

Spatial patterns of fish communities along two estuarine gradients in southern Florida

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Abstract

In tropical and subtropical estuaries, gradients of primary productivity and salinity are generally invoked to explain patterns in community structure and standing crops of fishes. We documented spatial and temporal patterns in fish community structure and standing crops along salinity and nutrient gradients in two subtropical drainages of Everglades National Park, USA. The Shark River drains into the Gulf of Mexico and experiences diurnal tides carrying relatively nutrient enriched waters, while Taylor River is more hydrologically isolated by the oligohaline Florida Bay and experiences no discernable lunar tides. We hypothesized that the more nutrient enriched system would support higher standing crops of fishes in its mangrove zone. We collected 50 species of fish from January 2000 to April 2004 at six sampling sites spanning fresh to brackish salinities in both the Shark and Taylor River drainages. Contrary to expectations, we observed lower standing crops and density of fishes in the more nutrient rich tidal mangrove forest of the Shark River than in the less nutrient rich mangrove habitats bordering the Taylor River. Tidal mangrove habitats in the Shark River were dominated by salt-tolerant fish and displayed lower species richness than mangrove communities in the Taylor River, which included more freshwater taxa and yielded relatively higher richness. These differences were maintained even after controlling for salinity at the time of sampling. Small-scale topographic relief differs between these two systems, possibly created by tidal action in the Shark River. We propose that this difference in topography limits movement of fishes from upstream marshes into the fringing mangrove forest in the Shark River system, but not the Taylor River system. Understanding the influence of habitat structure, including connectivity, on aquatic communities is important to anticipate effects of construction and operational alternatives associated with restoration of the Everglades ecosystem.

Introduction

Estuaries are generally considered to be highly productive ecosystems because of inputs of organic matter from the watershed at the fresh-saltwater interface (Nixon, 1980; Day et al., 1989). Though Odum's (1980) hypothesized net export of estuarine productivity to marine habitats has not been

universally documented (Dame, 1986; Dame & Allen, 1996), estuarine habitats are known to be important nursery grounds for many fishes and invertebrates with life cycles linking these habitats (Norcross & Shaw, 1984; Stancyk, 1986; Deegan, 1993; Dean et al., 2005). Fluctuating salinities, interacting with other environmental gradients, make estuaries a physiologically challenging

habitat for fishes and limit the species able to spend time there (Evens, 1993; Hurst & Conover, 2002; Peterson et al., 2004). Thus, fish productivity in these dynamic environments may not follow patterns seen in primary production (Peterson, 2003).

Nutrient dynamics, salinity fluctuation, and seasonal hydrology have been emphasized as organizing processes shaping aquatic community and ecosystem dynamics in estuaries and wetlands of southern Florida (Lorenz, 1999; Rudnick et al., 1999; Turner et al., 1999; Ley & McIvor, 2002; Childers et al., 2006). Two drainages in the southern Everglades National Park (ENP) characterize a dichotomy in nutrient availability and tidal range. Taylor Slough (TS) drains into the Taylor River and then into Florida Bay, is hydrologically isolated from the Gulf of Mexico, lacks discernable tides (Holmquist et al., 1989), and is highly oligotrophic (Rudnick et al., 1999; Childers et al., 2006). In contrast, Shark River Slough (SRS) drains into the Shark River and the Gulf of Mexico, has moderate diurnal tidal fluctuations (average tidal range 1 m; Levesque, 2004), and is less oligotrophic (Rudnick et al., 1999; Childers et al., 2006). Based on these patterns, we hypothesized that low nutrient

availability would limit fish standing crops, as an index of secondary production, in the Taylor River estuary compared to the Shark River estuary. We report results from a 5-year observational study of fish communities in the upstream freshwater wetlands, transitional wetlands, and downstream estuarine zones of the SRS and TS drainages.

Methods

Study area and sampling techniques

The Everglades was historically a continuous wetland system with water flowing south towards Florida Bay (Taylor Slough) or southwest towards the Gulf of Mexico (Shark Slough). Everglades wetlands derived freshwater inputs from Lake Okeechobee and seasonal rainfall. A gradual dry-down of the non-tidal marsh surfaces occurred as the dry season progressed. Water drainage patterns of SRS and TS have been altered by canal construction, water diversion, and urban and agricultural development (Light & Dineen, 1994). The net result has been an overall compartmen-

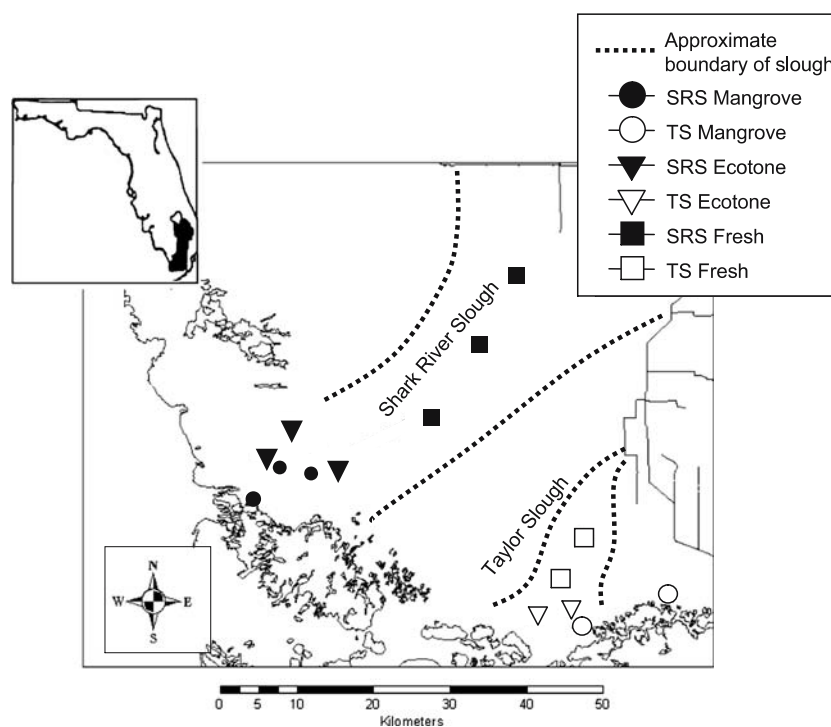


Figure 1. Map of Everglades National Park and fish sampling locations in SRS and TS.

talization of the freshwater portions of the ecosystem. The headwaters of these sloughs are located in the freshwater Everglades, and are dominated by sawgrass (*Cladium jamaicense*) stands and deeper wet prairies characterized by spikerush (*Eleocharis cellulosa*). The slough waters flow through a mangrove zone of oligohaline or mesohaline salinity before emptying into the more marine environments of the Gulf of Mexico (Shark River) and of Florida Bay (Taylor River). A mixture of *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans* characterizes the mangrove zone.

Our study sites were located in the Shark and Taylor River drainages, from the upstream freshwater sloughs to the mangrove-dominated river systems (Fig. 1). We grouped our sampling sites into three regions nested within drainages: upstream freshwater sites in SRS (SRS: 3 sites) and TS (TS: 3 sites); at the mangrove-marsh ecotone (SRSE: 2 sites; TSE: 2 sites); and mangrove sites along the Shark River (SRM: 3 sites) and Taylor River (TRM: 2 sites). These areas vary in salinity from fresh water (salinity of 0‰ throughout the study) to greater than seawater (39.4‰). All but one of our mangrove sites experienced salinities fluctuating from oligohaline (1–6‰) to at or near seawater within each year of the study (Table 1). All sampling sites were permanent sampling locations that were revisited throughout the study. However, the specific definition of a ‘site’ varied somewhat among regions because of sampling technique, described below.

We used enclosure net sampling (Rozas & Minello, 1997) throughout the entire region although precise technique varied between the freshwater prairie and mangrove-dominated estuarine habitats as necessitated by the structure of

the vegetation. We used a modified 6 m² bottomless lift net (Rozas, 1992) to collect fishes among the dense prop roots of the SRS mangrove zone, while fish were collected by a 9 m² drop-trap (Lorenz et al., 1997) in the more open TS mangrove zone. In SRS, three lift nets were set at each of three locations along the riverine gradient within the closed-canopy, intertidal, fringing forest. Bottomless lift nets buried in the forest floor were triggered at slack high tide. The ebb tide concentrated the entrained fishes in the perimeter trench of each net from which the catch was cleared at low tide. Two groups of three drop-net samples were collected in each sampling event in the Taylor River mangrove zone. These traps enclosed small mangrove trees and their prop roots, three in flats habitats and three in adjacent channel habitat. These data from TS were combined as a mean that was weighted by the relative coverage of these to habitats in a square kilometer encompassing the study sites (Lorenz et al., 1997). Nets were maintained in fixed positions and resampled periodically for both drop and lift nets because of difficulties placing these nets in the mangroves; spatial replicates were from different nets at a study site. All freshwater samples were collected with a 1 m² throw trap (Jordan et al., 1997). Seven samples were collected at randomly identified locations within 100 m by 100 m permanent plots (approximate dimensions) in wet prairie habitat at each study site on each sampling date (Wolski et al., 2004). There were three such plots at each freshwater study site. All data were adjusted to biomass per m² (g/m²) for each species to permit quantitative comparisons among study sites.

We collected fish samples in one or more months during the dry season (January through April), wet season (June through September) and between seasons (October, December) from January, 2000, through April, 2004. This design allowed us to capture the seasonal changes in hydrology and salinity characteristic of the Greater Everglades Ecosystem. At the upstream freshwater sites, we collected 21 1 m² throw trap samples (seven samples in three plots) at each study site in the months of February, April, July, October, and December. At the mangrove sites along the Taylor River, six 9 m² samples were collected in January, February, March, April, June, September, November, and December.

Table 1. Range of salinities (‰) observed at our study sites between 2000 and 2004

Site	Min	Max
Shark River Slough (SRS)	0	0
Taylor Slough (TS)	0	0
Shark River Slough ecotone (SRSE) ^a	0	20
Taylor Slough ecotone (TSE) ^a	0	6
Shark River mangrove (SRM)	0.3	34.4
Taylor River mangrove (TRM)	0.0	39.4

^aSites only visited in wet and dry season, 2004–2005.

Table 2. Species collected in this study with sites where collected

Family	Species	Code	Common name	SRS	SRM	SRSE	TS	TRM	TSE
Lepisosteidae	<i>Lepisosteus platyrhincus</i>	lepplat	Florida gar	Y			Y		
Batrachoididae	<i>Opsanus beta</i>	opsbet	toadfish					Y	
Esocidae	<i>Esox americanus</i>	esoame	redfin pickerel	Y					
	<i>Esox niger</i>	esonig	chain pickerel				Y		
Cypinidae	<i>Notemigonus crysoleucas</i>	notcry	golden shiner				Y		
	<i>Notropis petersoni</i>	notpet	coastal shiner				Y		
Catostomidae	<i>Erimyzon sucetta</i>	erisuc	lake chubsucker	Y			Y		
Ictaluridae	<i>Ameriurus natalis</i>	amenat	yellow bullhead	Y			Y		
	<i>Noturus gyrinus</i>	notgyr	tadpole madtom	Y			Y		
Clariidae	<i>Clarias batrachus</i>	clabat	walking catfish	Y					
Belonidae	<i>Strongylura notata</i>	strnot	redfin needlefish		Y			Y	
	<i>Strongylura timucu</i>	strtim	timucu		Y				
Cyprinodontidae	<i>Adinia xenica</i>	adixen	diamond killifish					Y	
	<i>Cyprinodon variegatus</i>	cypvar	sheepshead minnow	Y	Y	Y	Y	Y	Y
	<i>Floridichthys carpio</i>	flocar	goldspotted killifish					Y	
	<i>Fundulus chrysotus</i>	funchr	golden topminnow	Y			Y	Y	
	<i>Fundulus confluentus</i>	funcon	marsh killifish	Y	Y	Y	Y	Y	Y
	<i>Fundulus grandis</i>	fungra	gulf killifish		Y	Y		Y	
	<i>Fundulus seminolis</i>	funsem	Seminole killifish				Y		
	<i>Fundulus similis</i>	funsim	longnose killifish					Y	
	<i>Jordanella floridae</i>	jorflo	flagfish	Y		Y	Y	Y	
	<i>Lucania goodei</i>	lucgoo	bluefin killifish	Y			Y	Y	
	<i>Lucania parva</i>	lucpar	rainwater killifish		Y	Y		Y	
	<i>Rivulus marmoratus</i>	rivmar	mangrove rivulus		Y				
	Poeciliidae	<i>Belonesox belizanus</i>	belbel	pike killifish	Y	Y		Y	Y
<i>Gambusia holbrooki</i>		gamhol	eastern mosquitofish	Y	Y	Y	Y	Y	
<i>Heterandria formosa</i>		hetfor	least killifish	Y			Y	Y	
<i>Poecilia latipinna</i>		poelat	sailfin molly	Y	Y	Y	Y	Y	Y
Atherinidae	<i>Labidesthes sicculus</i>	labsic	brook silverside	Y			Y		
	<i>Menidia peninsulae</i>	menpen	tidewater silverside					Y	
Centrarchidae	<i>Elassoma evergladei</i>	elaeve	Everglades pygmy sunfish	Y			Y	Y	
	<i>Enneacanthus gloriosus</i>	ennglo	bluespotted sunfish	Y			Y		
	<i>Lepomis gulosus</i>	lepgul	warmouth	Y			Y		
	<i>Lepomis macrochirus</i>	lepmac	bluegill	Y			Y		
	<i>Lepomis marginatus</i>	lepmar	dollar sunfish	Y			Y	Y	
	<i>Lepomis microlophus</i>	lepmic	reardear sunfish	Y			Y		
	<i>Lepomis punctatus</i>	leppun	spotted sunfish	Y			Y	Y	
Gerreidae	<i>Micropterus salmoides</i>	micsal	largemouth bass				Y		
	<i>Gerridae spp.</i>	gerspp	mojarras		Y			Y	
	<i>Eucinostomus gula</i>	eucgul	silver jenny		Y				
Cichlidae	<i>Cichlasoma urophthalmus</i>	cicuro	Mayan cichlid	Y	Y	Y	Y	Y	Y
	<i>Cichlasoma bimaculatum</i>	cicbim	black acara	Y			Y		
	<i>Oreochromis aureus</i>	oreaur	blue tilapia	Y					
	<i>Tilapia mariae</i>	tilmar	spotted tilapia					Y	

Continued on p. 391

Table 2. (Continued)

Family	Species	Code	Common name	SRS	SRM	SRSE	TS	TRM	TSE
Gobiidae	<i>Bathygobius soporator</i>	batsop	frillfin goby		Y				
	<i>Gobiosoma bosci</i>	gobbos	naked goby					Y	
	<i>Gobiosoma robustum</i>	gobrob	code goby					Y	
	<i>Lophogobius cyprinoides</i>	lopcyp	crested goby					Y	
	<i>Microgobius gulosus</i>	micgul	clown goby					Y	
Soleidae	<i>Trinectes maculatus</i>	trimac	hogchoker					Y	
			No. of species	26	16	8	28	29	5

Code indicates notation used in Table 4 for each species. Regional abbreviations defined in Table 1.

Collections were less regular in the Shark River mangrove zone because of logistical challenges accessing the sites. In this region, three 6 m² samples were collected at each study site each year of the study spanning the wet and dry seasons of 2000, 2001, and 2003 (2000: March, April, May, June, July, and September; 2001: January, April, June, August, October, and December; 2002: February and April; 2003: February, May, July, and September; 2004: April).

Data analyses

We analyzed community composition and fish biomass along freshwater to estuarine gradients in two sloughs of the Everglades. We analyzed the biomass and, separately, density of all fish species summed with Proc Mixed in SAS to model site means with reduced maximum likelihood (REML). We modeled temporal autocorrelation using a one-step autoregressive model and tested for effects among regions, sites within regions, years, and seasons within years. Biomass and density data were log transformed, $(n + 1)$ to adjust for zeros.

We examined patterns of community structure through analysis of Bray-Curtis dissimilarity matrices calculated from relative biomass and, separately, relative density for each species at each sampling event. Relative mass and density were transformed by taking the fourth root to upweight the impact of rare taxa on the analysis. We used Analysis of Similarities (ANOSIM) to test hypotheses of species compositional differences and change across discrete sites and dates (Clark, 1993; Clark & Warwick, 1994; Philippi et al., 1998), and the corresponding Mantel tests

(McCune & Grice, 2002) to identify relationships of dissimilarity with salinity at the time of capture. Nonmetric multidimensional scaling (NMDS) was used to illustrate the spatial and temporal patterns that emerged (Kruskal & Wish, 1978). ANOSIM hypotheses were tested with data from each site and sample event as the raw data. Our ordination results were similar for density and biomass data, so we report the latter.

Results

We collected 50 species from the six study regions between 2000 and 2004 (Table 2). The regions with the highest species richness are TRM, TS, and SRS (29, 28, 26 species, respectively). The ecotonal regions had the lowest number of species collected, though these areas had a relatively low sampling effort and the data are not comparable to the better-studied areas. Between 2000 and 2004, only 16 species were collected in the SRSM region.

Over the course of the study, we observed consistent differences among the regions in both fish biomass and density (Fig. 2; Region: mass $F_{3,7} = 25.36$, $p = 0.004$; density $F_{3,7} = 48.83$, $p < 0.001$; Year: mass NS, density NS; Region by Year: mass NS, density $F_{12,27} = 3.5$, $p = 0.003$). Contrary to our predictions, both fish biomass and density were greatest at the SRS and TS regions, and least at the SRM region (Table 3; Fig. 2). The TRM region supported a lower density of fish than the TS region upstream, but a similar standing crop (Table 3). Given the unexpectedly low fish captures in Shark River estuarine mangroves, we did two things: (1) determined the recovery efficiency of marked fishes of the two most common

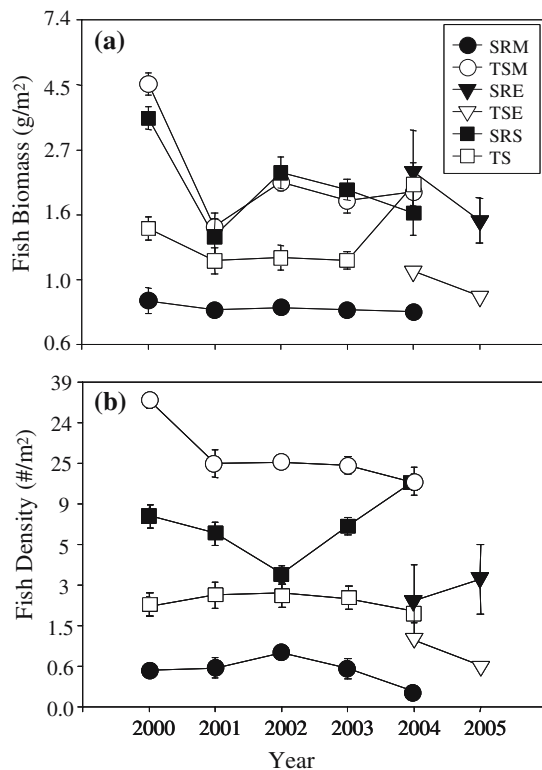


Figure 2. Estimated annual average standing crops (least-squares means) in six study regions. Means \pm one standard error are reported. (a) Biomass, (b) Density.

species; and (2) sampled at the mangrove-marsh ecotone in wet season 2004 and dry season 2005 to determine if this pattern extended beyond the mangrove forest immediately adjacent to the Shark River. Recovery efficiency from SRM modified lift nets was uniformly high (>90%) for both species tested (mangrove rivulus, frillfin goby) eliminating a possibility of net bias contributing to low biomass observed. The ecotonal

Table 3. Comparisons of average density and biomass from the four study regions of this study

Region	Density (No./m ²)	Mass (g/m ²)
Shark River Slough (SRS)	15.7 ^a	2.19 ^a
Shark River Mangroves (SRM)	0.55 ^b	0.03 ^b
Taylor Slough (TS)	6.58 ^c	1.26 ^{a,c}
Taylor River mangroves (TRM)	2.40 ^d	0.91 ^c

Letters indicate means that are not different in Tukey-adjusted pairwise comparison.

mangrove sites were accessed by helicopter and were randomly selected from the matrix of wet prairie habitats interspersed between the mangrove-lined creeks at the headwaters of the Shark and Taylor Rivers. Collections from the SRS ecotonal region yielded similar fish biomass and density to the freshwater sites upstream and more than the nearby SRM sites (Fig. 2), while collections from the TS ecotone yielded lower standing crops and density than those made at TS or TRM.

Community structure varied consistently among the four study regions analyzed (mass $R = 0.411$, $p = 0.001$) with little directional change over years (Fig. 3). The two mangrove ecotonal sites were added late in the study and had too few samples to be included in the analyses. Of the 25 species collected at the upstream freshwater study sites, 17 were restricted to freshwater (69%); five of these were limited to TS and three to SRS (Table 2). Five of the 13 species collected at SRM sites were only found at SRM (38%), while 11 of the 27 fishes collected at the TRM sites were only found at TRM there (40%). Three of the fish species collected at the SRM region were also collected upstream in the SRS freshwater (23%).

Though all the regions were distinguishable by ANOSIM, the SRM region displayed greater separation than the other regions in our NMDS plots (Figs. 3, 4). This separation resulted from the presence of several species typical of saline conditions (redfin needlefish, gulf killifish, frillfin goby, crested goby, and rainwater killifish; Table 4). Two of these species (redfin needlefish and frillfin goby) were not collected at the TSM region, accounting for their separation in the NMDS. A number of species typical of freshwaters were also collected at the TSM region and these assemblages clustered between the freshwater sites and SRM sites (Table 4, Fig. 4); no typically freshwater species were collected at SRM sites though the most upstream one had salinities < 6‰ most of the wet season. Mayan cichlids, a non-native species, accounted for the greatest proportion of biomass of all species at the TSM sites (Table 4). SRM density data indicated a dominance of mangrove rivulus, in contrast to the mass data that were dominated by a relatively small number of large needlefish (Table 4). This difference had no effect on the distinctive findings for SRM compared to all other study regions, because mangrove rivulus

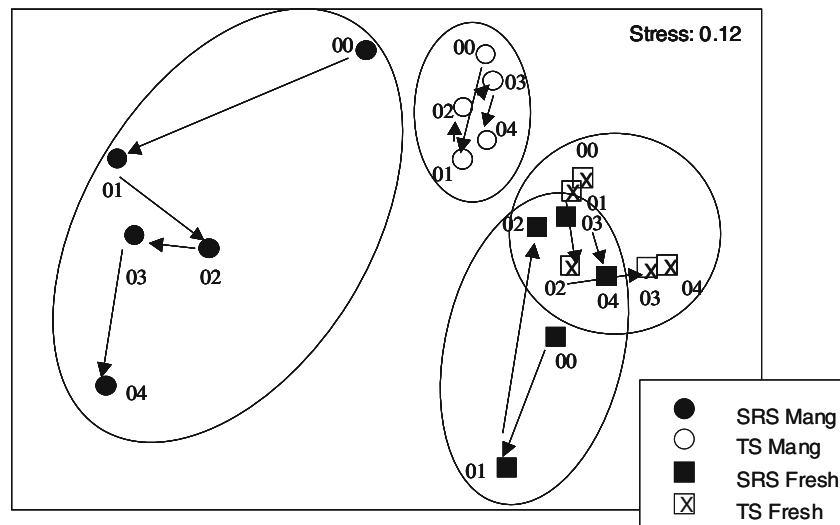


Figure 3. NMDS ordination of study sites illustrating changes in fish community composition from 2000–2004 based on relative mass. These plots illustrate annual regional means to reduce clutter. Years are plotted separately for each region and connected by arrows to indicate the temporal sequence and circles enclose data from a single region.

was unique to this region and needlefish were very rarely collected in TSM.

The ecotonal sites in both drainages were primarily home to fish that lived throughout the salinity gradient. All but one of the eight species collected at the SRSE sites were also collected at the SRM site and six of the eight were also collected in the freshwater SRS sites located upstream. A similar pattern was noted at the TSE sites; all five species obtained at the TSE sites were also collected at both the upstream freshwater sites and the mangrove sites in that drainage. While our sampling effort was inadequate to consider these to be exhaustive species lists for the ecotone regions, we believe they do indicate spatial patterns in species composition.

Fish abundance (standing crops and density) was linked to salinity, but through the differences we observed among our study regions. Standing crops were related to salinity in the total data set (mass $F_{1,242} = 81.791$, $p < 0.001$, $R^2 = 0.253$; density $F_{1,541} = 141.949$, $p < 0.001$, $R^2 = 0.212$). However, if region was included in a statistical model, neither salinity nor salinity-by-region interaction was significant; all the variation in density and standing crops is explained by region. Mantel correlations indicated dissimilarity in relative mass of fish assemblages was correlated with difference in salinities at the time of capture

($r = 0.527$, $p < 0.001$). This correlation remained, but was reduced in magnitude, when data from the two mangrove regions were analyzed separately (SRM $r = 0.366$, $p < 0.001$; TRM $r = 0.189$, $p < 0.001$). NMDS ordinations illustrate that SRM sites had distinct community structure even though salinities at TSM sites were often similar to those recorded at SRM (Fig. 4B, size of circles is proportional to salinity at time of capture).

Discussion

Our data failed to support our initial hypothesis that differences in nutrient availability and primary productivity between our two drainages would explain spatial patterns of fish standing crops or density. Furthermore, salinity gradients also failed to explain the markedly lower standing crops and density of fishes in the SRM region compared to the TRM region. Community composition in the Taylor River drainage indicated marked seasonal overlap of fish species and relative abundance between the freshwater and mangrove-dominated habitats, in contrast to the Shark River drainage where fish assemblages in the mangrove habitats were dominated by salt-tolerant species absent from upstream. Sampling in the marsh-mangrove ecotone adjacent to the

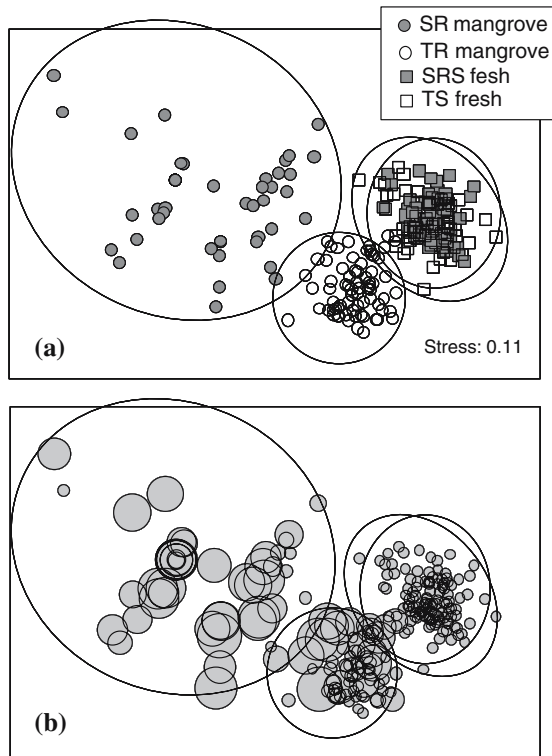


Figure 4. NMDS ordination of individual sampling events illustrating separation of community composition among regions and relationships with salinity. (a) NMDS coded by region, circles enclose data from a single region. (b) Same NMDS plot as in (a), but symbol size is proportional to salinity scaled from smallest (salinity = 0) to largest (salinity = 39.4 ‰). Circles enclose data from a single region, also as in (a).

mangrove-lined river channels of the Shark River where our initial efforts were directed, indicated higher standing crops and density and more freshwater taxa than in the mangrove zone even though salinities were similar. In the following discussion, we propose an alternative to our original productivity-based hypothesis to explain these patterns.

Floodplains of low-gradient rivers in the coastal plain of the southeastern United States provide an analogous environment to the one we have observed in the Shark River upstream of Tarpon Bay. When high flows spill over the banks of the main channel and into the adjacent floodplain, the decreasing velocity causes sediment to settle out, producing natural levees along the main channel higher than the backwater swamps in the floodplain. As flows decrease and water levels

recede, the downstream flow returns to the main channel. The hydroperiod of the backwater swamps is determined by the restricted drainage back into the main channel via incisions or rivulets across the levees, by evaporation, and by transpiration from vegetation and lasts much longer than the flood duration (Hupp, 2000; Noe & Hupp, 2005). Similar processes are seen in salt marshes (McIvor & Rozas, 1996). We hypothesize that in the Shark River system, tidally flooded forests are hydrologically isolated from adjacent marshes (our mangrove ecotone zone) and fish must move into the river channel at low tide, with its diverse community of piscivores, or seek refuge in small creeks, under logs or leaf litter, or in crab burrows. This pattern is supported by data from Light Detection and Ranging imagery (LIDAR). This LIDAR detector bounces a 33 kHz pulsed infrared (1.1 μm) laser every 1 m in a 350-m wide swath and bare ground elevations are estimated from the last return at each spot (Zhang et al., 2003). These data suggest natural levees disconnecting the main channel from the surrounding marshes in Shark River, but show no signs of elevated levees along the more diffuse TS (Fig. 5).

Mangrove rivulus was a dominant species at the Shark River sites, possibly because they are well adapted for seeking refuge in these microhabitats on the marsh surface, while few other species can thrive in such circumstances. In contrast, a diverse community of small fishes is sustained in the TS mangrove zone. Also, though the most upstream of our Shark River mangrove sites and all of our Taylor River mangrove sites experienced periods of near zero salinity, only TS was found to harbor numbers of freshwater species at these times. Laymen et al. (2004) report similar effects of habitat connectivity on fish species density in mangrove-dominated estuaries in the Bahamas, where levees with culverts have restricted access among habitats in some areas, but not others. High habitat connectance facilitating recolonization in fluctuating environments may provide a general explanation for peaks in species richness across landscapes (Tockner et al., 1998; Ward et al., 1999; Amoros & Bornette, 2002; Wiens, 2002; He & Hubbell, 2003).

We propose that hydrologic connectivity (water-mediated transfer of matter, energy, or organisms within or between elements of a

Table 4. Relative density and mass of fishes by study region

Density (No./m ²)				Mass (g/m ²)			
Species	Density	Contrib%	Cum%	Species	Mass	Contrib%	Cum%
Taylor Slough (TS)							
jorflo	1.63	23.13	23.13	jorflo	0.29	20.45	20.45
lucgoo	2.98	22.2	45.33	lucgoo	0.26	16.2	36.65
gamhol	1.48	21.53	66.86	funcon	0.1	15.38	52.03
funchr	0.61	13.69	80.55	gamhol	0.11	13.56	65.59
funcon	0.24	7.74	88.29	funchr	0.18	12.18	77.76
hetfor	0.57	4.38	92.67	cicuro	0.45	6.43	84.2
				hetfor	0.02	3.63	87.82
				cypvar	0.03	3.44	91.26
Shark River Slough (SRS)							
gamhol	6.07	23.24	23.24	gamhol	0.3	16.38	16.38
jorflo	3.11	16.81	40.04	jorflo	0.55	15.58	31.96
hetfor	4.93	16.45	56.5	lucgoo	0.26	11.91	43.87
lucgoo	3.86	13.01	69.51	funchr	0.12	10.69	54.57
funchr	0.77	12.1	81.61	hetfor	0.1	10.6	65.17
poelat	1.87	6.75	88.37	poelat	0.34	8.91	74.08
funcon	0.42	5.46	93.83	funcon	0.14	8.52	82.61
				cicuro	0.49	5.24	87.85
				leppun	0.19	3.81	91.66
Taylor River mangroves (TRM)							
lucpar	0.65	24.15	24.15	cicuro	1.42	18.12	18.12
cypvar	0.5	18.47	42.61	lucpar	0.19	17.89	36.02
poelat	0.33	15.2	57.81	cypvar	0.35	17.24	53.25
cicuro	0.31	12.44	70.25	poelat	0.53	17.22	70.47
funcon	0.14	6.31	76.56	funcon	0.17	6.51	76.99
gamhol	0.33	5.83	82.39	lepspp	0.19	4.7	81.69
micgul	0.16	5.18	87.57	micgul	0.06	4.55	86.24
lepspp	0.08	3.52	91.09	gamhol	0.07	4.27	90.51
Shark River mangroves (SRM)							
rivmar	0.47	84.56	84.56	strnot	0.13	76.06	76.06
batsop	0.03	5.97	90.53	batsop	0.06	9.29	85.35
				eucsp	0.06	4.22	89.57
				lucpar	0.04	3.03	92.61

Density and mass are the means for each region. Contrib% is the relative abundance in that region and Cum% indicates the proportion of the total for each species. Species codes are defined in Table 3.

hydrologic cycle; Pringle 2001) permits fish biomass and species richness to increase as a function of linkage between adjacent habitats in this ecosystem, primarily because of water level fluctuation on the daily, seasonal, and yearly time scales. Tidally flooded forest bordering the Shark River dries once or twice daily, leaving only intermittent aquatic refuge for fishes. The only option for most

species is to move into the deep channels of the Shark River because passage to nearby transitional mangrove habitats is blocked. Furthermore, mangrove habitats downstream from Tarpon Bay are characterized by an abundance of tidal creeks and cuts that form a physical barrier to fish movement between upstream marshes and tidal forests. These hydrological features create stressful

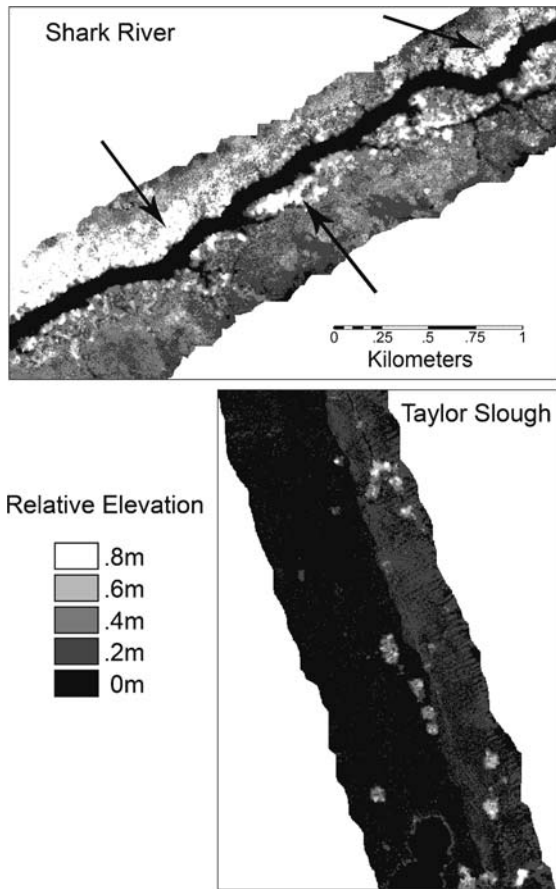


Figure 5. Estimated bare-ground elevations from LIDAR for Shark River and Taylor Slough. Relative elevation indicates difference of elevation in meters from the lowest surface (water) in late dry season, April 2003. Arrows point to natural topographic highpoints along the main channel of Shark River, 0.4–0.6 m above the surrounding marshes and 0.8–1 m above the water level in the channel. The corresponding location along Taylor Slough has isolated elevated spots, but no relief separating channel and marsh habitats, as well as a more diffuse channel structure. The ~ 0.1 m difference between the left and right along the Taylor Slough transect reflect unrectifiable drift in elevations from the two flight lines that produced this image.

(from drying and low oxygen) and risky (high predator density in creeks and river channels) habitats that result in a low standing crop of marsh-surface fishes (McIvor & Rozas, 1996). In contrast, in the Taylor River drainage there is no diurnal tide and few barriers to movement from upstream transitional mangrove and freshwater wetlands. In many dry seasons, flats habitats of the Taylor River become exposed, but fishes there can disperse to nearby shallow creeks or upstream to

other local low points. Upon reflooding, fishes can recolonize the mangrove zone from up or downstream, unlike in the Shark River. Thus, the time scale of water-level fluctuation (daily in upper Shark River drainage and seasonally in the upper Taylor River drainage) shapes both the topography and hydrological linkage between habitats. We propose that connectivity is low in the Shark River mangrove system, even over short distances, in comparison to the Taylor River System. From this proposal, we hypothesize that landscape connectivity contributes to explaining why our initial expectations of higher standing stocks in the more nutrient rich Shark River system were not supported. We propose that presence or absence of tidal variation in these two systems shapes landscape features that dictate inter-habitat connectivity and spatial patterns of predation risk and physiological stress. These spatial patterns act as filters of the regional fish species pool (Poff, 1997), while predation, salinity, and oxygen stress determine local community dynamics and act as proximate causes of spatial structure in estuarine fish communities.

There are a number of caveats to this study, not the least being its purely observational basis. One key limitation is that we are focused on standing crops of small fishes. Clearly, significant components of secondary production of this system are in the channel as large piscivorous fishes. We know that some of these fishes move into the estuarine habitats we studied, but were not collected quantitatively by our sampling gear. Prior to a separate sampling effort targeting these fish, our interpretations are speculative. Another limitation of this study comes in placement of our lift nets in homogeneous sections of fringing forest, distant from small tidal creeks or intertidal rivulets that could provide ebb-tide refuge for fishes. Our estimates of standing crops may not be representative of fringing forests that include more extensive adjacent shallow refuge. An analogous study of fishes on marsh surfaces immediately adjacent to a large river by Rozas & Odum (1987) found that the abundance and biomass of marsh-surface fishes was diminished here relative to abundance and biomass on marsh surfaces adjacent to smaller shallower streams of lower order. Perhaps most important, detailed analyses of topography and its influence of fish movement are needed in our study

habitats to test our new hypothesis and conceptual model.

Comparisons of results among fish-collection techniques must always be made with caution. In this study, we combine data from three sampling programs that are designed to best capture density dynamics of fishes at the study sites. It would be desirable to compare capture efficiency (efficiency of both capture and removal from a trap) among the studies. Capture efficiency has been estimated for the throw-trap technique (Jordan et al., 1997), while only fish removal efficiency has been estimated for the mangrove techniques. All techniques yield comparable and high removal efficiencies (e.g., see results for lift net). We have compared drop trap and throw trap collections made in the same marsh at the same time, and density estimates were indistinguishable (Trexler & Lorenz, unpublished data), but no such comparisons have been made with the lift nets used in SRM. Additional work is needed to fully resolve the direct comparability of our data.

Everglades restoration is expected to increase the amount of freshwater reaching the mangrove zone by restoring some of the 'natural' sheetflow. Salinity changes will likely influence the nature of the vegetation and algal base. Invertebrate and vertebrate communities will respond to these changes in food resource and habitat structure, and food web complexities are likely to change. Altering water flow will affect habitat connectance in long- and short- hydroperiod freshwater marshes as well as linkages between mangroves and their surrounding marsh habitats in the transitional zones (Sklar & Browder, 1998). The issue of habitat connectance should be explored in future work to determine whether new connections between previously disconnected habitats will affect fish standing crops and community composition.

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