SEASONAL FISH COMMUNITY VARIATION IN HEADWATER MANGROVE CREEKS IN THE SOUTHWESTERN EVERGLADES: AN EXAMINATION OF THEIR ROLE AS DRY-DOWN REFUGES

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ABSTRACT

The connectivity between the fish community of estuarine mangroves and that of freshwater habitats upstream remains poorly understood. In the Florida Everglades, mangrove-lined creeks link freshwater marshes to estuarine habitats downstream and may act as dry-season refuges for freshwater fishes. We examined seasonal dynamics in the fish community of ecotonal creeks in the southwestern region of Everglades National Park, specifically Rookery Branch and the North and Watson rivers. Twelve low-order creeks were sampled via electrofishing, gill nets, and minnow traps during the wet season, transition period, and dry season in 2004–2005. Catches were greater in Rookery Branch than in the North and Watson rivers, particularly during the transition period. Community composition varied seasonally in Rookery Branch, and to a greater extent for the larger species, reflecting a pulse of freshwater taxa into creeks as marshes upstream dried periodically. The pulse was short-lived, a later sample showed substantial decreases in freshwater fish numbers. No evidence of a similar influx was seen in the North and Watson rivers, which drain shorter hydroperiod marshes and exhibit higher salinities. These results suggest that headwater creeks can serve as important dry-season refugia. Increased freshwater flow resulting from Everglades restoration may enhance this connectivity.

Biological connectivity between fish communities of mangrove regions and those of other marine and coastal habitats (e.g., coral reefs, seagrass beds, sand, and mudflats), although deserving further attention, has been explored in a number of recent studies (see reviews by Beck et al., 2001, Gillanders et al., 2003; Sheridan and Hays, 2003; Mason et al., 2005; Sheaves, 2005; Faunce and Serafy, 2006). The presence of mangroves along coastal areas enhances the richness, abundance, and biomass of fishes in marine habitats (e.g., coral reefs; Nagelkerken et al., 2002; Dorenbosch et al., 2004; Mumby et al., 2004). Mangroves provide nursery grounds for larval and juvenile marine fishes and crustaceans (Robertson and Duke, 1987; Laegdsgaard and Johnson, 1995; Nagelkerken et al., 2000) due to their high prey abundance (Robertson et al., 1988; Sheridan, 1997) and their role as a predation refuge (Primavera, 1998; Acosta and Butler, 1999). Juvenile survival may be enhanced in shallow mangrove habitats where structural complexity, shading, and turbidity are relatively high (Laegdsgaard and Johnson, 2001; Ellis and Bell, 2004). Mobile marine fishes use mangrove habitats transiently as foraging grounds (Blaber and Milton, 1990; Chong et al., 1990), reproductive grounds (Chaves and Bouchereau, 2000), or move in when environmental conditions in diel or seasonal cycles are favorable (e.g., at high tide or with increased salinity or temperature; Ley et al., 1999; Barletta et al., 2005).

By comparison, the connectivity between fish communities in mangrove regions and upstream freshwater habitats has received much less attention. A reason for this is that in many mangrove systems, the freshwater influence is small, and the contribution of freshwater fishes to the estuarine community is limited (Pinto and Punchihewa, 1996; Laroche et al., 1997; Kuo et al., 1999; Nordlie, 2003; Hindell and Jenkins,

2004). In the Greater Everglades Ecosystem, shallow vegetated freshwater marshes transition into an extensive region of tidal mangrove forests (up to 15 km in width, over 60,000 ha of mangroves), which dominates the landscape along the southwest Florida coast (Smith et al., 1994). At the ecotone, mangrove-lined creeks drain upland marshes into a network of interconnecting estuarine rivers, bays, and mangrove forests. The ecosystem is rainfall-driven, marked by strong seasonality (high rainfall in the summer and fall, low in the winter and spring), which greatly influences the spatial extent of inundation of freshwater marshes, as well as the salinity regime of this broad estuarine region (Gunderson and Loftus, 1993).

As in other estuarine systems, salinity levels play an important role in structuring the plant and animal communities of the Greater Everglades Ecosystem (Montague and Ley, 1993; Serafy et al., 1997; Ley et al., 1999; Lorenz, 1999; Faunce et al., 2004). Historically, large volumes of freshwater reached estuarine areas, particularly during the wet season (Fennema et al., 1994). Today, drainage, channelization, and impoundment of marshes have greatly diminished the freshwater inflow into estuarine areas, resulting in substantially higher and more variable salinity regimes (Smith et al., 1989; Montague and Ley, 1993; Light and Dineen, 1994; McIvor et al., 1994). Fish community response to the natural and the anthropogenically-derived variation in freshwater inflow and salinity has been relatively well-studied in the southern and eastern parts of the ecosystem, namely, Florida Bay and Biscayne Bay (Thayer et al., 1987; Montague and Ley, 1993; Serafy et al., 1997; Ley et al., 1999; Lorenz, 1999; Serafy et al., 2003; Faunce et al., 2004; Lorenz and Serafy, 2006); but remains understudied along the southwest region (but see Green et al., 2006), where the mangrove zone is substantially more extensive than in the southern and eastern parts (Smith et al., 1994). Mangrove creeks along this area also drain generally longer hydroperiod marshes than the southern and eastern regions (Fenema et al., 1994). These marshes (Shark Slough) support more diverse and abundant fish assemblages than southern marshes (Taylor Slough) (Trexler et al., 2001; Chick et al., 2004; Green et al., 2006); thus high connectivity between the mangrove and freshwater fish communities may be expected.

In this study, we examined variation in the fish community of headwater mangrove creeks in response to seasonal fluctuations in freshwater flow and salinity in the southwestern region of Everglades National Park (ENP). In particular, we explored the role of low-order, ecotonal mangrove creeks as dry-season refuges for freshwater fishes. As marsh water levels drop, fishes are forced into deeper habitats such as alligator holes, solution holes, canals (Kushlan, 1974; Nelson and Loftus, 1996; Chick et al., 2004; Kobza et al., 2004; Rehage and Trexler, 2006), and presumably headwater creeks. We sampled the fish community in the uppermost stretches of creeks, where habitat may be most suitable for freshwater species because of proximity to marshes and low salinity regimes. A secondary goal of this study was to compare sampling efficiency among gears. Sampling with electrofishing and gill nets targeted large fishes, whereas minnow traps targeted small fishes. Sampling focused on two regions: Rookery Branch (RB) and the North and Watson rivers (NW) (Fig. 1). Headwater creeks in the RB region link the main freshwater drainage of the southern Everglades (Shark Slough) to Tarpon Bay, and the Shark and Harney rivers. Creeks in the NW area are headwaters of the North and Watson rivers which flow into Whitewater Bay. In neither system have the fish communities in the oligohaline reaches received enough attention to describe their seasonal and long-term dynamics beyond surveys

that provided inventory data (Tabb and Manning, 1961; Odum, 1971; Loftus and Kushlan, 1987), despite their historical importance as a prey source for wading birds (Ogden, 1994) and their key role in the mangrove food web (Odum, 1971).

Methods

Site Description.—We sampled the large and small fish community in the oligohaline to mesohaline headwater reaches of six creeks in the RB region and six creeks in the NW region (Fig. 1). RB sites included four creeks in the main stem of Rookery Branch, as well as Squawk and Otter creeks (RB7 and RB12, respectively). NW sites were located along three Watson River creeks and three North River creeks. Creeks in NW drain shorter hydroperiod marshes than RB creeks. By hydroperiod, we refer to the number of days the marsh is flooded in a yearly cycle. Marshes are typically considered dry if water levels drop below 5 cm, at which depth little standing water remains (Loftus and Eklund, 1994). According to data from hydrologic stations P35 and P38 (Fig. 1), over the past 20-yr period (1986–2006), the hydroperiod averages 332 d of flooding (± 8.3 d) in marshes upstream of RB creeks, and 305 d (± 13.5 d) in marshes upstream of NW creeks. Nutrient concentrations are similar between regions: relatively high nitrogen (approximately 1 mg L^{-1}) and low phosphorus concentrations (below 0.02 mg L^{-1}) are characteristic of both RB and NW waters (Levesque, 2004).

Sampling Effort.—All sampling was conducted in the main channel of headwater creeks and in the uppermost boat-accessible 600 m reach of each creek. Sampling included only first and second order creeks (Strahler, 1957). Creek shorelines were vegetated by riverine mangrove forests dominated by red mangrove, *Rhizophora mangle* Linnaeus, 1753 (Lugo and Snedaker, 1974). Creek depth at sampling locations averaged 1.37 m (± 0.03 m, n = 108); width averaged 10.8 m (± 1.0 m, n = 107). Sampling was conducted during November 2004, February 2005, and April 2005, corresponding to the wet season, the transition between wet and dry
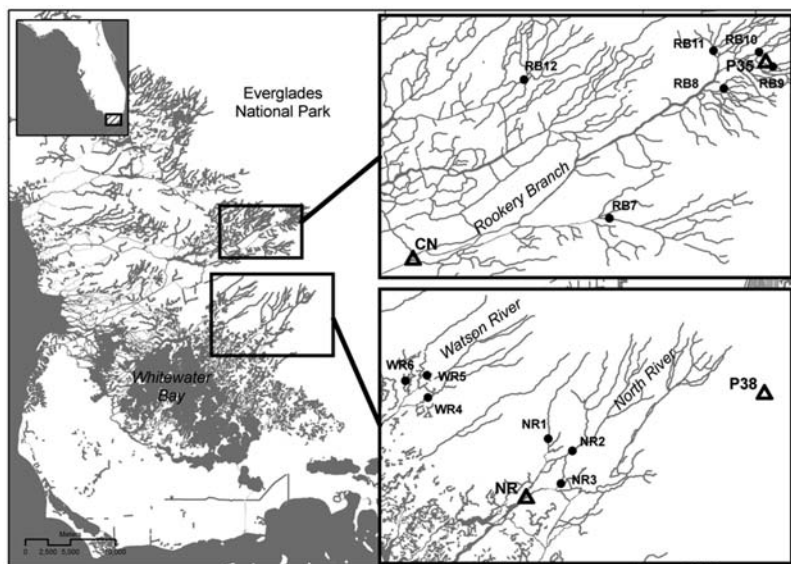

Figure 1. Map of southwestern Everglades National Park showing location of headwater creeks included in this study. Twelve creeks (filled circles) were sampled: six in the North and Watson rivers (NR1-3 and WR4-6) and six in the Rookery Branch region (RB7-12). Location of four reference NPS hydrological stations is indicated by open triangles (see Figure 2 for data from these stations). Distance from sampling sites to stations varies. CN and NR stations are located in creek channels downstream of sites sampled (CN is 4200 m downstream from RB7 and NR is 900 m downstream from NR3). P35 and P38 are located in freshwater marshes upstream of creeks (P35 is 300 m from RB9 and P38 is 6300 m from NR2).
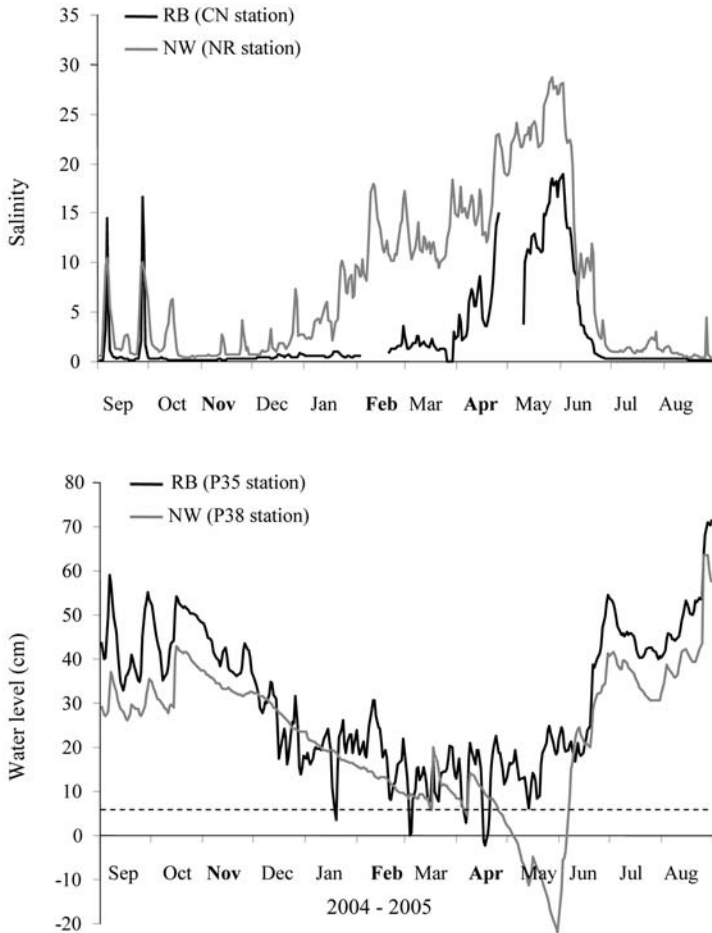
Figure 2. (A) Mean daily salinity and (B) water levels collected by the nearest four NPS monitoring stations to study headwater creeks. See Figure 1 for approximate location of stations in reference to sites. Bold lettering indicates sampling months. Dotted line indicates 5-cm water depth cutoff used for calculation of marsh hydroperiod (see text for explanation).

seasons (hereafter "transition"), and dry season. Daily marsh water level and creek salinity measurements were obtained from the nearest National Park Service (NPS) hydrologic stations (Figs. 1 and 2). While sampling, we measured salinity at creek sites with a YSI° 85 unit (Fig. 3).

Large-fish Sampling.—Large fishes (55–750 mm standard length, SL) were sampled using a boat-mounted electrofishing unit (two-anode, one-cathode Smith-Root° generator-powered pulsator 9.0 unit rated to a maximum salinity of 15). Electrofishing has been shown to be an effective method for sampling larger fishes in other Everglades habitats (Nelson and Loftus, 1996; Chick et al., 1999). At each creek, sampling was conducted in three 5-min (pedal time) bouts (three bouts × six creeks × two regions × three seasons = 108 electrofishing samples). For all bouts, electrofishing power was standardized to 1500 watts according to temperature and salinity conditions (Burkhardt and Gutreuter, 1995). On average, each bout sampled 122.6 m (± 2.8 m, n = 108) of creek shoreline. Bouts were distributed evenly over the 600-m segment of creek, so that each bout was considered an independent sampling unit. For each bout, we randomly selected a creek shoreline and made a single pass with the electrofish-
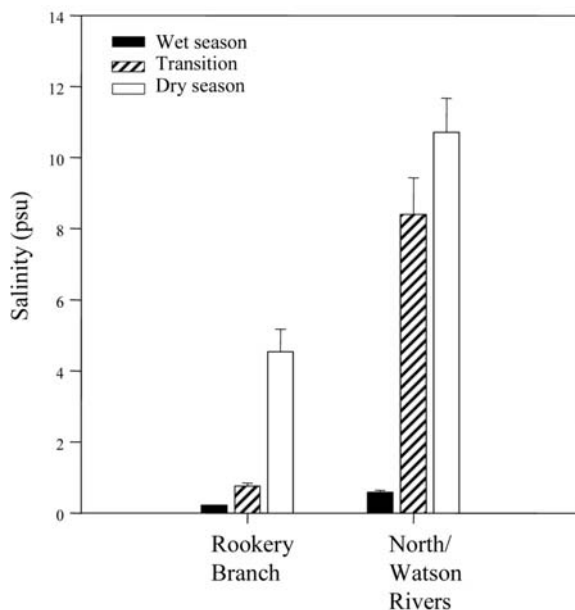
Figure 3. Salinities over the three sampling seasons in the two study regions: the North and Watson rivers and Rookery Branch. Shown are means ± 1 standard error (SE).

ing boat. All fish captured were identified to species, measured to nearest mm SL, weighed to nearest g, and released after full recovery. Non-indigenous species were collected and brought to the laboratory for processing.

We sampled the upper 100-m reaches of each creek with two passive techniques—experimental gill nets and minnow traps. Gill nets are commonly used to monitor fish populations in a wide range of habitats, typically targeting highly mobile and large-bodied species (e.g., Hubert and O'Shea, 1992). Experimental gill nets have panels of several mesh sizes, thus reducing the potential for size or single-species selectivity (Argent and Kimmel, 2005). Nets were 38 m long, with six mesh sizes (25.4, 38.1, 50.8, 63.5, and 76.2 mm). One net was set in the upper 100 m of each creek (one gill net × six creeks × two regions × three seasons = 36 gill net samples). Logistic constrains prevented us from obtaining greater gill-net sample sizes that would be comparable to electrofishing sample sizes. To comply with NPS regulations, gill nets were set mid-channel, parallel to the direction of current flow, and for only 30-min periods. All fishes captured were identified, measured, and weighed in the field, then released.

SMALL-FISH SAMPLING.—Small fishes (< 50 mm SL) were sampled with 3-mm, metal-mesh minnow traps (25.4 mm opening) deployed unbaited, overnight along creek banks. Minnow traps are a commonly used and easily replicable sampling device, but it suffers from several sampling biases (Rozas and Minello, 1997), one of which is trap placement. Minnow traps are typically set on the substrate, where they are unlikely to be encountered by water-column or surface dwellers (Layman and Smith, 2001). In this study, we deployed minnow traps in pairs; one set on the substrate and a second suspended just beneath the water surface, secured to mangrove prop roots. In each creek, we deployed three pairs of traps during the November 2005 sampling event, but increased effort to five pairs for subsequent sampling events (November: six traps × six creeks × two regions = 72 samples, February and April: 10 traps × six creeks × two regions x two seasons = 240 samples; total sample size is 312). Fish captures from minnow traps were preserved in 10% formalin and brought to the laboratory for processing.

STATISTICAL ANALYSES.—We examined variation in the abundance of fishes among regions and creeks and as a function of season with nested, repeated-measures ANOVA or ANCOVA models. Season was the repeated measure in our analyses, and nesting allowed us to

account for spatial variation among regions (RB and NW); creeks were nested within regions. Focal response variables included: CPUE for the large fishes caught in electrofishing (number 5-min^{-1} pedal time) and gill nets (number 30-min^{-1} soak time), CPUE for the small fishes caught in minnow traps (number 24 h^{-1}), and the proportion of CPUE that was freshwater in electrofishing and minnow trap samples (CPUE was too low in gill net samples). Species were classified as either marine, estuarine, or freshwater (Table 1) based upon their habitat occurrence (per Loftus and Kushlan, 1987; Loftus, 2000). Preliminary analyses examined seasonal and spatial variation in the number of species caught in all gears, but results were indistinguishable from analyses of CPUE; and thus, are not presented here.

A two-way ANOVA was used to examine seasonal and spatial variation in salinity levels. Salinity was used as a covariate in analyses of the large fish data; no salinity measurements were made at the time of minnow trap deployment. To better satisfy assumptions of parametric tests, CPUEs were ln (observed value + 1)-transformed and proportions were subject to angular transformations prior to analyses. Post-hoc pairwise comparisons were performed using Tukey-corrected contrasts. If salinity was a significant covariate, simple linear regressions were used to examine the relationship between response variables and salinity. All analyses were performed using Proc Mixed in SAS Version 9.1.3˚.

We used analyses of similarity (ANOSIM) based on Bray-Curtis similarity matrices to test for effects of region, season, and gear (electrofishing vs gill net, and top vs bottom minnow trap) on fish community structure (Clarke and Warwick, 2001). Dissimilarity matrices were constructed based on ln (observed value + 1)-transformed estimates of the relative abundance of all taxa in samples, except for the gear comparison of gillnets and electrofishing, where a presence/absence matrix was used. Analyses included 28 taxa from electrofishing samples, 10 taxa from gill nets, and 22 taxa from minnow traps (Table 1). We followed ANOSIM analyses with percentage of similarity analyses (SIMPER) to determine which taxa contributed most to groupings observed among samples. We constructed non-metric multi-dimensional scaling (NMDS) plots to illustrate dissimilarity among groups. In these plots, the distance between data points is proportional to the degree of similarity between samples. All community structure analyses were conducted using Primer© Version 5.2.9.

Results

Freshwater Flow and Salinity.—Salinity levels near our study sites increased substantially with the yearly onset of the dry season as flows from upstream freshwater marshes decreased (Fig. 2). In 2005, these increases occurred earlier in NW creeks than in RB creeks (Fig. 2A). Maximum salinities were higher in the vicinity of our NW sites than near RB sites (29 and 19, respectively). Hydroperiod was shorter in marshes upstream of NW sites than in those upstream of RB sites. Marshes upstream of NW sites were flooded for 357 d in 2004–2005; whereas marshes upstream of RB creeks were flooded for 324 d (Fig. 2B). Marshes upstream of RB also dried more frequently, but for short periods of time. In contrast, marshes upstream of the North River dried less frequently, but once dry, remained dry for a longer period of time. At our study creeks, salinity varied both among sites and across seasons (ANOVA: significant season by region interaction, $F_{2, 102}$ = 18.6, P = 0.0001; Fig. 3). Salinities were comparable between regions during the wet season sample, but diverged as the dry season progressed, reaching 10 in NW but < 5 in RB (Tukey pairwise comparisons of RB vs NW, P < 0.0001 for both the transition period and dry season).

Estimates of Abundance.—Fish abundance in the oligohaline to mesohaline reaches of mangrove creeks, as estimated by electrofishing, gill net, and minnow trap CPUE, was consistently higher in RB creeks than in NW creeks (Figs. 4,5). CPUE varied as a function of season (significant season by region interactions for all three

Table 1. Number of fishes caught (catch per unit effort, CPUE) by the three sampling methods in headwater creeks in the North and Watson rivers and Rookery Branch over three sampling events (W = wet, T = transition, and D = Dry) in 2004–2005. Species were classified according to their occurrence in FW = freshwater habitats, EF = oligohaline to mesohaline reaches of estuarine habitats, E = mesohaline to polyhaline reaches of estuarine habitats, and M = marine habitats (Loftus and Kushlan, 1987; Loftus, 2000).

| Species | | | CPUE | | | | | | | | |
| Scientific name | Common name | Occurrence | Electrofishing | | | Gill nets | | | Minnow traps | | |
			W	T	D	W	T	D	W	T	D
Lepisosteus platyrhincus DeKay, 1842	Florida gar	FW, EF, E	8	351	246	1	31	23			
Amia calva Linnaeus, 1766	bowfin	FW, EF	1	52	3						
Megalops atlanticus Valenciennes, 1847	Tarpon	EF, E, M					8				
Anguilla rostrata (Lesueur, 1817)	American eel	EF, E	5	6	2						
Notropis petersoni Fowler, 1942	coastal shiner	FW, EF	17	42						468	
Ariopsis felis (Linnaeus, 1766)	hardhead catfish	EF, E, M						1			
Esox americanus Gmelin, 1789	redfin pickerel	FW		2							
Opsanus beta (Goode and Bean, 1880)	gulf toadfish	E, M									2
Mugil cephalus Linnaeus, 1758	striped mullet	EF, E, M	9	56	19						
Menidia beryllina (Cope, 1867)	inland silverside	EF, E	7		2						4
Strongylura notata (Poey, 1860)	Atlantic needlefish	EF, E, M			1						
Strongylura sp.	unidentified needlefish	EF, E, M		2	5						
Fundulus chrysotus (Günther, 1866)	golden topminnow	FW, EF								11	
Lucania goodei Jordan, 1880	bluefin killifish	FW, EF							15	1,016	119
Lucania parva (Baird and Girard, 1855)	rainwater killifish	EF, E, M							13	49	97
Gambusia holbrooki Girard, 1859	eastern mosquitofish	FW, EF, E, M							137	390	357
Heterandria formosa Agassiz, 1855	least killifish	FW, EF							2	25	44
Poecilia latipinna (Lesueur, 1821)	sailfin molly	FW, EF, E, M							21		
Cyprinodon variegatus Lacépède, 1803	sheepshead minnow	FW, EF, E, M									1
Centropomus undecimalis (Bloch, 1792)	Snook	EF, E, M	33	102	14		1	1			
Enneacanthus gloriosus (Holbrook, 1855)	bluespotted sunfish	FW		6					4	102	2
Lepomis gulosus (Cuvier, 1829)	Warmouth	FW, EF							1	1	
Lepomis macrochirus Rafinesque, 1819	Bluegill	FW, EF	1	1							

Table 1. Continued.

| Species			CPUE								
			Electrofishing			Gill nets			Minnow traps		
Scientific name	Common name	Occurrence	W	T	D	W	T	D	W	T	D
Lepomis marginatus (Holbrook, 1855)	dollar sunfish	FW	1	213	2					216	11
Lepomis microlophus (Günther, 1859)	Redear	FW, EF	2	31	1						
Lepomis punctatus (Valenciennes, 1831)	spotted sunfish	FW, EF	5	38	5						
Lepomis sp.	unidentified sunfishes	FW, EF		8							
Micropterus salmoides (Lacépède, 1802)	largemouth bass	FW, EF	7	100	7						
Caranx hippos (Linnaeus, 1766)	crevalle jack	EF, E, M			2		1	1		3	2
Lutjanus griseus (Linnaeus, 1758)	gray snapper	EF, E, M	11				1	1			
Eucinostomus harengulus Goode and Bean, 1879	tidewater mojarra	EF, E, M	113	2	2				2		
Eugerres plumieri (Cuvier, 1830)	striped mojarra	EF, E, M	111	12	11			3	2		
Archosargus probatocephalus (Walbaum, 1792)	Sheepshead	EF, E, M	2			2					
Cynoscion nebulosus (Cuvier, 1830)	spotted seatrout	E, M									1
Sciaenops ocellatus (Linnaeus, 1766)	Redfish	EF, E, M	5	6							
Elassoma evergladei Jordan, 1884	Everglades pygmy sunfish	FW, EF							2		
Cichlasoma urophthalmus (Günther, 1862)[a]	Mayan cichlid	FW, EF	5	21	16			1	2		
Oreochromis aureus (Steindachner, 1864)[a]	Blue tilapia	FW, EF		15	10		3	1			
Tilapia mariae Boulenger, 1899[a]	spotted tilapia	FW, EF	3						3		
Gobiosoma bosc (Lacépède, 1800)	naked goby	EF, E							1	3	2
Lophogobius cyprinoides (Pallas, 1770)	crested goby	EF, E, M	17						4	1	
Microgobius gulosus (Girard, 1858)	clown goby	EF, E, M							3	2	4
Trinectes maculatus (Bloch and Schneider, 1801)	Hogchoker	EF, E, M	4							3	2
CPUE total by season			368	1,066	348	6	47	31	210	2,287	646
Total number of samples				108			36			312	
Total CPUE by gear				1,782			84			3,143	
Total taxa				27			10			22	

[a] Non-indigenous species
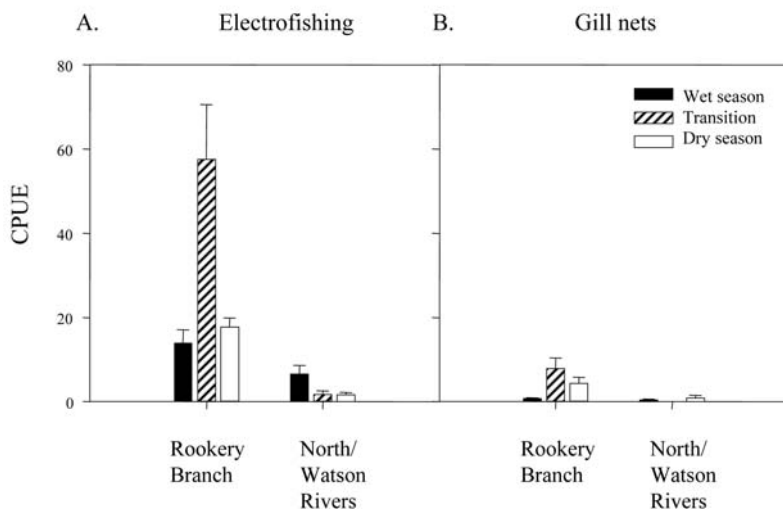
Figure 4. (A) Electrofishing and (B) gill net catch-per-unit effort (CPUE) over the three sampling seasons in the two study regions. Shown are means ± 1 SE.

CPUEs, Table 2), but season had a different effect in the two sampled regions. Across sampling gears, CPUE was highest in RB samples during the transition period. CPUE increased four-fold in electrofishing samples, eight-fold in gill nets, and nine-fold in minnow traps between the wet and transition samples (electrofishing, P = 0.009; gill nets, P = 0.002; minnow traps, P = 0.0001). The abundance of large species, such as Florida gar, bowfin, snook, largemouth bass, Mayan cichlid, and sunfishes peaked in the transition period. Among the small fishes, catches of bluefin killifish, eastern mosquitofish, coastal shiners, and smaller-bodied sunfishes also peaked during the transition period (Table 1). RB CPUE decreased significantly, returning to wet-season levels, in the dry season for electrofishing and minnow traps, but not for gill nets (electrofishing, P = 0.003; minnow traps, P = 0.0001).

In NW creeks, electrofishing CPUE was highest in the wet season (wet vs dry, P = 0.03; wet vs transition, P = 0.01; Fig. 4A), whereas no seasonal variation was detected in minnow trap nor gill net CPUE (Figs. 4B, 5). There was a trend for electrofishing CPUE to be negatively related to salinity (Table 2). The relationship had a relatively better fit in NW than in RB creeks (NW, P = 0.0001, r^2 = 0.27; RB, P = 0.045, r^2 = 0.08; Fig. 6). We detected no relationship between salinity and gill net CPUE (Table 2).

All gears varied significantly among creeks within the two study regions, and this variation was affected by season (Table 2). In NW, electrofishing CPUE was higher in North River creeks than in Watson River creeks (P = 0.003), although CPUE in gill nets and minnow traps did not differ. Seasonally, electrofishing CPUE was higher in North River headwaters in the transition and dry-season samples (P = 0.06 and P = 0.0006, respectively), but not in the wet season. In RB, electrofishing CPUE was lower in Squawk Creek (RB 7, Fig. 1) than in other creeks, particularly in the transition sample (P < 0.05). Minnow trap and gill net CPUE were significantly higher in Otter Creek (RB 12, Fig. 1) than in Squawk Creek (P = 0.0006 and P = 0.02, respectively), while CPUE in other RB creeks was intermediate.
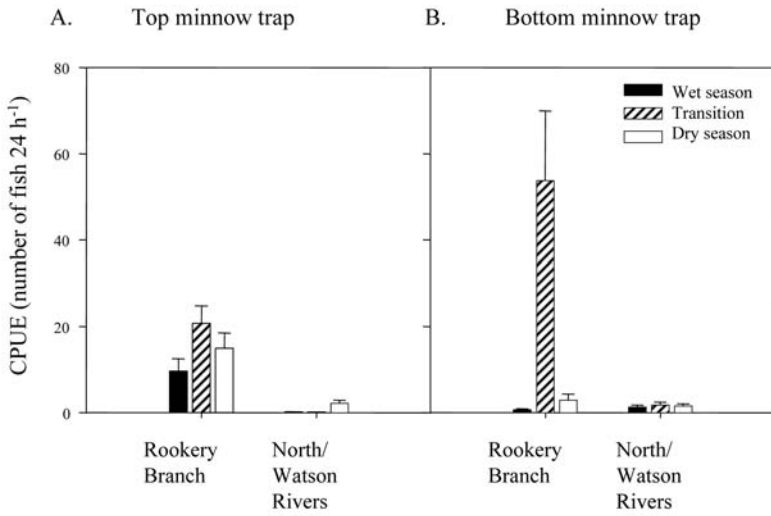
Figure 5. CPUE in minnow traps shown separately by trap placement: (A) top vs (B) bottom of water column) over the three sampling seasons and in the two study regions. Shown are means ± 1 SE.

LARGE-FISH COMMUNITY STRUCTURE.—The composition of electrofishing catches varied equally between regions and among seasons (Table 3). Community structure was similar between NR and RB creeks in the wet season, but diverged considerably during the transition and dry seasons (wet, R = 0.12, P = 0.14; transition, R = 0.54, P = 0.002; dry, R = 0.74, P = 0.002; Fig. 7A). This divergence can be explained by increases in the relative contribution of freshwater taxa to the creek community. The contribution of freshwater species to CPUE was comparable between regions in the wet season (5% in NW vs 20% in RB; P = 0.225), but differed significantly in later samples (Fig. 8A). NW catches remained < 10% freshwater, whereas in RB, 80%–90% of the catch was composed of freshwater taxa during the transition and dry seasons (transition, P = 0.0011; dry season, P = 0.0001). During these drier samples, Florida gar, largemouth bass, bowfin, Mayan cichlid, and several sunfish species were almost

Table 2. Summary of results of nested, repeated-measures ANOVA and ANCOVAs testing the effects of season, region, creek, placement (for minnow traps only), and salinity on catch-per-unit-effort (CPUE) from electrofishing, gill nets, and minnow traps.

| Source of variation	Electrofishing CPUE			Gill-net CPUE			Minnow-trap CPUE		
	df	F	P	df	F	P	df	F	P
Season	2, 42	6.7	0.0031	2, 14	3.7	0.0502	2, 200	26.9	0.0001
Region	1, 55	60.4	0.0001	1, 11	9.3	0.0113	1, 220	46.8	0.0001
Placement							1, 112	2.6	0.1077
Season × region	2, 45	14.5	0.0001	2, 16	4.1	0.0368	2, 200	31.7	0.0001
Season × placement							2, 198	21	0.0001
Region × placement							1, 112	19.1	0.0001
Region × season × placement							2, 198	9.5	0.0001
Creek (region)	3, 38	8.4	0.0002	3, 6	6.9	0.0202	4, 140	4.8	0.0012
Creek (region) × season	6, 37	2.3	0.0558	6, 14	0.8	0.5973	6, 201	4.1	0.0006
Salinity	1, 41	3.8	0.058	1, 13	0.01	0.9453			
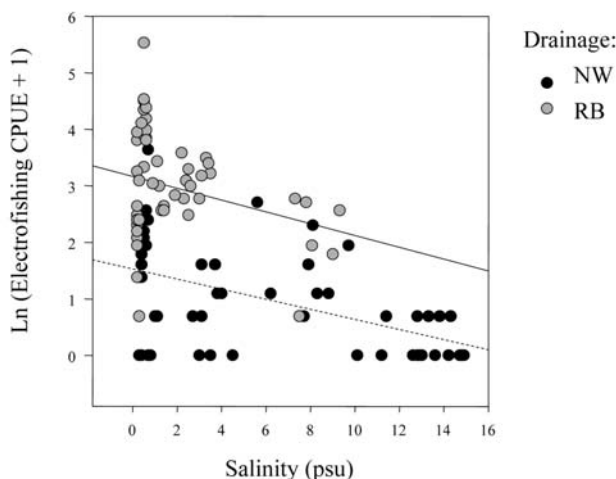
Figure 6. Estimates of large fish abundance (CPUE) in electrofishing samples (Log-transformed) plotted as a function of salinity. Separate least-squares regressions were fitted to the two regions: Rookery Branch (RB, solid line) and the North and Watson rivers (NW, dotted line).

exclusively caught in RB creeks. The relative abundance of snook was also higher in RB, whereas needlefishes and tidewater mojarras were exclusively caught in NW creeks. Composition of gill net samples was similar between regions during the wet season, but tended to differ in the dry season sample (wet, R = 0.29, P = 0.20; dry, R = 0.65, P = 0.10; Fig. 7B). Florida gar was dominant in RB gill net samples, whereas NW gill nets were dominated by a small number of striped mojarras.

Small-fish Community Structure.—Variation in the small community structure was higher between regions than among seasons (Table 3, Fig. 9A), yet the proportion of freshwater species in traps varied as a function of both season and region (Table 4). The contribution of freshwater species to the RB small fish fauna showed no seasonal variation, averaging 96% throughout the study (Fig. 8B). In NW, however, the contribution of freshwater species decreased significantly between the wet and dry seasons, from 24% to 2% (P = 0.024). Minnow trap CPUE in NW primarily contained estuarine species (rainwater killifish, tidewater mojarra, and clown goby), whereas the RB community primarily contained freshwater species (eastern mosquitofish, sailfin molly, bluefin killifish, least killifish, dollar sunfish, and bluespotted sunfish; Table 1).

Gear Comparison.—Large fish catches averaged 16.5 fish 5-min^{-1} bout in electrofishing samples, whereas gill nets only averaged 2.3 fish per 30-min set (Fig. 4). Gill nets failed to detect the marked seasonal variation in the numbers of large fresh-

Table 3. Summary of ANOSIM results testing variation in fish-community structure as a function of region, season, and gear in electrofishing, gill net, and minnow trap samples.

Target community	Sampling method	Region		Season		Gear comparison	
		Global R	P	Global R	P	Global R	P
Large fishes (> 50 mm)	Electrofishing	0.446	0.001	0.416	0.001	0.279[a]	0.002
Large fishes (> 50 mm)	Gill nets	0.511	0.019	0.275	0.012		
Large fishes (> 50 mm)	Minnow traps	0.641	0.001	0.1	0.001	0.135[b]	0.002

[a] Comparison of electrofishing and gill nets
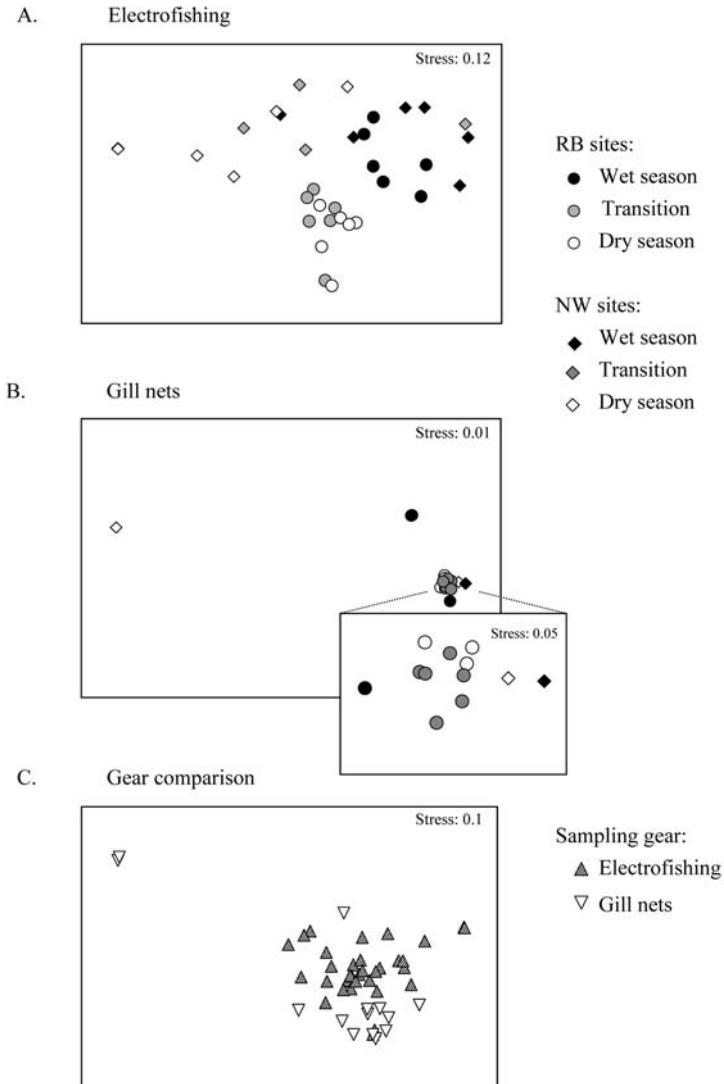[b] Comparison of minnow trap placement: top vs bottom of water column

Figure 7. Two-dimensional non-metric MDS ordinations illustrating large fish (50–750 mm SL) community structure in (A) electrofishing samples, (B) gill net samples, and (C) gill net vs electrofishing samples based on Bray-Curtis similarities of log-transformed, standardized CPUE.

water fishes present in creeks seen in the electrofishing data, particularly in RB (Fig. 4A). Electrofishing and gill-net samples also differed significantly in composition, although this dissimilarity was less than that observed as a function of spatial or seasonal factors (Table 3, Fig. 7C). Florida gar was the most abundant species caught using both methods, but numbers caught by electrofishing were higher than those caught using gill nets. CPUE of snook, striped mullet, largemouth bass, mojarras, and largemouth bass were also higher in electrofishing samples than in gill nets.

In minnow traps, mean CPUE was similar between the top and bottom trap, but placement affected the magnitude of CPUE variation across seasons and between regions (Table 2). For instance, CPUE in RB doubled between the wet and transition
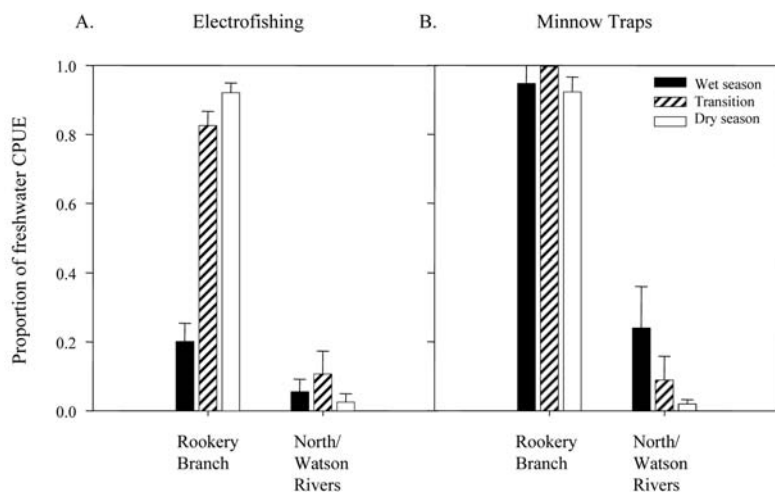
Figure 8. Average proportion of (A) electrofishing and (B) minnow trap CPUE composed of freshwater species over the three sampling seasons in the two study regions. Only species known to occur in freshwater marshes (listed as FW in Table 1) were included in these analyses. Shown are means ± 1 SE.

samples in the top trap, but increased by 50 times in the bottom trap (P = 0.0001 for both cases, Fig. 5). Large numbers of sunfishes, bluefin killifish, and coastal shiners accounted for this increase in the bottom trap (Table 1). In NW headwaters, seasonal variation in CPUE was detected only in the top trap. In spite of very low catches, CPUE increased between the transition period and the dry season (P = 0.0001; Fig. 5A). Dissimilarity between minnow trap samples as a function of trap placement was lower than the separation observed when comparing gill nets and electrofishing samples (Table 3, Fig. 9B). The contribution of freshwater species was higher in the top than in the bottom trap (80.6% and 54.2%, respectively; Table 4). Eastern mosquitofish and least killifish were more abundant in traps placed at the top of the water column, whereas bluefin killifish, rainwater killifish, clown gobies, and dollar sunfish were more abundant in traps placed at the bottom of the water column.

Table 4. Summary of nested, repeated-measures ANCOVA and ANOVA analyses testing variation in the proportion of CPUE that is composed of freshwater taxa (FW in Table 1) per sample as a function of region, season, and placement (for minnow traps only) in electrofishing and minnow trap samples.

	Proportion of freshwater CPUE					
	Electrofishing samples			Minnow trap samples		
Source of variation	df	F	P	df	F	P
Season	2, 61	5.8	0.0049	2, 129	5.7	0.0044
Region	1, 58	38.7	0.0001	1, 128	199.7	0.0001
Placement				1, 103	18.1	0.0001
Season × region	2, 63	16.9	0.0001	2, 130	4.1	0.0191
Season × placement				2, 129	5.1	0.007
Region × placement				1, 103	0.1	0.7619
Region × season × placement				2, 129	7.9	0.0006
Creek (region)	3, 29	3.4	0.0319	4, 105	0.9	0.4609
Creek (region) × season	6, 53	1.1	0.3533	6, 115	1.1	0.3586
Salinity	1, 61	0.04	0.8399			

A.   Seasonal and drainage variation
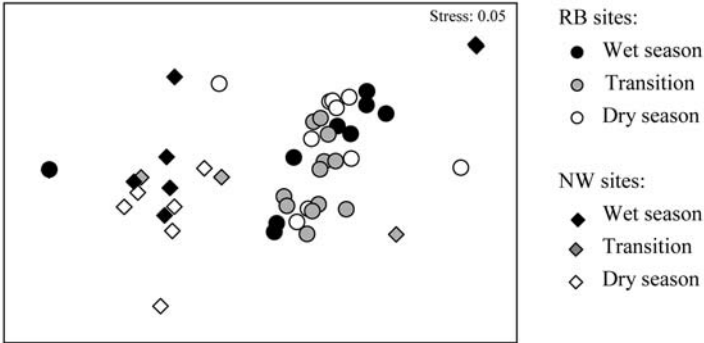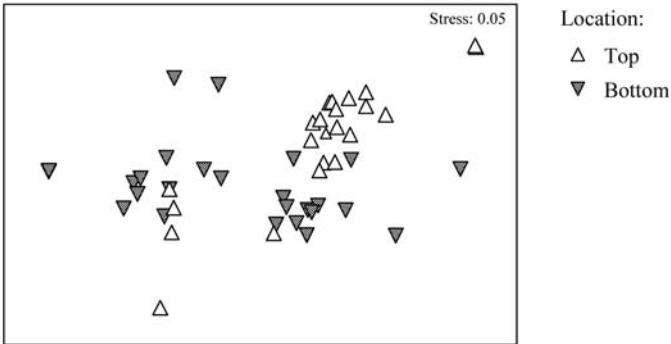

B.   Trap placement

Figure 9. Two-dimensional non-metric MDS ordinations illustrating variation in small fish community structure (< 5 cm SL): (A) among seasons and sites and (B) as a function of trap placement. MDS plots are based on Bray-Curtis similarities of standardized minnow traps CPUE.

DISCUSSION

Disturbance from recurrent, seasonal dry-down events has a strong structuring effect on freshwater fish communities inhabiting Everglades marshes (Kushlan, 1974; Loftus and Eklund, 1994; Trexler et al., 2001, 2005; Chick et al., 2004). In response to dry-down, fish move from marshes to deeper habitats such as alligator holes, solution holes, and canals (Nelson and Loftus, 1996; Trexler et al., 2001; Kobza et al., 2004; Rehage and Trexler, 2006). Thus, access to dry-season refuges is a key element underlying long-term population dynamics in freshwater fishes (DeAngelis et al., 1997). Our results indicate that mangrove creek headwaters in the southern part of the ecosystem can also serve as important dry-season refugia, particularly for large-bodied species, whose abundance is strongly limited by seasonal dry-down (Trexler et al., 2001, 2005; Chick et al., 2004). A pulse of freshwater fishes was detected in RB creeks in February as marshes upstream began to dry periodically, which resulted in marked seasonal variation in patterns of abundance and composition in RB headwaters. The pulse was composed of both predatory species, such as Florida

gar, bowfin, and centrarchids; and of the small cyprinodontoids, although some species (e.g., mosquitofish) appeared to reside in creek all-year around. No evidence of a similar pulse was noted in the North and Watson rivers, where the contribution of freshwater taxa to the community was consistently small (0%–24%) and showed lower seasonal variation.

Mangrove fish communities are highly variable in both short (tidal) and longer time scales (seasonal) because of pronounced environmental fluctuations (Kupschus and Tremain, 2001). Seasonal changes in the abundance and composition of tropical and subtropical fish communities have been reported in mangrove systems throughout the world, including Madagascar (Laroche et al., 1997), Brazil (Barletta et al., 2005), Australia (Loneragan et al., 1986), the Solomon Islands (Blaber and Milton, 1990), Taiwan (Lin and Shao, 1999), and Mexico (Yanez-Arancibia et al., 1988). Of these examples, mangrove creeks of the Caeté River estuary in Brazil (Barletta et al., 2005) exhibit the greatest freshwater inflow and may closely resemble the mangrove creeks at our Everglades sites. However, the directionality of seasonal variation in RB and NW creeks is opposite that of Caeté, where the influx of freshwater species occurs during the wet season when salinities are low. Seasonal community dynamics have also been shown in Everglades mangrove regions (Thayer et al., 1987; Ley et al., 1999; Lorenz et al., 1999; Faunce et al., 2004). In Florida Bay and Whitewater Bay, Thayer et al. (1987) reported increases in both fish numbers and biomass during the wet season. Our results from NW fit their findings. Fish abundances varied monthly in mangrove creeks of southeastern Florida Bay, with those of freshwater species increasing during February and March (Faunce et al., 2004), as seen in our RB sites.

Several factors may be responsible for the lack of a freshwater species influx in NW headwaters. Marshes upstream of NW creeks have shorter hydroperiods than those upstream of RB sites, and consequently may contain lower densities of fishes, particularly of the large species (Lorenz, 1999; Trexler et al., 2001, 2005; Chick et al., 2004). Freshwater fishes may be absent from NW creeks simply because the pool of potential marsh migrants is small. Secondly, salinity levels are higher in NW than RB headwaters, and may approach or exceed the physiological tolerances or preferences for some of the freshwater species such as centrarchids (Loftus and Kushlan, 1987). However, other marsh inhabitants exhibit high salinity tolerances (Lorenz and Serafy, 2006; Nordlie, 2006), and should find suitable salinity conditions in NW, despite the fact that there were rarely caught there.

Thirdly, the pattern of marsh dry-down differed between regions, and marshes upstream of NW remained flooded beyond our dry-season sample. A pulse of freshwater species could have possibly occurred later in the season, and would have been missed by our sampling. Other studies, however, suggest that marsh fishes move into deep-water refugia well in advance of low-water conditions (Chick et al., 2004; Rehage and Trexler, 2006). Even in long-hydroperiod marshes that rarely dry, and where direct mortality due to dry-down conditions is unlikely, large-fish densities decrease significantly in the open marsh during the dry season and concentrate in deep-water refuges. Marsh water-levels upstream of NW were low (close to 5 cm); therefore, a pulse of migrants should have occurred by our April sample. Furthermore, salinities in later months exceeded 15 in NW, which is too stressful for many of the potential migrants. Another explanation may be a higher abundance of alternative dry-down refuges (e.g., solution and alligator holes) in marshes upstream of NW relative to RB. However, abiotic (high ammonia and low oxygen) and biotic (high predation) condi-

tions in these alternative refuges are often stressful (Nelson and Loftus, 1996; Kobza et al., 2004), and could make these refuges less preferred relative to creeks. Lastly, small differences in local topography (e.g., the presence of berms along creeks) could limit fish movement in and out of creeks, perhaps to a greater extent in NW than RB sites (Green et al., 2006).

The pulse of freshwater species in RB occurred early in the dry season, and despite the fact that RB assemblages remained dominated by freshwater species in the later sample, their abundances decreased considerably. This decrease could be explained by a large-scale return of the freshwater taxa to marshes, if marshes had reflooded. However, this was unlikely in 2005 since water levels in upstream marshes at the time of our transition and dry season samples were relatively low and similar (11 and 13 cm, respectively). Alternatively, the increase in salinity between the transition and dry samples in RB (from < 1 to 5) could explain the decline in freshwater species through mortality or movement to more suitable salinity environments. An important source of mortality could also be predation. Mangrove habitats provide important foraging grounds for marine and estuarine piscivores (Blaber and Milton, 1990; Chong et al., 1990). Even though mangroves can provide a refuge from predation because of their high habitat complexity (Primavera, 1998; Acosta and Butler, 1999), the abundance of predators is not necessarily lower in these shallow coastal habitats (Sheaves, 2001). In RB creeks, piscine predators such as snook, Florida gar, large-mouth bass, and bowfin were abundant early in the dry season and could account for the declines in the cyprinodontoids between February and April. Top predators, such as alligators, wading birds, and bull sharks could possibly account for the decreases in the abundance of the larger freshwater species. More extensive, paired sampling in creeks, marshes (including other dry-down refuges), and downstream portions of the estuary is needed to discriminate between these and other plausible explanations for the timing and extent of pulsing of freshwater taxa into headwater creeks.

Results from studies that rely on a single gear type to sample mangrove fishes may be restricted in their applicability because of gear selectivity (Rozas and Minello, 1997). CPUE in gill nets was appreciably lower than that for electrofishing, and catch composition differed between gears. This suggests that gill nets with the 30-min soak times used in our study do not provide a reliable index of abundance, nor detect seasonal variation in community structure, even if previous studies have shown that gill nets may be better at capturing certain aspects of target fish populations, such as size structure, relative to electrofishing (Colvin, 2002). Comparison of the small-fish CPUE showed that minnow-trap placement in the water column strongly affects catch numbers and species composition. This is likely explained by variation in microhabitat use among small-fish species; a factor that needs to be considered if sampling is targeted to multiple species.

The influx of freshwater species into RB headwater creeks may enhance estuarine fish abundance and richness, and should provide an important prey source for marine and estuarine piscine predators, as well as for avian predators. Interannual variation in drying patterns may create circumstances in which other creek headwater habitats (including NW) may serve as dry-season refugia. In other parts of the ecotone, factors such as high salinity and local topography could limit the connectivity between mangrove and upstream marsh habitats (i.e., Green et al., 2006). Ongoing restoration of the Greater Everglades ecosystem aimed at re-establishing historical freshwater flows (CERP, 1999), could greatly enhance this connectivity.

Increased freshwater flows are expected to result in reduced salinities, prolonged pooling of freshwater, and a spatially-expanded and seasonally-extended oligohaline zone at that marsh-mangrove ecotone, including our study creeks (Davis et al., 2005). These conditions should make large portions of the mangrove region suitable for freshwater species. In northern parts of Florida Bay, increased freshwater flow has resulted in higher abundance and biomass of small-bodied freshwater taxa, and thus the recovery of the demersal forage fish community (Lorenz, 1999; Lorenz and Serafy, 2006). Similar effects could occur in our study area in southwestern Everglades, but overall responses of freshwater fishes are somewhat uncertain. Increased freshwater flow and decrease salinity are expected the influence multiple components of marine, estuarine, and freshwater food webs and how these interact over a complex and heterogeneous ecotonal landscape. Further research is needed to develop predictions and gain a better understanding of the net effects of hydrological restoration on the freshwater fish community of mangrove headwaters.

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