



Community structure of fishes inhabiting aquatic refuges in a threatened Karst wetland and its implications for ecosystem management

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Abstract

We illustrate the importance of subsurface refuges for conservation of aquatic fauna with our studies of karstic wetlands in Everglades National Park, Florida, USA. Managers have proposed that water levels there should not fall more than 46 cm below ground level for more than 90 days annually. In four areas, 84% of solution holes were less than 46 cm deep and holes deeper than 1 m were rare ($<3 \text{ km}^{-2}$). Null-model analysis indicated no “structure” in the solution-hole fish communities early in the dry season, but that structure emerged as drying progressed. Native cyprinodontiforms were abundant in shallow solution holes that dry annually under current management, while predatory species (often non-native) tended to dominate deeper holes. Water quality was correlated with hole volume and with composition of late dry-season fish communities. Tremendous losses of fish biomass occurred when water levels fell below 46 cm from ground surface. Most native taxa were unlikely to survive in the deep refuges that held predatory non-native taxa.

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1. Introduction

Mismanagement of water resources by re-distribution or over-extraction is a global problem affecting the quantity and quality of aquatic habitats for wildlife and humans (Ostrom et al., 1999). Lowering of water tables by pumping is a common result of flood control, agriculture, and human consumption of water. Temporary aquatic habitats, and the organisms that live there, are especially at risk from lowered water tables. Many species of amphibians (Kiesecker et al., 2001), fishes (Matthews, 1998; Tonn, 1990) and vernal-pool organisms (Preisser et al., 2000) have been affected. For aquatic organisms, maintenance of habitat quality requires the assurance of enough water to maintain aquatic refuges in most years, with the expectation that the species will

re-colonize from distant refuges after extreme events. Thus, an important goal for wetland management is setting minimum hydrological standards that assure the quality of refuges for aquatic organisms through drought events. Unfortunately, the rapid loss of wetlands in recent years, coupled with the invasion of non-native species, has exacerbated the challenge of managing such habitats through stressful years (Mack et al., 2000). Successful management requires the establishment of standards based on understanding the responses of sensitive organisms to drought.

The Rocky Glades is a short-hydroperiod, karst wetland that once covered a large area on the eastern fringe of the Florida Everglades, USA (Craighead, 1971; Snyder et al., 1990), but which has experienced marked drainage. Development has reduced this habitat by more than half to approximately 8030 ha, primarily in Everglades National Park (US Fish & Wildlife Service, 1999; Fig. 1). Beginning in the 1960s, the water table in

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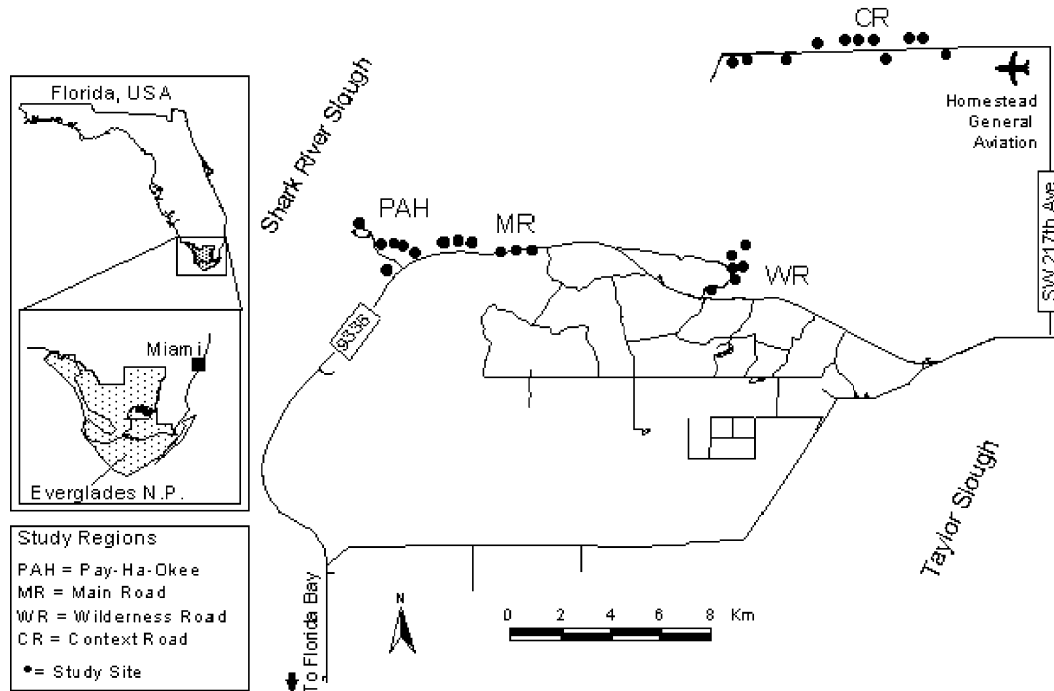


Fig. 1. Sampling regions in the Rocky Glades indicated by letters PAH, MR, WR, and CR. Solid circles indicate the solution holes sampled for this study. A region for the transect study was defined as the area within 1.6 km of the solution holes in each region, and bounded on one side by the access road.

the Rocky Glades was lowered to drain areas for agricultural and urban development. This action reduced the duration and level of surface-water inundation, lowered ground water levels, and changed the time of maximum surface-water depth to approximately one month earlier than pre-drainage (Loftus et al., 1992). Those changes resulted in complete drying of most aquatic refuges in all but the wettest years, presumably decreasing the survival of aquatic organisms. The Rocky Glades will be greatly affected by changes in water delivery proposed by the initiative to restore the Everglades ecosystem (US Fish & Wildlife Service, 1999).

The highest elevations of the Rocky Glades today are inundated approximately 20–60 days a year (US Fish & Wildlife Service, 1999), with maximum hydroperiods of 5–6 months. The surface of the Rocky Glades is weathered limestone, with numerous depressions (solution holes) that serve as refuges for aquatic organisms during dry conditions (Loftus et al., 1992). These solution holes range in diameter from a few centimeters to several meters, often with very complex internal topography. They range in depth from shallow depressions a few centimeters deep to holes that extend several meters into the surficial aquifer. The substrate within the holes is variable; many holes contain marl soil or detritus that occlude free access to deeper cavities, but may hold moisture necessary for survival of some aquatic invertebrates (Loftus and Reid, 2000). Others have little or no soil development.

Secondary production of aquatic organisms in the Rocky Glades appears to be limited by mortality through the annual dry season when aquatic habitats are reduced to solution holes (Loftus et al., 1992). Few published studies of dispersal and colonization of dry-season refuges in the Everglades are available (Acosta and Perry, 2001). Loftus et al. (1992) noted the presence of organisms in seven solution holes in the Rocky Glades. Their data demonstrated that fish and aquatic invertebrates were able to survive through a severe drought in 1990–1991 by reaching ground water in deep solution holes. However, deep solution holes are uncommon. The role of the abundant shallow holes as refuges in years with more typical rainfall and ground-water conditions remains to be established. Complicating this picture, several non-native fish species invaded this region in the early 1990s, where they are, at times, abundant (Trexler et al., 2001). The impact of these species on native fish communities is unknown.

This study sought to provide baseline information on the use of solution holes by fishes during the South Florida dry season and to identify the characteristics that determine the quality of these habitats as refuges for fishes. We also provide information on the distribution and potential effects of introduced species on fish communities in solution-hole refuges of the Rocky Glades. We addressed the following questions: what is the distribution and density of solution holes across the Rocky Glades?; when, and in what patterns, do fishes colonize and persist within dry-season refuges?; once

colonized, do the abiotic characteristics of solution holes such as depth, water quality, or habitat complexity determine fish community structure there?; finally, how does community structure of fishes change as the dry season progresses?

2. Methods

2.1. The physical environment

South Florida experiences a wet–dry season hydrology, with the wet season typically from May to November and the dry season from December to April (Chen and Gerber, 1990). During the dry season of 2000, we conducted a survey of solution holes in four short-hydroperiod regions (Fig. 1) to document the frequency and characteristics of solution holes. We randomly selected ten plots in each region and surveyed ten 50-m transects radiating randomly from the center of the plot, for a total of 500 linear meters per plot. We measured the length, width, and average depth of all solution holes at least 50 cm × 50 cm × 30 cm (length × width × depth) that each transect crossed.

We measured environmental parameters in solution holes where we routinely collected fish. Depth was measured at a fixed position in each hole to document water-level fluctuation. We measured as an index of solution-hole complexity the length of a chain laid over the bottom of each hole along its longest axis relative to the linear distance across that axis. At least once every 3 weeks during the dry season, we deployed Hydrolab Scouts® in each hole between 0800 and 1400 to estimate water temperature, dissolved oxygen, specific conductivity, and pH. Additionally, water samples were taken from each hole approximately every three months for analysis of chlorophyll *a* and ammonium.

2.2. Patterns of fish abundance

We used Gee® minnow traps to estimate catch-per-unit-effort (CPUE) of fish in each solution hole. We determined that the minnow trap was the best method to capture fishes in solution holes, given the complex dimensions, small spaces, and jagged surfaces. Previous studies have shown minnow traps to be relatively inefficient, and at times biased, in their sampling (Pot et al., 1984; He and Lodge, 1990; Jackson and Harvey, 1997). Therefore, we supplemented our minnow trap collections with weekly visual estimates of species composition by counting all fish observed during a 5-min interval. We wrapped the traps in 2 mm mesh and standardized the funnel entrance diameter to 30 mm. The top of the trap was placed approximately 5 mm above the water surface to allow fish access to the surface during low-oxygen conditions to minimize overnight mortality.

We standardized effort by setting the traps for approximately 24 h. When traps were checked, we measured the total length (TL) of each specimen, marked it by a fin clip, and returned it live to the hole where it was captured. Fin clipping did not uniquely identify individuals or their time of capture, but did identify fishes collected previously.

During 1999, we sampled 11 solution holes at Context Road (CR), two at Wilderness Road (WR), two at Main Road (MR), and four at Pa-Hay-Okee (PAH) (Fig. 1). In 2000, we added four solution holes at WR, four at MR, and two at PAH. Because of the increased number of holes in the second year, it was necessary to decrease the frequency of dry-season sampling from weekly in 1999 to every 2.5–3 weeks in 2000. Access to many study sites was difficult, so it was not possible to sample all solution holes in a single week. We sampled year-round, though the frequency of trapping was increased during the dry season when water levels fluctuated. We averaged data collected within six time intervals, with each hole sampled at least once, to standardize the temporal comparisons. The time intervals could not be standardized between years because the rate of drying and rainfall dictated the sampling regime each year.

We used a 1-m² throw trap (Kushlan, 1981; Chick et al., 1992; Jordan et al., 1997) to collect fishes on the marsh surface during the wet season. This allowed us to determine if the same community of fishes in the open marsh during the wet season colonized adjacent solution holes when drying commenced. Throw-trap sampling was conducted every three months during times of surface flooding. We used a throw trap with a 46 cm weighted-mesh curtain on the bottom to sample fishes on the uneven limestone surface of the Rocky Glades. Limited surface water caused the number of throw traps sampled to vary among study regions and between years.

2.3. Statistical methods

We tested for evidence of changing fish abundance as the dry season progressed each year. We used repeated measures analysis of variance (ANOVA) to compare the change in species CPUE between adjacent time intervals and among study regions (CR, MR, PAH, and WR). We followed this with a null-model analysis to test for non-random patterns of species co-occurrence in solution-hole assemblage using the algorithm SIM4 in the EcoSim™ software (<http://homepages.together.net/~gentsmin/ecosim.htm>). This analysis is robust to type I errors and works well with count data (Gotelli, 2000; Gotelli and Entsminger, 2001). Matrices of species presence-absence by sample were produced from minnow trap and visual survey data for time intervals 1–4; time intervals 5 and 6 were excluded because the shallow

holes had dried. Species that accounted for fewer than 5% of the total number of fish captured were excluded from analyses, because rare taxa can be overly influential in simulation tests. We ran the analysis twice to standardize the number of solution holes considered in temporal comparisons; we ran the analyses with all solution holes containing water at a particular time period and with only those solution holes that still contained water at the final dry season sampling period. Both schemes gave the same results, so only the latter is discussed.

We compared each presence-absence matrix with 1000 random matrices generated from the data to provide an index of the average number of co-occurrences between all possible pairs of species (“checkerboard units” or C-scores; Stone and Roberts, 1990). This index provided a standardized effect score to scale the results in units of standard deviations and allowed comparisons among tests (Gotelli, 2000). A standardized effect score of ± 2 is statistically significant at the $P=0.05$ level and indicates that deterministic forces (e.g. competition or predation) may influence the community. We illustrated the results of the null-model analysis with cluster analysis to group fish communities with non-random co-occurrence patterns based on the relative Sorenson distance measure (Faith et al., 1987).

We used principal components analysis (PCA) to identify latent patterns in the environmental data from individual solution holes late in the dry season (sampling intervals 3–5, early March–mid June). Most holes retaining water at this time (1999: $N=14$; 2000: $N=17$) appeared twice in this data set, providing an indication of temporal trends. We were unable to analyze time intervals separately because drying did not occur uniformly across the study area and we did not sample enough holes to provide robust ordinations at any single point in time. Our analysis fails to account explicitly for temporal autocorrelation within solution-hole communities, with the practical implication of treating the two samples as independent observations comparable to different holes. If two samples from the same hole are more similar than two samples from different holes (the most likely error), our conclusions underestimate general patterns of community–environment relationships. We interpreted factors that explained the first 70% of variance in these environmental parameters.

We used a Mantel analysis to test for correlations between the pairwise Euclidean distance of each of these factors in all solution holes and a matrix of pairwise comparisons of fish collected in the same holes using relative Sorenson similarity indices (Mantel, 1967; Douglas and Endler, 1982). The Sorenson indices were calculated on the abundance of each species relativized to the most abundant taxon in each sample. We used non-metric multidimensional scaling (NMDS) to illustrate relationships between environmental parameters

and fish community data. The NMDS ordination method is based on rank-distances and is not susceptible to problems associated with zero truncation, common in ecological data (Beals, 1984). The NMDS ordination procedure produced coordinates for solution-hole samples of fish CPUE on a common scale that was rotated to maximize variation in the environmental variable indicated to be significantly correlated with the fish community by the Mantel test.

3. Results

3.1. Physical environment

The densities and depths of solution holes differed among the four study regions (Fig. 2). CR and MR had relatively high densities of solution holes, while far fewer holes were present in the same spatial area at PAH (163, 129, and 17, respectively). Although the average solution-hole depth did not differ among the four areas surveyed, no holes 0.5 m or deeper were noted at PAH, and few deeper than 0.6 m were noted at MR (Fig. 2). Overall, solution holes deeper than 0.5 m comprised only 11% of the total measured.

Water depths declined and rebounded seasonally in all of the solution holes between January 1999 and July 2000 (Fig. 3). During both 1999 and 2000, water depths in solution holes did not decrease uniformly in each region (repeated measure ANOVA time-by-region interaction: 1999, $F_{15, 70}=2.788$, $P=0.002$; 2000, $F_{15, 125}=3.975$, $P<0.001$). On average, water receded fastest at CR in 1999 (CR=2.7 cm/day, MR=1.9 cm/day, WR=1.7 cm/day, PAH=2.0 cm/day), but in 2000 it receded fastest at MR (CR=1.5 cm/day, MR=2.6 cm/day, WR=1.9 cm/day, PAH=2.0 cm/day).

Water chemistry varied seasonally in both years and became potentially harmful to fish in the late dry season. Ammonium and chlorophyll *a* concentrations increased in both dry seasons and decreased in the wet seasons (Table 1). Generally, the shortest hydroperiod regions, MR and WR, had the greatest concentration of chlorophyll *a*. The long hydroperiod region, PAH, had some of the lowest chlorophyll *a* concentrations. There was no clear relationship between ammonium concentration and hydroperiod of the region, although the highest concentrations occurred at MR and WR, the shortest hydroperiod areas.

Most other water-quality measures also varied from the wet to dry season. Dissolved oxygen was generally higher in solution holes during the wet season than the dry season, and was at times near 0 mg/l in the dry season. The confidence intervals about the dry-season estimates of ammonium, chlorophyll *a*, and dissolved oxygen were generally larger than reported for wet-season samples (as a proportion of the mean estimate,

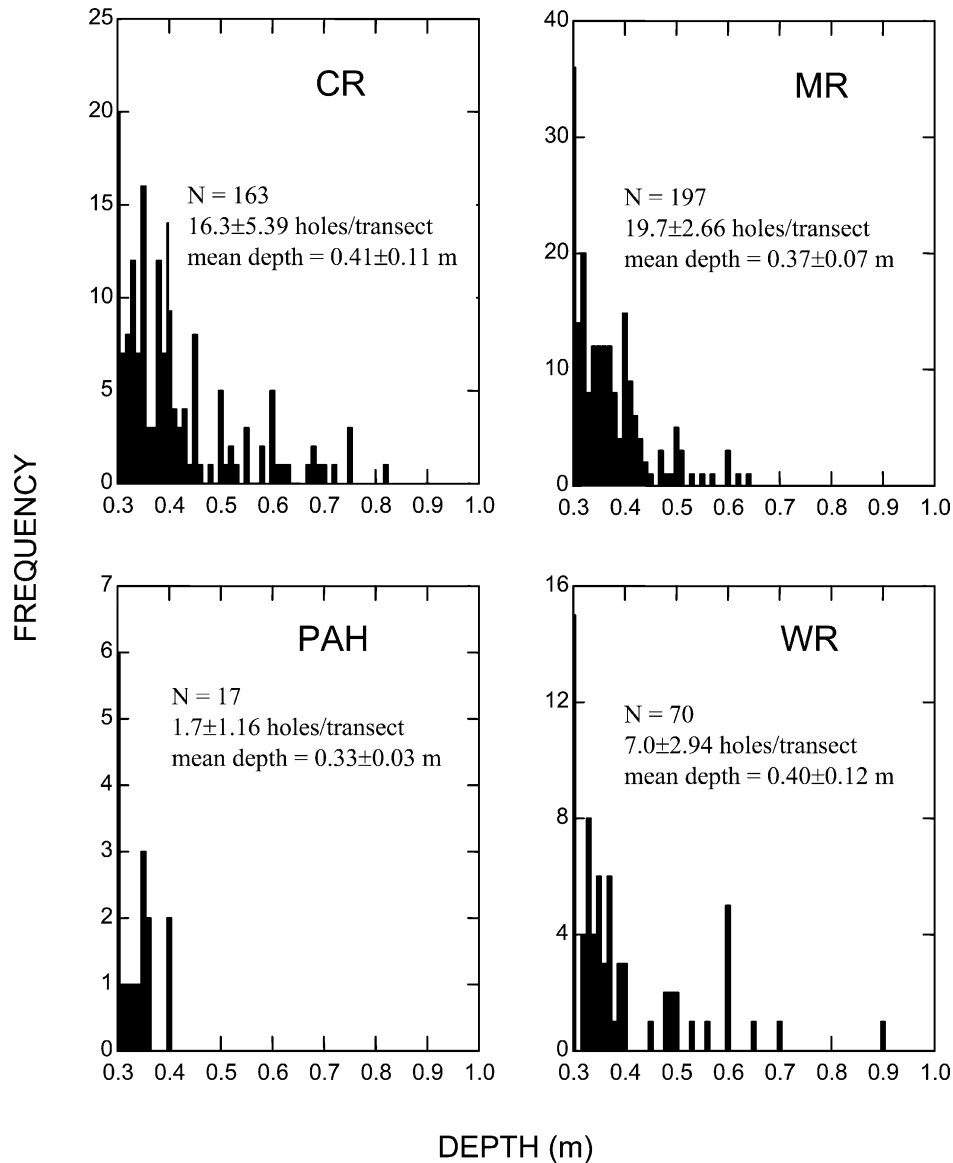


Fig. 2. Frequency of refuges and their depths measured in a survey across the Rocky Glades. Note variation in scale on Y-axes from different study sites. Transects totaling 5000 m were surveyed in each region; N is the number of solution holes encountered that were greater than $0.5 \text{ m} \times 0.5 \text{ m} \times 0.3 \text{ m}$ ($l \times w \times d$).

Table 1). The difference in water temperature between dry and wet seasons (generally cooler in the dry than the wet) was more marked in 2000 than in 1999. In all four regions in both years, pH varied from neutral during the dry season to weakly basic during the wet season (Table 1).

In both years, PCA revealed similar patterns of correlation among the water quality parameters (dissolved oxygen, pH, ammonium, and chlorophyll *a*) and hole volume from late dry-season solution holes (Table 2). Ammonium and chlorophyll *a* varied together in both years (1999 Axis 3; 2000 Axis 2), and with the opposite sign as dissolved oxygen and pH (1999 Axis 1; 2000 Axis 1 and Axis 3). Hole volume was positively correlated with ammonium and chlorophyll *a*

(1999 Axis 1 and Axis 3; 2000 Axis 1), while volume was inversely correlated with dissolved oxygen and pH (1999 Axis 1; 2000 Axis 1).

3.2. Patterns of fish abundance

3.2.1. Minnow traps in solution holes

We collected more than 3500 fishes of 17 species between the dry season of 1999 and the wet season of 2000 (Table 3). Over twice as many samples were taken in 1999 than in 2000, but the distribution of sampling effort among regions was more equitable in 2000. Eastern mosquitofish was the most numerous species taken, comprising over 20% of specimens in both years. Eastern mosquitofish, yellow bullhead, marsh killifish, flagfish,

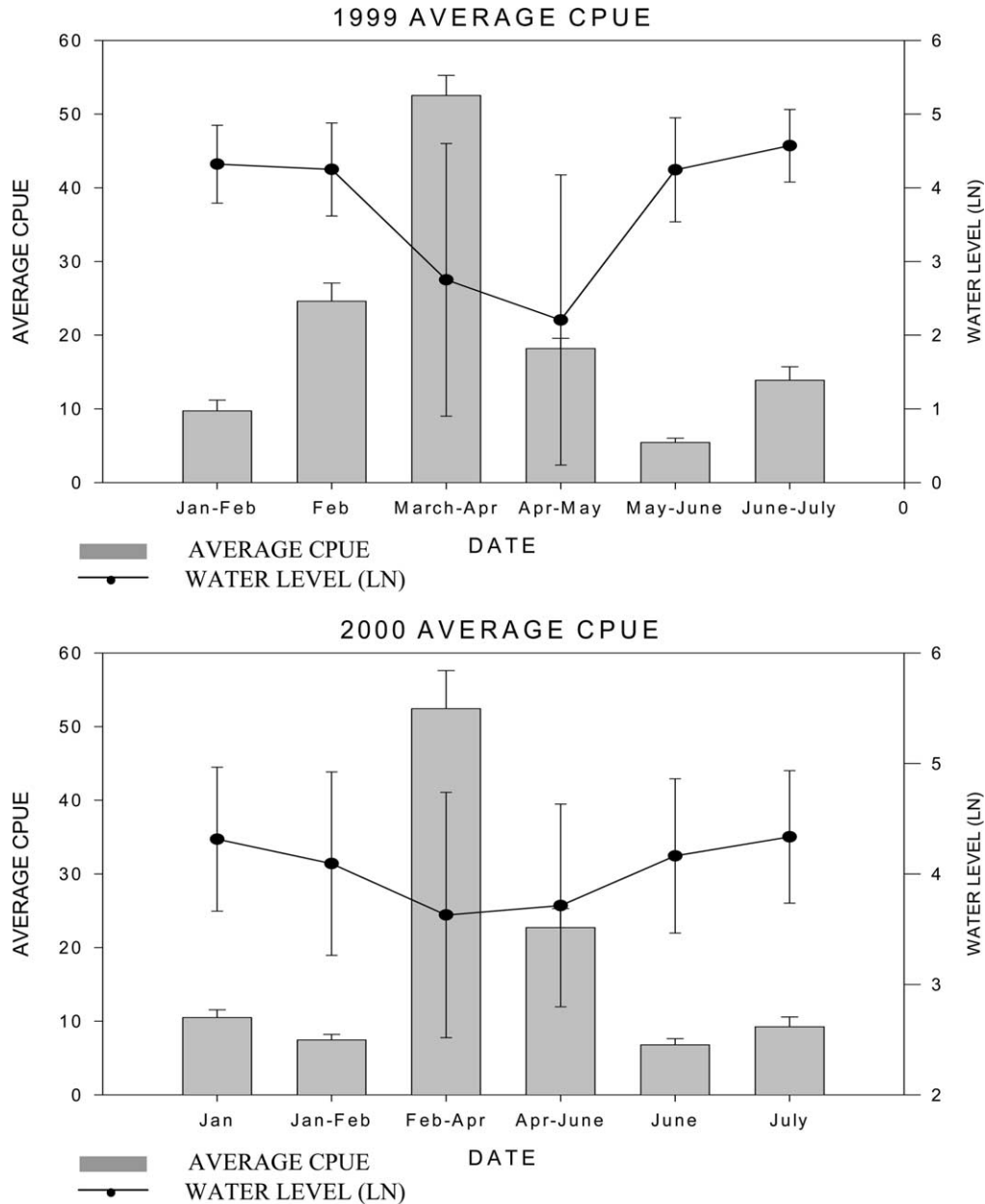


Fig. 3. The average CPUE of all fish species at all sites for 1999 and 2000 plotted by time interval. Natural-log values of water level (cm + 1) are also indicated.

bluefin killifish, and black acara comprised over 75% of the specimens collected in both years (Table 3). There was also an indication of regional differences in relative abundance. For example, eastern mosquitofish was the dominant species at three of the four regions, yet comprised fewer than 10% of the specimens at WR both years. Black acara was abundant at WR both years. Bluefin killifish represented a greater proportion of specimens collected at three of the sites in 1999 than in 2000 (Table 3). This probably reflects the greater sampling effort outside of the dry-season months in 1999, because this species was not common in holes when isolated from the marsh surface.

Non-native species were common during both years. In the 1999 dry season, they accounted for 50% of the fishes collected at MR and 23% of those at WR. At CR and PAH, we found fewer non-native specimens, accounting for 16 and 3% of fishes trapped, respectively. During 2000, non-native fish accounted for 32% of all fishes collected at WR, and 18% of those at MR, but at CR and PAH, they comprised only 8 and 1% of the fishes, respectively. The patterns of CPUE of introduced fishes were similar in both years.

The average CPUE of fish collected in all solution holes increased from the start to the middle of the dry season, then decreased during the late dry season in

Table 1

Small-sample tests of differences in water quality in solution holes between wet and dry seasons in 1999 and 2000

Parameter	df	t-score	Dry-season	Wet-season
1999 (insufficient data were collected at CR this year)				
<i>MR</i>				
Chlorophyll <i>a</i>	35	6.14*	85.9±55.0	1.1±0.2
Ammonium	20	48.8*	910.6±199.9	1.4±0.8
Temperature	20	0.05	20.8±0.8	20.8±5.0
Dissolved O ₂	22	4.35*	1.3±1.3	3.8±1.4
pH	10	4.27*	7.4±0.2	8.2±0.3
<i>WR</i>				
Chlorophyll <i>a</i>	8	1.58	5.1±2.8	1.6±0.5
Ammonium	8	2.23	60.4±52.5	0.6±0.2
Temperature	18	0.06	22.5±0.7	22.4±5.7
Dissolved O ₂	31	0.99	1.0±1.0	2.9±3.0
pH	29	2.40	7.1±0.1	7.7±0.5
<i>PAH</i>				
Chlorophyll <i>a</i>	33	4.39*	3.8±3.2	0.7±0.2
Ammonium	32	4.20*	406.9±0.7	0.7±0.3
Temperature	32	2.30	22.0±1.5	23.9±3.2
Dissolved O ₂	31	6.88*	2.1±1.8	3.8±1.8
pH	29	29.02*	7.4±0.1	8.5±0.1
2000				
<i>CR</i>				
Chlorophyll <i>a</i>	80	2.38	4.1±6.3	0.8±0.7
Ammonium	80	1.95	82.2±189.4	3.2±5.1
Temperature	53	22.30*	21.4±0.8	28.3±1.5
Dissolved O ₂	53	4.16*	1.9±0.7	3.0±1.3
pH	53	6.36*	7.4±0.2	7.7±0.3
<i>MR</i>				
Chlorophyll <i>a</i>	19	3.76*	18.4±15.2	1.0±0.2
Ammonium	19	3.30*	455.3±457.9	0.7±0.2
Temperature	18	16.40*	20.6±1.0	27.0±0.8
Dissolved O ₂	18	4.74*	1.0±0.8	2.5±0.6
pH	18	7.67*	7.3±0.1	7.6±0.1
<i>WR</i>				
Chlorophyll <i>a</i>	28	0.59	3.0±4.7	2.2±1.7
Ammonium	30	0.83	67.6±250.2	7.2±8.9
Temperature	23	6.81*	21.9±1.3	25.1±0.9
Dissolved O ₂	23	9.82*	0.9±1.1	4.4±5.8
pH	23	6.70*	7.2±0.1	7.5±0.1
<i>PAH</i>				
Chlorophyll <i>a</i>	32	2.35	2.9±2.4	1.2±0.8
Ammonium	32	4.20*	82.2±129.2	1.3±0.9
Temperature	27	10.45*	21.5±1.3	26.5±0.5
Dissolved O ₂	27	4.15*	1.4±0.7	2.4±0.7
pH	27	1.88	7.5±0.1	7.6±0.1

Means and 95% confidence intervals are reported; asterisks indicate $P < 0.006$, which is indicative of statistical significance with correction for multiple testing (nominal $P = 0.05/8$ tests = 0.006). Seasons: 1999, dry: 20 January–20 April; wet: 4 July–17 December; 2000, dry: 24 January–12 April; wet: 8 June–15 June. Units listed on Table 2.

Table 2

Results from PCA of environmental variables reported separately by year

Variables	Axis 1 <i>r</i>	Axis 2 <i>r</i>	Axis 3 <i>r</i>
<i>1999 N = 27</i>			
Average water depth (cm)	−0.394	0.799	−0.029
Complexity (cm)	0.129	0.700	0.564
Vegetative cover (%)	0.163	−0.596	0.260
Average substrate depth (cm)	−0.159	−0.296	0.430
Average depth from ground surface to substrate	0.017	0.839	0.416
Volume (cm ³)	0.194	0.463	−0.575
Chlorophyll <i>a</i> (ug/l)	0.444	0.280	−0.707
Ammonium, NH ₄ (uM)	0.679	0.011	−0.464
Water temperature (C°)	−0.863	0.026	−0.095
Dissolved oxygen (mg/l)	−0.897	−0.084	−0.221
PH	−0.853	−0.184	−0.292
Specific conductivity (uS/cm ²)	0.786	−0.219	0.183
Variance explained (%)	31.8	22.2	16.4
<i>2000 N = 33</i>			
Ave. water depth (cm)	0.351	0.721	−0.38
Complexity (cm)	0.311	−0.422	0.285
Vegetative cover (%)	−0.646	0.365	0.115
Ave. substrate depth (cm)	0.303	−0.303	−0.396
Ave. depth from ground surface to substrate	0.212	0.679	−0.573
Volume (cm ³)	−0.637	0.483	0.005
Chlorophyll <i>a</i> (ug/l)	−0.818	−0.059	−0.035
Ammonium, NH ₄ (uM)	−0.820	−0.053	−0.084
Water temperature (C°)	0.334	0.631	0.429
Dissolved oxygen (mg/l)	0.313	0.043	0.583
PH	0.086	0.459	0.705
Specific conductivity (uS/cm ²)	−0.486	−0.029	0.247
Variance explained (%)	24.8	18.6	15.1

N indicates the number of solution holes in each sample. Solution-hole volume was measured as the long axis × short axis × average depth.

both 1999 and 2000 (Fig. 3). During 1999, the CPUE of all species increased early in the dry season (February – March), then declined as the dry season progressed (April–May), increasing again in late dry season. In 2000, CPUE again increased both early in the early dry season (Feb–Mar) and early in the wet season (June–July) (Fig. 3). In 1999, the CPUE of eight species displayed significant temporal variation over the course of the dry season (eastern mosquitofish, bluefin killifish, flagfish, sailfin molly, sunfish spp., golden topminnow, black acara, and yellow bullhead). The CPUE of only four species varied over the same season in 2000 (eastern mosquitofish, bluefin killifish, black acara, and yellow bullhead). In 1999, contrasts of CPUE between adjacent time intervals indicated that eastern mosquitofish, sailfin molly, golden topminnow, and black acara increased in abundance early in the dry season; CPUE of most of these declined as the dry season progressed. Bluefin killifish displayed a marked increase in CPUE in

Table 3

Number of specimens and frequency (%) of each species collected from solution holes in the 1999 and 2000 sampling seasons

Species common name	Yr	CR	PAH	MR	WR	Total
Esocidae						
<i>Esox niger</i>	99	1 (0.07)	0	0	0	1 (0.04)
Chain pickerel	00	0	0	0	0	0
Catostomidae						
<i>Erimyzon sucetta</i>	99	0	2 (0.2)	0	0	2 (0.08)
Lake chubsucker	00	0	0	0	1 (1.2)	1 (0.1)
Ictaluridae						
<i>Ameiurus natalis</i>	99	317 (24.3)	42 (3.8)	14 (8.4)	4 (4.6)	377 (14.2)
Yellow bullhead	00	116 (37.7)	3 (1.2)	22 (19.5)	13 (15.5)	154 (20.1)
<i>Noturus gyrinus</i>	99	0	3 (0.3)	1 (0.6)	0	4 (0.2)
Tadpole madtom	00	0	0	0	0	0
Clariidae*						
<i>Clarias batrachus</i> *	99	3 (0.2)	0	7 (4.2)	1 (1.1)	11 (0.4)
Walking catfish	00	0	1 (0.4)	0	1 (1.2)	2 (0.3)
Cyprinodontidae						
<i>Jordanella floridae</i>	99	18 (1.4)	234 (21.2)	11 (6.6)	7 (8.0)	270 (10.2)
Flagfish	00	6 (2.0)	51 (19.5)	5 (4.4)	9 (10.7)	71 (9.3)
Fundulidae						
<i>Fundulus chrysotus</i>	99	24 (1.9)	145 (13.1)	0	0	169 (6.4)
Golden topminnow	00	0	16 (6.1)	7 (6.2)	1 (1.2)	24 (3.1)
<i>Fundulus confluentus</i>	99	18 (1.4)	137 (12.4)	1 (0.6)	0	156 (5.9)
Marsh killifish	00	18 (5.8)	72 (27.6)	15 (13.3)	22 (26.2)	127 (16.6)
<i>Lucania goodei</i>	99	64 (5.0)	176 (15.9)	11 (6.6)	33 (37.5)	284 (10.7)
Bluefin killifish	00	44 (14.3)	9 (3.5)	7 (6.2)	0	60 (7.8)
Poeciliidae						
<i>Belonesox belizanus</i> *	99	53 (4.0)	14 (1.3)	12 (7.2)	2 (2.3)	81 (3.1)
Pike killifish	00	0	0	6 (5.3)	0	6 (0.8)
<i>Gambusia holbrooki</i>	99	455 (35)	192 (17.4)	13 (7.8)	1 (1.1)	661 (24.9)
Eastern mosquitofish	00	66 (21.5)	101 (38.7)	20 (17.7)	7 (8.3)	194 (25.4)
<i>Heterandria formosa</i>	99	29 (2.2)	9 (0.8)	2 (1.2)	0	40 (1.5)
Least killifish	00	25 (8.1)	0	2 (1.8)	1 (1.2)	28 (3.7)
<i>Poecilia latipinna</i>	99	15 (1.2)	10 (0.9)	3 (1.8)	13 (14.8)	41 (1.5)
Sailfin molly	00	1 (0.3)	4 (1.5)	0	0	5 (0.7)
Centrarchidae						
<i>Elassoma evergladei</i>	99	30 (2.3)	5 (0.5)	0	0	35 (1.3)
Everglades pygmy sunfish	00	0	0	0	0	0
<i>Lepomis spp</i>	99	114 (8.8)	121 (11.0)	28 (16.8)	10 (11.4)	273 (10.3)
Sunfish	00	6 (2.0)	2 (0.8)	16 (14.2)	3 (3.6)	27 (3.5)
Cichlidae*						
<i>Cichlasoma bimaculatum</i> *	99	126 (9.7)	0	57 (34.1)	12 (13.6)	195 (7.3)
Black acara	00	21 (6.8)	2 (0.8)	11 (9.7)	25 (29.8)	59 (7.7)
<i>Cichlasoma urophthalmus</i> *	99	33 (2.5)	14 (1.3)	7 (4.2)	5 (5.7)	59 (2.2)
Mayan cichlid	00	4 (1.3)	0	3 (2.7)	1 (1.2)	8 (1.1)
Total fish						
	99	1300	1,104	167	88	2659
	00	307	261	113	84	765
Number of samples						
	99	277	146	66	62	551
	00	73	46	29	43	191

The row total indicates the total number of each species for the study and its relative frequency, indicated in parentheses. The number of solution holes and sampling effort per hole varied among study regions and between years. Asterisks denote non-native species.

the late dry season/early wet season (May – June) after early rains flooded the marsh, reconnecting the solution holes to surface waters. During 2000, eastern mosquitofish, black acara, and yellow bullhead CPUE increased in mid-dry season (February – March), later declining; bluefin killifish displayed a similar late dry-season increase in abundance (see Kobza 2001 for details of statistical results).

The recapture rates of fish in solution holes differed between 1999 and 2000 sampling (proportion of fish recaptured: $\bar{X}_{1999}=0.037$, $\bar{X}_{2000}=0.011$, $N=697$, $Z=3.26$, $P<0.002$). In both years and at all study sites, the percentage of fish recaptured increased from early dry season (when water level receded enough to isolate solution holes from the marsh surface) to a maximum late in the dry season. For example, the percentage of fish recaptured at CR in 1999 ranged from 5% early in the season to 100% by the time the holes dried out (see Kobza, 2001 for more details on the patterns of recapture).

3.2.2. Throw traps on the marsh surface

Early in the dry season, fewer species of fish were collected by throw trap from the marsh surface during the wet season than by minnow traps in adjacent solution holes (Table 4). In both years, the lowest percent similarity between the surface collections and solution-hole collections was at WR. Species identities matched well between the marsh surface and solution holes in 1999, and relatively rare species were collected in only one area. That year, a small number of Everglades pygmy sunfish (*Elassoma evergladei*) and juvenile sunfishes (*Lepomis spp.*) were taken in solution-hole samples but not marsh samples. In 2000, small numbers of sailfin molly, brook silverside (*Labidesthes sicculus*), and sheepshead minnow (*Cyprinodon variegatus*) were collected in the marsh samples but not solution holes, whereas juvenile sunfish, yellow bullhead, black acara, and bluefin killifish were collected in holes but not on the marsh. Overall fish abundance was estimated to be greater in 1999 than in 2000 for both methods.

Table 4

Species richness and species in common from samples collected in wet-season, open-marsh samples and early dry-season solution-hole samples

	Year	CR	MR	WR	PAH
<i>Species richness</i>					
Open water	1999	10	9	4	8
	2000	6	10	2	8
Solution holes	1999	15	13	10	14
	2000	10	11	11	10
Species in common	1999	10/15, 66%	8/13, 62%	3/10, 30%	8/14, 57%
	2000	4/10, 40%	10/11, 91%	2/11, 18%	7/10, 70%

Species in common reported as open-marsh samples/solution-hole samples.

3.3. Assemblage structure

3.3.1. Discrimination of fish assemblage structure

Null-model analysis indicated that non-random patterns of species co-occurrence emerged in individual solution holes as the dry season progressed. In both years, only the final dry-season interval displayed a significant non-random pattern of species co-occurrence (1999: effect size = 2.088, $P=0.014$; 2000: effect size = 2.329, $P=0.005$). We used cluster analysis to illustrate which species yielded the non-random patterns observed in that time interval. Distance measures from the cluster analysis indicated three groups in 1999 and four in 2000 (Fig. 4). In 1999, the three groups were characterized by eastern mosquitofish, yellow bullhead, and black acara (group 1); flagfish, sunfishes, marsh killifish, sailfin molly, Mayan cichlid, and pike killifish (group 2); and golden topminnows (group 3). These same species yielded four groups in 2000: eastern mosquitofish, yellow bullhead, and black acara (group 1); flagfish, golden topminnow, and marsh killifish (group 2); sailfin molly, pike killifish, and Mayan cichlid (group 3); and sunfish spp (group 4). Eastern mosquitofish, yellow bullhead, and black acara clustered closely in both years (Fig. 4).

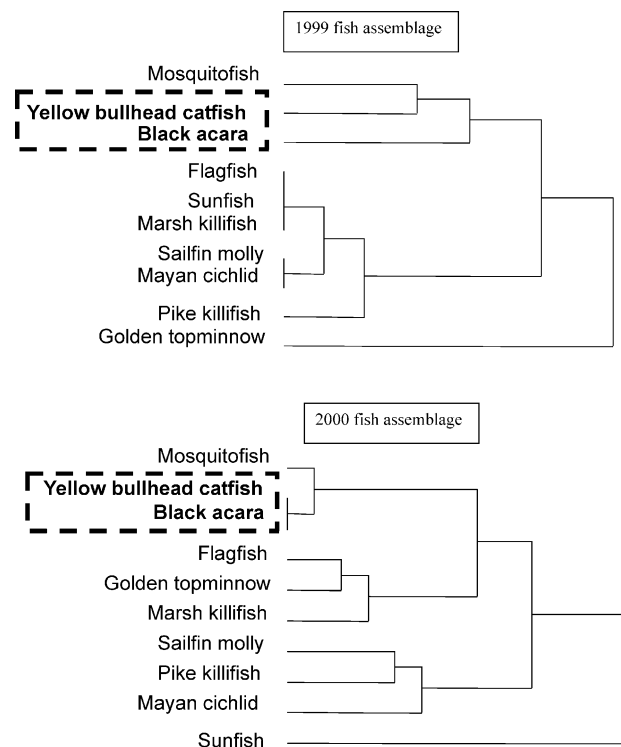


Fig. 4. Cluster analysis dendrogram of late dry-season fish communities. These analyses are based on presence-absence data of species within solution holes.

3.3.2. Environmental correlates with fish assemblage structure

Mantel analysis indicated that patterns of fish relative abundance were correlated with environmental parameters in late dry-season solution holes. Only PCA Axis 1 was correlated with the fish-similarity matrix in 1999 (Axis 1: standardized Mantel statistic $r=0.293$, $P=0.001$; Axis 2: standardized Mantel statistic $r=0.020$, $P=0.393$; Axis 3: standardized Mantel statistic $r=-0.033$, $P=0.414$). In 2000, Axis 2 and Axis 3 were significantly correlated with the fish-similarity matrix (Axis 1: standardized Mantel statistic $r=-0.48$, $P=0.210$; Axis 2: standardized Mantel statistic $r=0.148$, $P=0.019$; Axis 3: standardized Mantel statistic $r=0.141$, $P=0.014$).

NMDS illustrated the data in two dimensions in both 1999 and 2000. These two axes explained over 70% of the variation in the fish-similarity matrices in both years (1999: Axis 1 $R^2=0.356$, Axis 2 $R^2=0.437$; 2000: Axis 1 $R^2=0.522$, Axis 2 $R^2=0.273$). Axis 1 from the 1999 PCA analyses and Axis 3 from the 2000 PCA were both positively correlated with dissolved oxygen and pH, whereas Axis 2 in 2000 was positively correlated with solution-hole depth and temperature parameters. We obtained similar correlations for the environmental patterns in 2000 data with both Axis 2 and 3, so report only the results from Axis 3. The 1999 NMDS plot indicated that the solution-hole fish communities dominated by bluefin killifish grouped separately from those dominated by black acara, with those having a high relative abundance of eastern mosquitofish falling between (Fig. 5A). All solution-hole samples dominated by bluefin killifish were collected in early June, after the holes had been re-flooded by surface waters. Holes with a high relative abundance of yellow bullhead were intermediate, but overlapped more with those holding black acara than those holding bluefin killifish (not shown). These patterns represent an environmental gradient along Axis 1; black acara were found in holes with relatively high ammonium, and conductivity, and relatively low temperature, dissolved oxygen, and pH (correlation of NMDS Axis 1 with PCA Axis 1: $r=0.496$).

The 2000 NMDS plot revealed a separation of solution-hole fish communities similar to the previous year; black acara and yellow bullhead were the dominant species in communities that grouped separately from those dominated by bluefin killifish and eastern mosquitofish (Fig. 5B). The lone sample dominated by bluefin killifish was collected in late April, again after a rain event that permitted recolonization by fishes. Also similar to 1999, separation on Axis 1 maximized an environmental gradient characterized by black acara and yellow bullhead in holes with relatively low dissolved oxygen and pH; in contrast,

bluefin killifish and eastern mosquitofish were most common in holes with high oxygen and pH values (correlation of NMDS Axis 1 with PCA Axis 3: $r=0.549$).

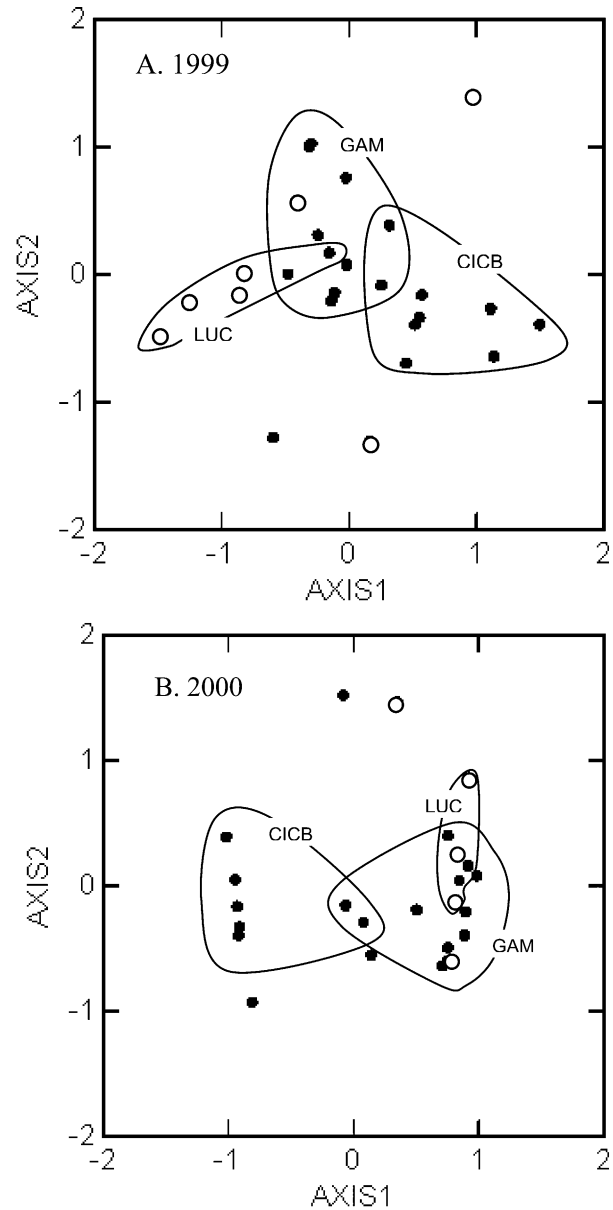


Fig. 5. NMDS ordinations illustrating patterns of similarity in solution-hole communities. Samples are grouped around three species assemblages highly correlated with the ordination axes and that indicated the general community relationships each year (GAM: eastern mosquitofish; LUC: bluefin killifish; CICB: black acara). Open circles indicate samples collected in late dry season, after an isolated rainfall event flooded the marsh, reconnecting the solution holes to the marsh surface. (A) Results for 1999. The ordination was rotated to maximize variation in PCA Axis 1, which was correlated with several water quality parameters (pH, ammonium, dissolved oxygen, and specific conductance). (B) Results for 2000. The ordination was rotated to maximize variation in PCA Axis 3, which was correlated with two water quality parameters (pH and dissolved oxygen).

4. Discussion

4.1. Marsh dry down and fish-community structure

Annually, receding surface waters force fishes inhabiting the karst wetlands of the Florida Everglades into solution holes that serve as aquatic refuges. We found that early in the dry season, soon after the holes became isolated from the marsh surface, the composition of the fish communities did not differ from random. However, apparent structure emerged in the late dry season, presumably from differential mortality, because our solution holes appeared to be closed systems (see below). Many studies have examined how stochastic processes act to structure fish communities (Grossman et al., 1982; Matthews, 1982; Schlosser, 1982; Kodric-Brown and Brown, 1993). Such processes may act as “filters” through which the members of a fish assemblage must pass (Tonn, 1990). Within a solution-hole refuge, the quality of the environment that a fish colonizes is influenced by the size of the solution-hole habitat (which remains relatively constant year to year), the complexity of the habitat (e.g. allochthonous debris, aquatic vegetation, and outcroppings) that may provide protection from predators or affect water quality, and the composition and density of fishes and invertebrates that share this refuge.

Our survey of solution holes indicated that the frequency of aquatic refuges deep enough to remain inundated through the entire dry season is low because of regional drainage effects on the Rocky Glades. Further, the pattern of increasing fish recaptures through the dry season, culminating in high recapture rates, suggests that the holes we studied were not connected to larger subterranean refuges by way of unseen crevices or channels in the limestone. However, further work is needed to evaluate the existence of such caverns because of their potential importance as refuge habitat (Loftus et al., 1992). At present, it appears groundwater levels lower than 0.5 m in our study areas lead to substantial mortality of fish and marked loss of productivity by aquatic animals (Acosta and Perry, 2001).

Negative correlations of temperature with both ammonium and chlorophyll *a* in both 1999 and 2000 resulted from the deepest solution holes, which had high concentrations of nutrients. As indicated by NMDS analysis, many native fishes occurred in solution holes with higher temperatures and lower chlorophyll *a* concentration, relative to holes where black acara were collected. This late dry-season pattern was probably related to the distribution of small-bodied (<30 mm) native species, most common in relatively shallow holes (<50 cm) possibly because of predation in deeper holes. Water temperatures in shallow holes were higher than in deeper ones. Chlorophyll *a* concentration was generally related to the amount of nutrients in the water, which

was often greater in large solution holes that held relatively large fish (yellow bullheads and black acara). Chlorophyll *a* and ammonium typically lagged behind decreasing dissolved oxygen, which in turn led to fish mortality events. The shallow refuges (<50 cm) generally did not experience the density of fishes that caused chlorophyll *a* increase.

Fish-community composition and density in holes at the start of the dry season may be important in determining dry-season habitat quality. The accumulation of fishes into refuges was a strong determinant of which individuals persist through the dry season. Once isolated, the fishes inhabiting solution holes compete for food and space, and prey on each other. We observed several instances of mass mortality in solution holes that initially had a large number of fishes. Generally, there was a sequence related to colonization: an increase in BOD leading to hypoxia, nutrient buildup, algal bloom, anoxia, fish mortality, and subsequent re-establishment of good water quality prior to rising water levels. However, in solution holes with low initial numbers of fish, this sequence did not occur and mass mortality events were not observed.

4.2. Non-native fishes

The Rocky Glades had a substantially higher relative abundance of non-native fishes than most other natural Everglades habitats surveyed by Trexler et al. (2001). We found that non-native fishes accounted for up to 50% of the total fishes caught at WR, while at PAH it was less than 5% of the total. The reasons for the high frequency of non-native fishes in some Rocky Glades locations are unclear, but presumably include a combination of proximity to sources of invasion, susceptibility of the native communities to invasion, and habitat characteristics amenable to the invading taxa. Water enters the Rocky Glades through both groundwater and surface flow from nearby canals that house numerous introduced fishes. New species have recently invaded the area (Kline and Perry, personal communication), suggesting that the availability of invaders is not the factor limiting their success. The high frequency of dry down, leading to high ammonium and low dissolved oxygen, may be stressful for native fishes and provide unique opportunities for invasion of hypoxia-tolerant exotic species.

Our data suggest that introduced fishes, especially black acara, may influence the assemblage of fishes that survive through the dry season in the Rocky Glades, and thus the fishes available locally to recolonize the marsh in the subsequent wet season. NMDS plots illustrated that the distribution of black acara displayed little overlap with the native fish species in both 1999 and 2000. Though not as common, the walking catfish was also present in the same solution holes as black

acara, as was the native yellow bullhead. Most samples in which black acara was relatively abundant were collected in the late dry season, when previously co-occurring small native species were absent. We cannot directly quantify the magnitude of the effect of non-native fishes on the assemblage of native fishes in refuges. However, the decline in small fishes through the dry season when they co-occurred with predatory native and non-native fishes implies that predation affects subsequent recolonization patterns.

We found no evidence that invasion sequence (“priority effects” Robinson and Dickerson, 1987) had an effect on the success of non-native species in these dry-season habitats. While the composition and density of fishes trapped in isolated pools influenced the resultant community, the timing of their arrival appeared inconsequential, probably because the solution holes were open to emigration and recolonization from the marsh surface prior to dry down and isolation. In these communities, interaction within the holes appeared relatively unimportant until the marsh surface dried and all fishes were isolated within the solution hole. Success is probably more contingent upon the environmental conditions of the habitat, and size and feeding habits of co-occurring species, than the invasion sequence (Moyle and Light, 1996).

4.3. Habitat heterogeneity

Habitat complexity and presence of aquatic vegetation probably influence the survivorship of fishes in refuges. We measured habitat complexity as habitat roughness or frequency of crevice microhabitats formed by the uneven dissolution of limestone rock. Generally, highly complex solution holes were shallow and wider than deep. Deep solution holes were generally simple in shape and had less surface area, while shallow holes had greater surface area and supported greater densities of emergent aquatic macrophytes such as sawgrass (*Cladium jamaicense*), arrowhead (*Sagittaria* spp.), and spikerush (*Eleocharis* spp.). The presence of macrophytes in relatively shallow holes may explain why hole complexity was positively correlated with dissolved oxygen in 2000. Deep holes may be relatively low-quality refuges for many native fishes, both in water quality and risk of predation.

Heterogeneity in refuge quality could influence the species richness of a regional community if refuges serve as a source of colonists for the surrounding marsh after wet season reflooding. We found that refuge frequency and quality varied among regions. Further, we found a corresponding community change among these regions. For example, PAH had the smallest number of solution holes, which were mainly shallow (<50 cm), but experienced the longest duration of flooding. That region typically supported larger populations of native

than non-native species in solution holes. In contrast, WR had relatively more deep refuges (>50 cm), but experienced the shortest duration of surface flooding. Many of the solution-hole samples in that region displayed the worst water quality. The refuges in WR generally contained a higher density of non-native than native fishes. CR had the largest number of solution holes with the largest range of refuge quality. There we observed more cases of native and non-native fishes co-occurring. Time was an important component in determining the distribution of species among solution-hole samples. For instance, the black acara was typically the dominant species in samples collected in the middle to late dry season, while other species tended to display greater relative abundance earlier in the dry season and in the wet season.

4.4. Implications for management

Water managers control the magnitude and timing of drying in the Rocky Glades. Severity of the annual dry-down event varies widely as a function of rainfall, but is also highly affected by management priorities. Our data, and previous work (Loftus et al., 1992), indicate that these decisions have major effects on the quality and abundance of aquatic refuges for fishes. This, in turn, may have major impacts on the biomass and composition of fish communities that inhabit the region, possibly even favoring non-native species. However, the larger significance of solution-hole refuges depends on whether they are, in fact, a major reservoir of post dry-season colonists for the local marshes and/or nearby areas of the Everglades. Samples of fishes collected in the surface marsh immediately following reflooding are not dominated by non-native fishes, as may be expected by our data from solution holes. This raises the possibility that cryptic or hidden refuges remain to be found in the region or that fishes migrate rapidly into the area from distant refuges upon reflooding. Recent data suggest that both of these mechanisms operate at our PAH and MR sites, but similar data have not been obtained elsewhere. Our data suggest, in fact, that the ecology at PAH and MR may differ from WR or CR. Further study will be needed to evaluate these alternatives.

There is evidence that annual maximum and minimum water levels were higher in the Rocky Glades prior to drainage of the area. Thus, even if solution holes are a sink habitat today, and if wet season colonists arrive from elsewhere, it is likely that they played a greater refuge role in the past. The loss of these refuges has probably had a major impact on the community dynamics of this region of the Everglades, an issue that should be addressed in upcoming plans for the restoration of this threatened habitat (Anonymous, 2000).

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References

- Anonymous. 2000. Comprehensive Everglades Restoration Plan. Master Program Management Plan Final—August 2000. Volume 1. South Florida Water Management District and US Army Corps of Engineers, Available: http://208.60.32.205/pm/mpmp_08182000.htm.
- Acosta, C.A., Perry, S.A., 2001. Impact of hydropattern disturbance on crayfish population dynamics in the seasonal wetlands of Everglades National Park, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11, 45–57.
- Beals, E.W., 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14, 1–55.
- Chen, E., Gerber, J.F., 1990. Climate. In: Myers, R.L., Ewel, J.J. (Eds.), *Ecosystems of Florida*. University of Central Florida Press, Orlando, pp. 11–34.
- Chick, J.H., Jordan, F., Smith, J.P., McIvor, C.C., 1992. A comparison of four enclosure traps and methods used to sample fishes in aquatic macrophytes. *Journal of Freshwater Ecology* 7, 353–361.
- Craighead, F.C., 1971. *The Trees of South Florida*. Univ. of Miami Press, Coral Gables.
- Douglas, M.E., Endler, J.A., 1982. Quantitative matrix comparisons in ecological and evolutionary investigations. *Journal of Theoretical Biology* 9, 777–795.
- Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57–68.
- Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81, 2606–2621.
- Gotelli, N.J., Entsminger, G.L., 2001. Swap and fill algorithms in null model analysis: rethinking the knight's tour. *Oecologia* 129, 281–291.
- Grossman, G.D., Moyle, P.B., Whitake Jr., J.O., 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *American Naturalist* 120, 423–454.
- He, X., Lodge, D.M., 1990. Using minnow traps to estimate fish population size: the importance of spatial distribution and relative species abundance. *Hydrobiologia* 190, 9–14.
- Jackson, D.A., Harvey, H.H., 1997. Qualitative and quantitative sampling of lake fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 2807–2813.
- Jordan, F., Coyne, S., Trexler, J.C., 1997. Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m² throw trap. *Transactions of the American Fisheries Society* 126, 1012–1020.
- Kiesecker, J.M., Blaustein, A.R., Belden, L.K., 2001. Complex causes of amphibian population declines. *Nature* 410, 681–684.
- Kobza, R. M., 2001. Community Structure of Fishes Inhabiting Hydrological Refuges in a Threatened Karstic Habitat. MS thesis, Florida International University, Miami.
- Kodric-Brown, A., Brown, J.H., 1993. Highly structured fish communities in Australian desert springs. *Ecology* 74, 1847–1855.
- Kushlan, J.A., 1981. Sampling characteristics of enclosure fish traps. *Transactions of the American Fisheries Society* 110, 557–562.
- Loftus, W.F., Reid, J.W., 2000. Copepod (Crustacea) emergence from soils from Everglades marshes with different hydroperiods. *Journal of Freshwater Ecology* 15, 515–523.
- Loftus, W.F., Johnson, R.A., Anderson, G.H., 1992. Ecological impacts of the reduction of groundwater levels in short-hydroperiod marshes of the Everglades. In: Stanford, J.A., Simons, J.J. (Eds.), *Proceedings of the First International Conference on Ground Water Ecology*. American Water Resources Association, pp. 199–208.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Cloutm, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689–710.
- Mantel, N., 1967. The detection of disease clustering and generalized regression approach. *Cancer Research* 27, 209–220.
- Matthews, W.J., 1982. Small fish community structure in Ozark streams: structured assembly patterns or random abundance of species? *American Midland Naturalist* 107, 42–54.
- Matthews, W.J., 1998. *Patterns in Freshwater Fish Ecology*. Chapman Hall, New York.
- Moyle, P.B., Light, T., 1996. Fish invasions in California: do abiotic factors determine success? *Ecology* 77, 1666–1670.
- Ostrom, E., Burger, J., Field, C.B., Norgaard, R.B., Policansky, D., 1999. Sustainability—revisiting the commons: local lessons, global challenges. *Science* 284, 278–282.
- Pot, W., Noakes, D.L.G., Ferguson, M.M., Coker, G., 1984. Quantitative sampling of fishes in a simple system: failure of conventional methods. *Hydrobiologia* 114, 249–254.
- Preisser, E.L., Kefer, J.Y., Lawrence, J.D., 2000. Vernal pool conservation in Connecticut: an assessment and recommendations. *Environmental Management* 26, 503–513.
- Robinson, J.E., Dickerson Jr., J.E., 1987. Does invasion sequence affect community structure? *Ecology* 68, 587–595.
- Schlosser, I.J., 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 52, 395–414.
- Snyder, J.R., Herndon, A., Robertson Jr., W.B., 1990. South Florida rocklands. In: Myers, R.L., Ewel, J.J. (Eds.), *Ecosystems of Florida*. University of Central Florida Press, Orlando, pp. 230–277.
- Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. *Oecologia* 85, 74–79.
- Tonn, W.M., 1990. Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society* 119, 337–352.
- Trexler, J.C., Loftus, W.F., Jordan, F., Lorenz, J., Chick, J., Kobza, R.M., 2001. Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views. *Biological Invasions* 2, 265–277.
- US Fish & Wildlife Service, 1999. *South Florida Multi-species Recovery Plan*. Southeast Region, Atlanta.