixty
330 percent of the models. When at least one pulse in activity was detected, we found that
331 immigration period occurred earlier than the foraging and emigration periods for all species, and
332 the emigration period occurred later than the foraging period for two out of four species.
333 Similarly, we found general trends in the mean duration of each period with foraging being the
334 longest and emigration and immigration being the shortest; however, these results were more
335 equivocal with only two species exhibiting shorter immigration period than foraging period, and
336 no detectable differences observed for any species between the emigration and the other two

337 periods. High variance in the estimates of emigration duration possibly reflects the inter-site
338 variability in wetland drying.

339 In contrast to the relatively consistent timing and duration of periods among species,
340 encounter-rate estimates revealed marked differences among species in response to hydrological
341 variation. Change-point analyses described eastern mosquitofish and flagfish data better and
342 indicated more responsiveness to hydrological variation than bluefin killifish and least killifish.
343 During the immigration period, encounter-rate estimates for eastern mosquitofish and flagfish
344 were higher than the encounter rates of least killifish and bluefin killifish in all other periods.
345 This suggests that eastern mosquitofish and flagfish are able to quickly disperse into newly
346 available habitats in relatively large numbers, while relatively few individuals of least killifish
347 and bluefin killifish are able to respond to flooding. These results may indicate heterogeneity in
348 behavioral adaptations enabling detection and response to environmental cues (Lytle and Poff
349 2004), and may explain differences in recovery observed in long hydroperiod environments
350 (Trexler et al. 2005, DeAngelis et al. 2005). Immigration and emigration encounter-rate
351 estimates for eastern mosquitofish were not different, and were higher than all other estimates
352 with the exception of the flagfish immigration estimate. Strong responses by eastern
353 mosquitofish to both flooding and drying is not surprising because this species is well
354 documented as a good disperser (Brown 1985, 1987, Capone and Kushlan 1991, Congdon 1994,
355 Rehage and Sih 2004, Ruetz et al. 2005), and has become invasive in many areas (Courtenay and
356 Meffe 1989, Pyke 2008). Our results suggest that its responsiveness to both flooding and drying
357 may contribute to its widespread success. Obaza et al. (2011) indicated that drift fences may be
358 slightly less efficient at capturing eastern mosquitofish than the other study species. Thus, the

359 results reported here are inconsistent with the species differences expected by this bias, and the
360 high encounter rate estimates for eastern mosquitofish are probably conservative.

361 Our results provide empirical support for the importance of dispersal for connecting local
362 fish communities in the Everglades. Species-specific differences in dispersal is a key component
363 of metacommunity models where patterns in community structure are shaped by both local (e.g.,
364 competition) and regional scale processes (e.g., dispersal). In particular, patch dynamics models
365 predict species that would normally be inferior competitors in a given patch can persist
366 regionally via superior colonization ability (e.g., a competition-colonization trade-off) (Leibold
367 et al. 2004). Empirical studies of Everglades fish communities where some species exhibit quick
368 recovery to disturbance followed by a decline in density (e.g., flagfish) while others recover
369 slowly but become dominant as time increases following a disturbance (e.g., bluefin and least
370 killifish) indicate that trade-offs between dispersal and competitive ability may be important in
371 explaining species coexistence in this system (Trexler et al. 2005; DeAngelis et al. 2005).
372 Eastern mosquitofish recovers quickly and persists at high densities through time, suggesting that
373 other mechanisms may explain its dynamics. In the present study, movement patterns were
374 consistent with previous estimates of interspecific differences in recovery, and reinforced the
375 inference that fish recovery to disturbance is driven by dispersal. Although there are likely other
376 mechanisms determining fish coexistence in this system, strong interspecific differences in
377 dispersal ability suggest that trade-offs operating at regional spatial scales may play a role in
378 mediating species coexistence in this system.

379 Overall, the results of our study are consistent with a conceptual model in which small
380 fishes in the Everglades display three periods of movement throughout the year: immigration,
381 foraging, and emigration. Although three periods of movement did not occur in every flooding

382 event, in the majority of flooding events that we analyzed the timing of the periods is relatively
383 consistent across species and there is evidence that the immigration period occurs over a
384 relatively short period of time. There are also interspecific differences in the magnitude of
385 response to flooding and drying that likely reflect differences in dispersal ability that may drive
386 larger scale patterns in response to disturbance. Although the drift-fence sampling methodology
387 also allows estimation of the direction fish are moving, in this study our focus was on differences
388 in overall activity levels in response to hydrological variation. Future research should explore
389 the potential directedness of movement in the immigration and emigration phases of this
390 seasonal cycle which would enhance our understanding of how fishes persist in this fluctuating
391 environment. The results of this study have important implications for predicting the
392 consequences of hydrological management of peripheral wetlands in the Everglades, and for
393 developing models for management assessment and evaluation (Trexler and Goss 2009, Jopp et
394 al. 2010). This study also reinforces the importance of regional scale processes influencing
395 Everglades fish communities and suggests that metacommunity theory may provide insight into
396 the mechanisms shaping fish community structure in this system.

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526

527 **Table 1.** Summary statistics for hydrologic data at each site across all years. DSF corresponds
528 to the number of consecutive days of wetland flooding (depth > 0). Events correspond to the
529 number of flooding events over the course of the study.

530

Site	Mean Hydroperiod	Mean DSF	Max DSF	Events
1	96.8	7.2	77	11
2	97.5	6.4	76	19
3	178.0	33.0	192	15
4	273.0	104.2	332	6
5	238.3	65.2	252	11
6	168.7	20.2	126	16

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544 **Table 2.** Encounter-rate (# of fish collected/24 hrs) summary statistics for all species at each site
 545 aggregated across years.

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Site	Species	Mean	Max
1	Eastern Mosquitofish	79.0	1998
1	Flagfish	7.3	85
1	Least Killifish	5.3	138
1	Bluefin Killifish	1.1	13
2	Eastern Mosquitofish	60.4	1427
2	Flagfish	36.2	595
2	Least Killifish	3.0	114
2	Bluefin Killifish	1.5	44
3	Eastern Mosquitofish	93.1	1837
3	Flagfish	12.4	364
3	Least Killifish	8.7	368
3	Bluefin Killifish	2.1	183
4	Eastern Mosquitofish	73.8	1714
4	Flagfish	19.5	234
4	Least Killifish	1.5	79
4	Bluefin Killifish	1.7	180
5	Eastern Mosquitofish	101.7	1648
5	Flagfish	24.4	494
5	Least Killifish	1.6	33
5	Bluefin Killifish	1.2	94
6	Eastern Mosquitofish	65.1	796
6	Flagfish	22.4	245
6	Least Killifish	2.0	73
6	Bluefin Killifish	0.5	25

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549 **Table 3.** Results from change-point analysis across all sites and years. Change points
550 correspond to the total number transitions between immigration, emigration and foraging
551 periods; % models with pulses is the percentage of models where the change-point analysis
552 detected at least one period with a pulse in activity (i.e., at least one change point within a
553 flooding event); immigration is the total number of segments occurring in the first (immigration)
554 period; emigration refers to the total number of segments in the last (emigration) period; both
555 corresponds to the total number of flooding events during which both immigration and
556 emigration periods occurred; mean and max r^2 correspond to the model fits aggregated across
557 years and sites, and the maximum r^2 , respectively.
558

Species	Change points	% Models with pulses	Immigration	Emigration	Both	Mean r^2	Max r^2
Eastern Mosquitofish	76	88	35	19	18	0.33	0.94
Flagfish	75	76	28	19	16	0.36	0.88
Least Killifish	56	63	24	15	13	0.20	0.65
Bluefin Killifish	65	73	26	18	14	0.24	0.81

560

561 Figure Legends

562 **Figure 1.** Location of the Rocky Glades region (stippled area) in Everglades National Park,
563 Florida, U.S.A., with study sites indicated by numbers. The Rocky Glades outside of ENP is not
564 stippled because it has been converted to agriculture.

565 **Figure 2.** A conceptual model of how fish-movement rate is related to the number of days since
566 wetland flooding. We hypothesized that there are three distinct periods of movement in response
567 to hydrologic variation: an immigration period with increased movement in response to
568 flooding; an emigration period with increased movement that is a response to drying; and a
569 foraging period between those two periods when movement is reduced.

570 **Figure 3.** Time-series graph of water depths during the study plotted separately for each site.
571 Sites are grouped by hydroperiod.

572 **Figure 4.** Estimates of the rank order of arrival means and 95% confidence intervals for each
573 species. Rankings were determined by assigning a rank based on the first instance a species was
574 collected during each flooding event (e.g., 1 = first species to arrive, 2 = second species to arrive,
575 etc.). Species were ranked equally if they arrived on the same day, and if they did not appear in
576 samples during a flooding event they were given a rank of one higher than the last species to
577 arrive (e.g., if the last species to arrive was ranked 3 then a species that did not appear would be
578 given a rank of 4). Non-overlapping confidence intervals indicate significant differences.

579 **Figure 5.** Plots of mean estimates from change-point analyses (colored lines) overlain on
580 observed data. The plots illustrate trends in encounter rates throughout a flooding event, with the
581 highest encounter rates during immigration and emigration periods, and lowest during foraging
582 periods. The graphs show data from Site 4, water years 2001, 2002, and 2003 (eastern
583 mosquitofish, bluefin killifish, and flagfish), and Site 3, water year 2001 (least killifish).

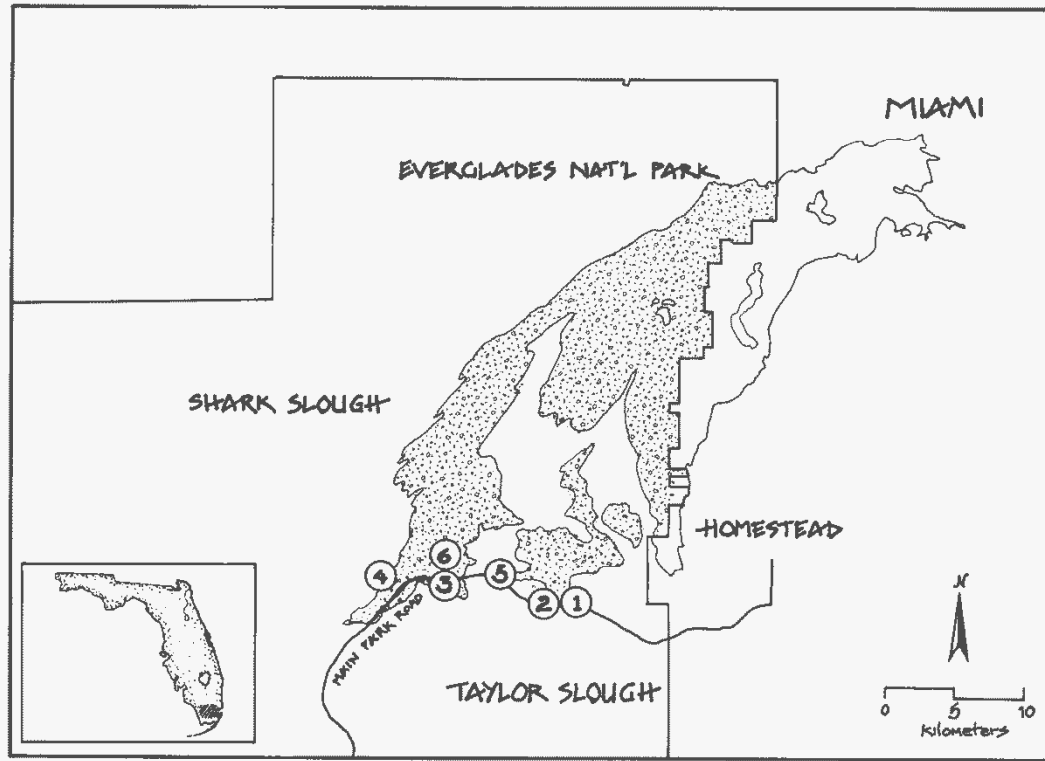
584 **Figure 6.** Estimates of the period timing means and 95% confidence intervals for each species.
585 Period timing corresponds to the ending of a particular period and is measured as a ratio of the
586 number days since flooding (DSF) observed at the change point for each period divided by the
587 maximum DSF observed in a flooding event. Non-overlapping confidence intervals indicate
588 significant differences.

589 **Figure 7.** Estimates of the period duration means and 95% confidence intervals for each species.
590 Period duration is the length of a period measured as a ratio of the total duration of a particular
591 period (measured in days) divided by the maximum number of days since flooding (DSF)
592 observed in a flooding event. Non-overlapping confidence intervals indicate significant
593 differences. Dotted lines correspond to the approximate mean estimate of all species for each
594 period.

595 **Figure 8.** Estimates of encounter rate means and 95% confidence intervals during each period
596 for each species. Non-overlapping confidence intervals indicate significant differences.

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598 Figure 1



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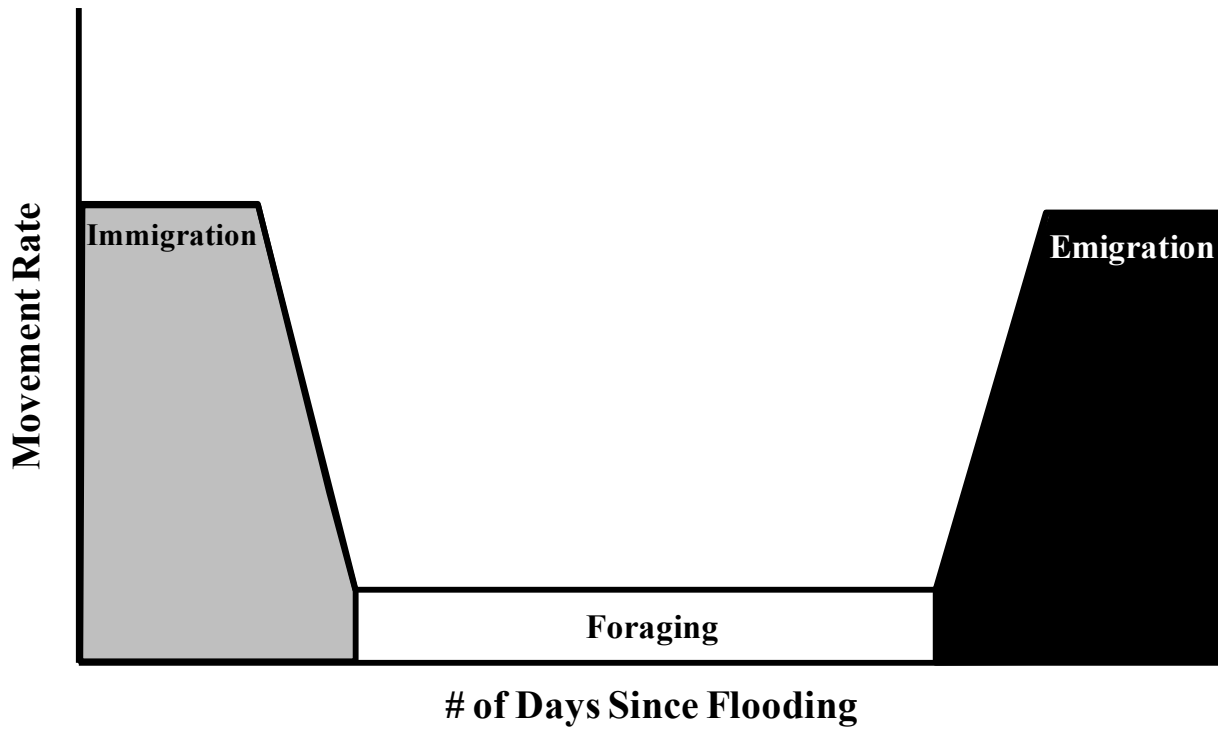
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608 Figure 2

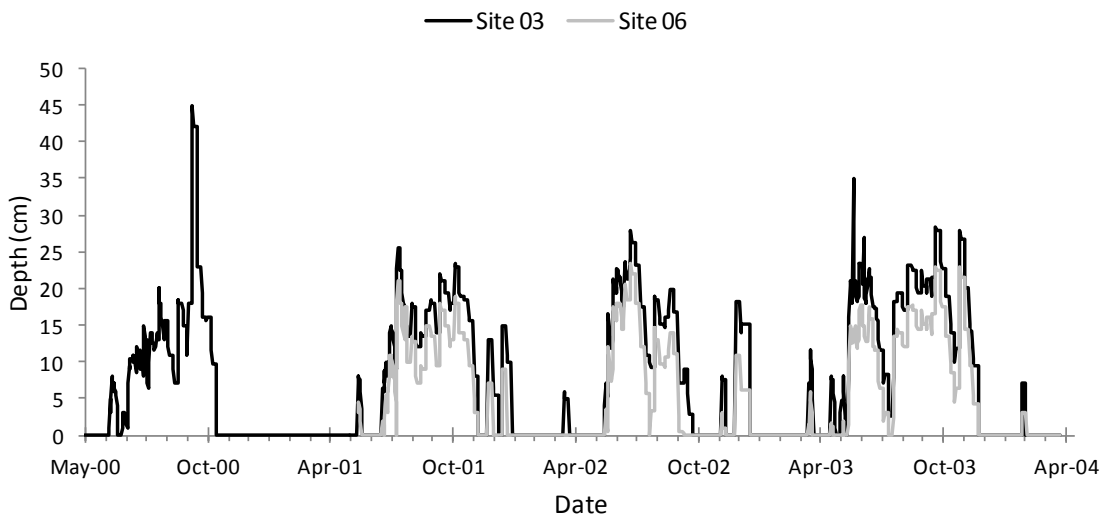
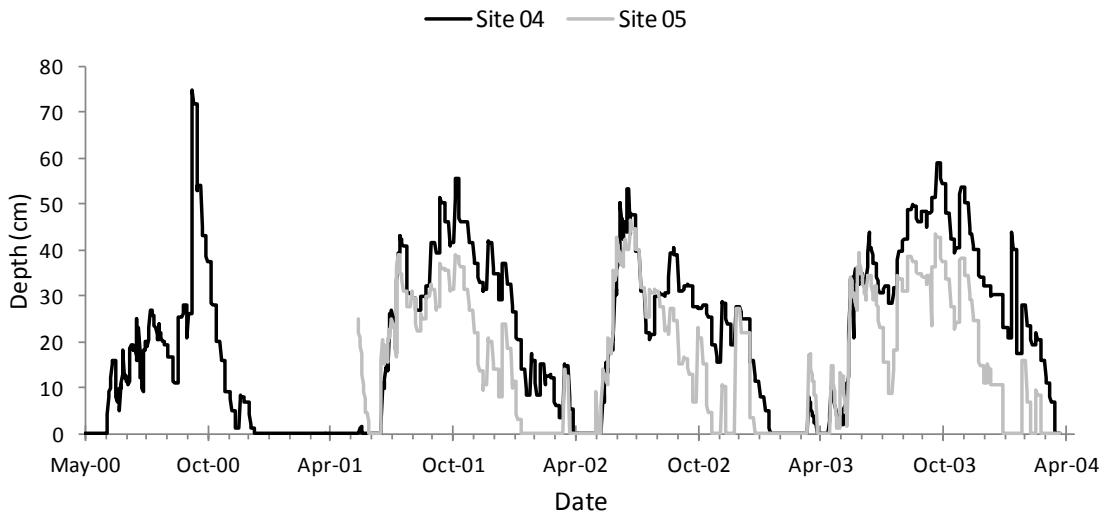
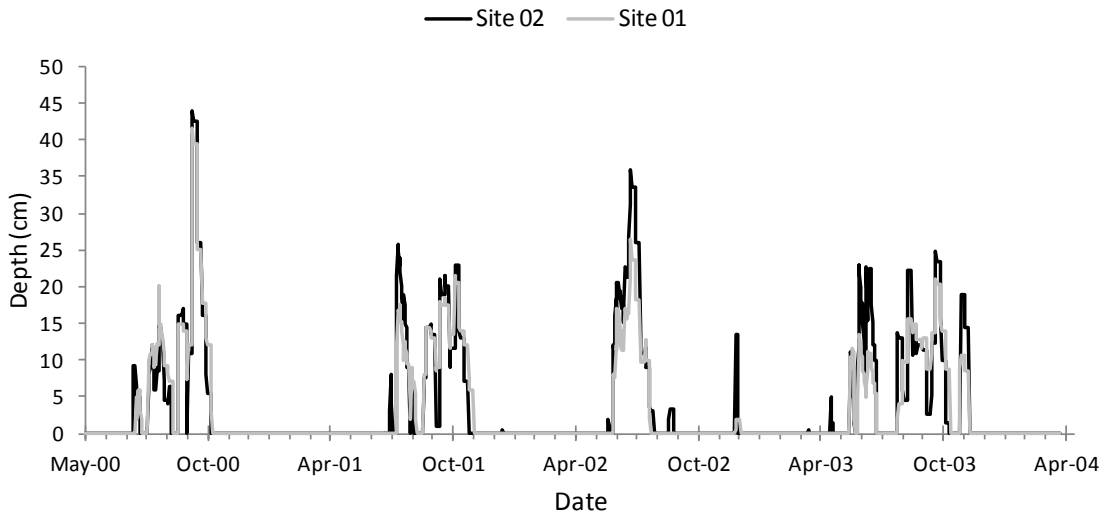


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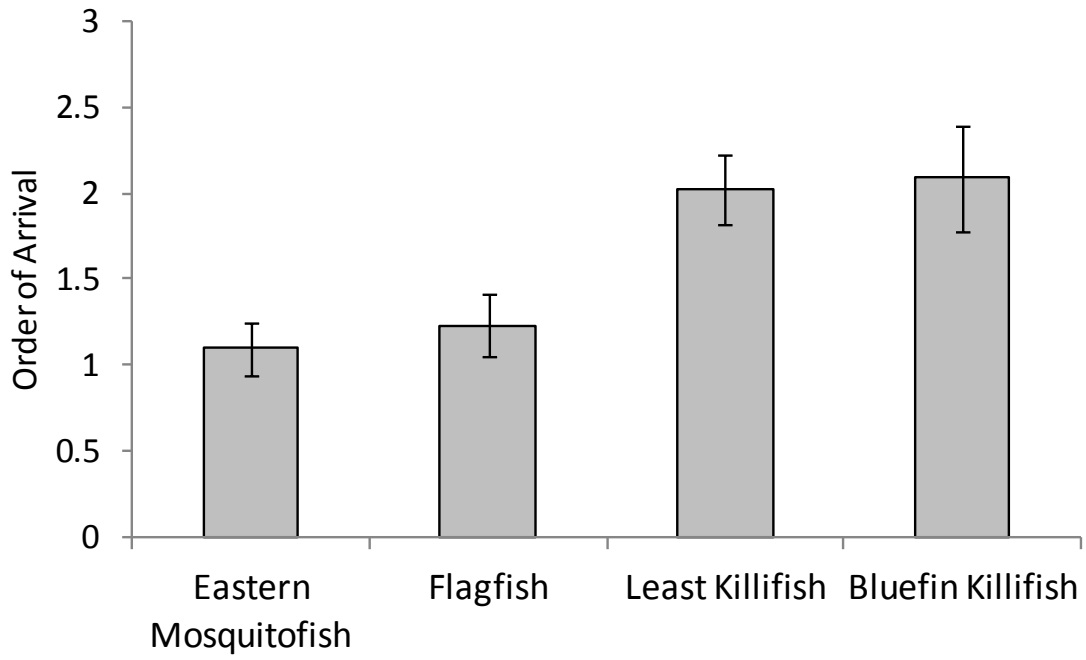
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612 Figure 3



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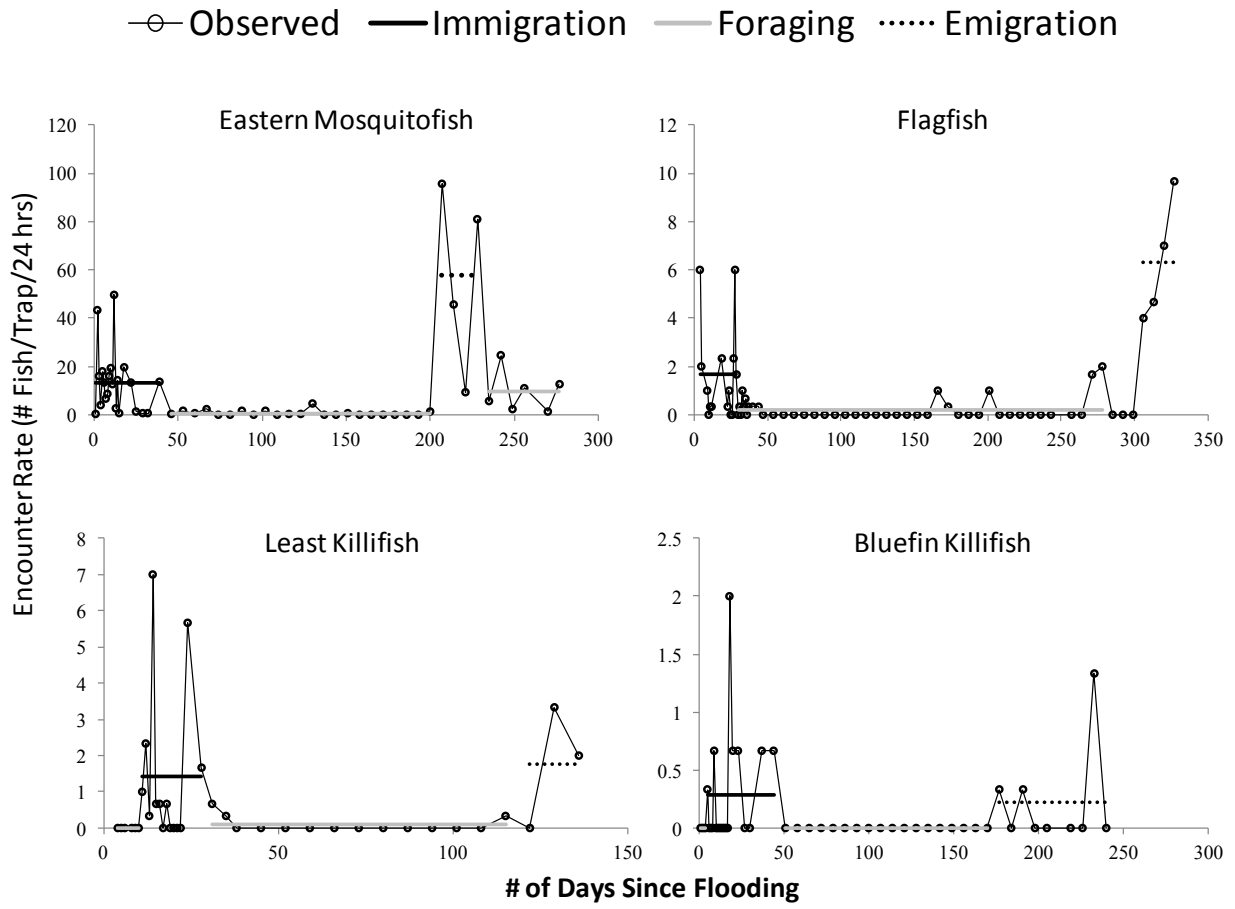
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619 Figure 5

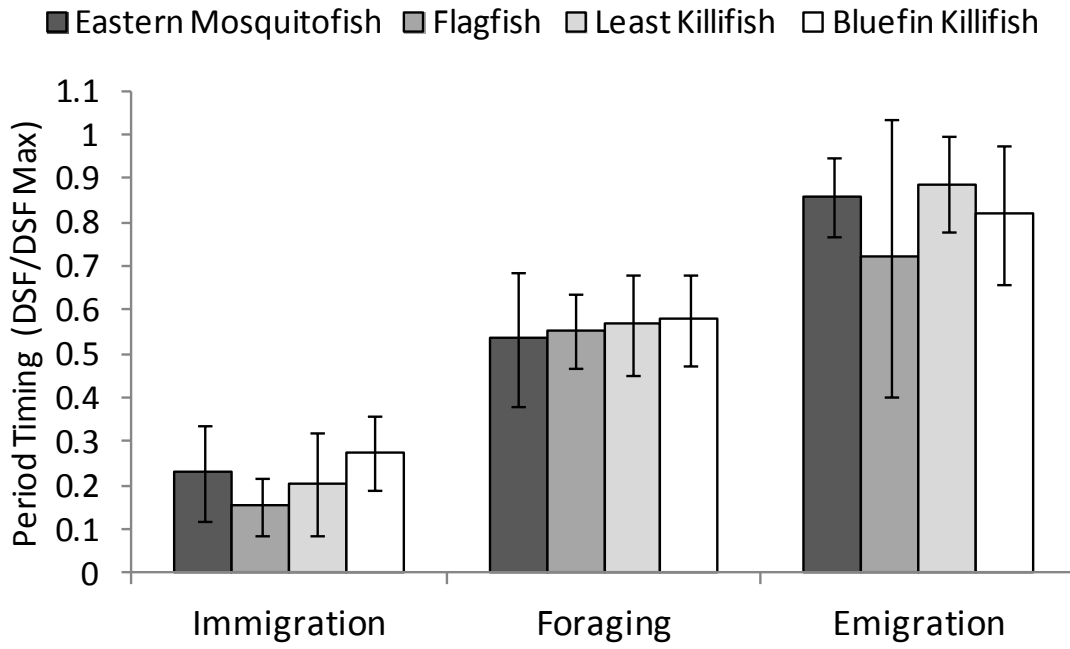


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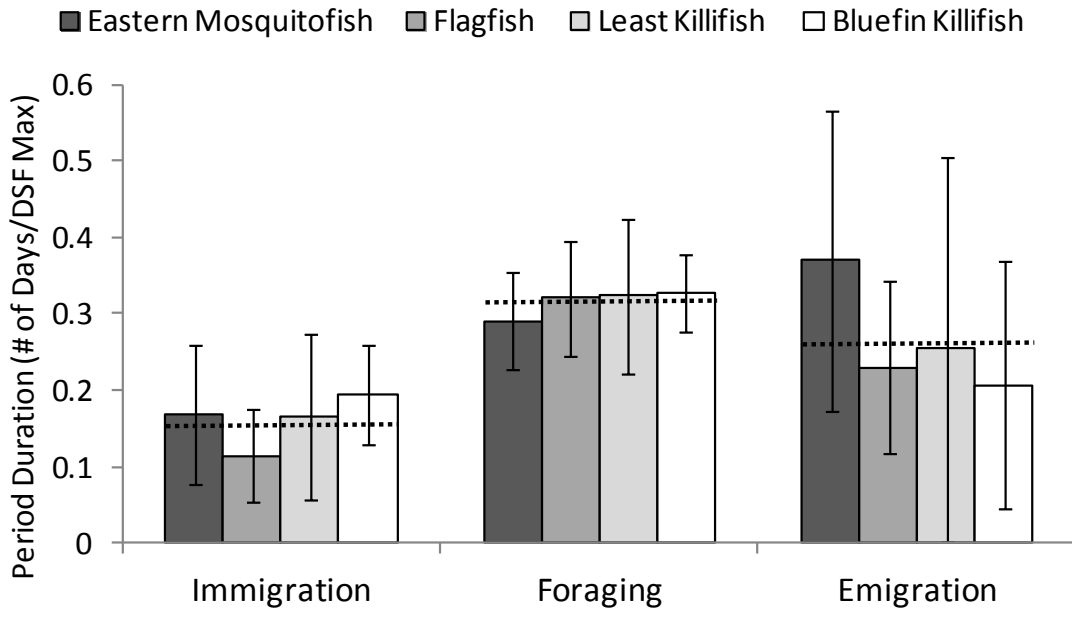
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623 Figure 6



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625 Figure 7

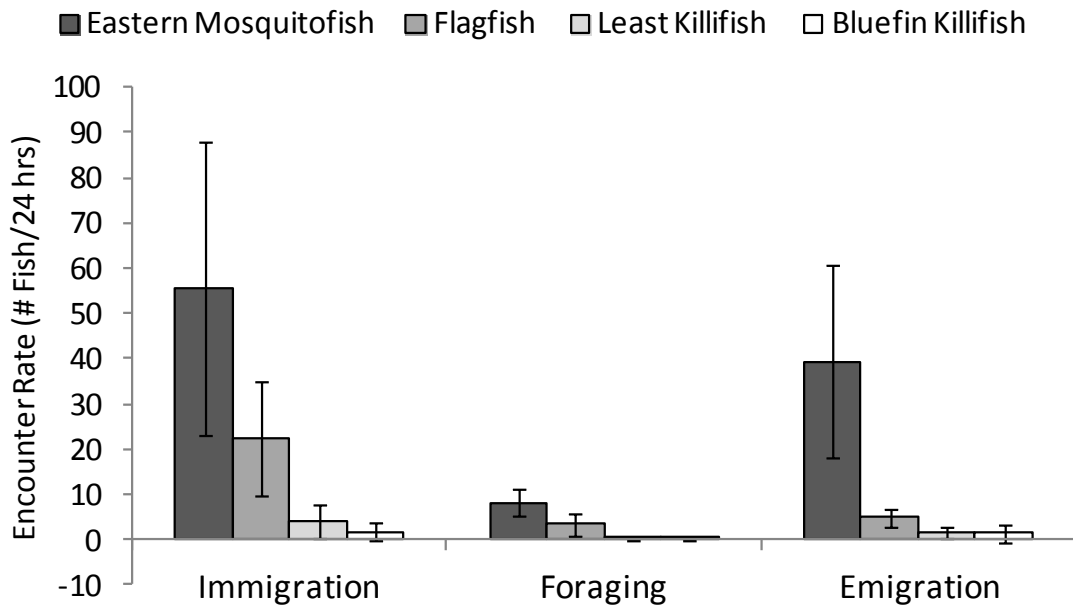


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629 Figure 8



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