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NOTE

Mainstem and Backwater Fish Assemblages in the Tidal Caloosahatchee River: Implications for Freshwater Inflow Studies

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Abstract Research strategies for investigating the freshwater-inflow requirements of estuarine fishes often integrate life-history information and correlative analyses of inflow and fish abundance. In tidal rivers, however, some fish have affinities for embayments, oxbows, and smaller tributaries, often referred to collectively as river "backwaters". The objective of this study was to determine whether freshwater and estuarine fish assemblages differed between backwaters and the mainstem of the tidal Caloosahatchee River, a highly managed river system located in an urban setting in southwest Florida. Nonmetric multidimensional scaling of 21.3-m seine data revealed that fish assemblages did indeed differ between the backwater and mainstem habitats in each of three river sections. Univariate analyses identified species that differed in abundance between the habitats, which included ecologically and economically important fishes in the region. For example, striped mullet *Mugil cephalus* and pinfish *Lagodon rhomboides* were more abundant along the river's mainstem; common snook *Centropomus undecimalis* and bluegill *Lepomis macrochirus* were more abundant in the river's backwaters. For those species that were more abundant along the mainstem of the river or showed no difference, studies that measure changes in the distribution and abundance of these species with varying inflow along the mainstem of the river are justified. However, for species that were more abundant in backwater areas, geomorphological features should be considered in the design of studies that assess factors affecting fish use.

Keywords Juvenile fish · Fish movement · Coastal geomorphology · Oxbows · Embayments · Tidal tributaries

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Introduction

Freshwater inflow from major rivers brings nutrients that fuel high levels of estuarine productivity and forms a salinity gradient that provides the physiochemical conditions favorable for juveniles of many marine species (Day et al. 1989). Management of freshwater resources often results in conflicts among various user groups, including fishing industries that depend on natural flow variability to provide the appropriate magnitude and timing of freshwater inflow to maintain estuary-dependent fish stocks (e.g., Baisre and Arboleya 2006). There is now broad acceptance among scientists and water managers that riverine and estuarine resources be considered legitimate users of water supplies (Flannery et al. 2002; Arthington et al. 2006). One of the most important challenges facing estuarine scientists and managers is to determine the necessary magnitude and timing of freshwater delivery to the estuary while maintaining sufficient supply for human populations (Alber 2002).

Appropriate research strategies for investigating the freshwater-inflow requirements of estuarine fishes should integrate life-history information and correlative analyses of inflow and fish abundance (Robins et al. 2005). Before such analyses can be conducted, however, scientists and managers must determine the appropriate sampling universe. Because inflow influences zones of primary productivity and environmental conditions, sampling fish assemblages along a gradient from tidal freshwater to higher salinities within river systems is particularly useful for measuring changes in fish distribution and abundance with varying inflow (Wagner and Austin 1999).

Another consideration when defining an appropriate sampling universe is landscape features within the estuarine systems. Such features within rivers include oxbows, embayments, and smaller tributaries often referred to collectively as river "backwaters." In freshwater portions of major rivers in the southeastern USA, backwater fish assemblages have been shown to be substantially different from those along the river's mainstem (Lehtinen et al. 1997). Backwaters provide the primary juvenile habitat for several recreationally important fishes, including largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus* (Scott and Nielson 1989; Nack et al. 1993; Lehtinen et al. 1997). For estuarine species, recent studies have shown that channel morphology accounts for recurring patterns and large differences in fish use among intertidal creeks (Visintainer et al. 2006; Allen et al. 2007). The authors of these studies recommended that geomorphological variation be considered when assessing factors affecting fish abundance along salinity and other environmental gradients. We hypothesize that freshwater and estuarine fish assemblages, and species-specific abundances, likely differ between the backwaters and mainstem of tidal rivers. The objective of this study was to compare the fish assemblages of the mainstem and backwater habitats of the tidal Caloosahatchee River, a highly managed river system located in an urban setting in southwest Florida.

Methods

Study Site

The Caloosahatchee River is part of a cross-Florida canal system that passes through Lake Okeechobee and connects the intracoastal waterways of Florida's east and west coasts. Water discharge to the Caloosahatchee River is regulated at three water-control structures (lock and dam) along the river. The Franklin Lock is farthest downstream and serves as the upriver boundary for tidal influence (Fig. 1). The upper tidal reaches of the river are relatively narrow (0.2 km), and the shorelines along the mainstem are highly altered as a result of channelization. Downstream of the confluence with the Orange River, the river abruptly widens to more than 1.5 km, and the littoral zone is characterized by expansive, shallow flats (<2 m deep). The remaining course of the river passes through two major cities (Fort Myers and Cape Coral), where more than 50% of the linear shoreline has been hardened with seawalls and rip-rap (estimated from aerial photography). Shorelines of remnant oxbows, embayments, and tidal tributaries are still composed of native vegetation, primarily red mangrove *Rhizophora mangle* and are therefore conspicuous features compared to the highly altered shorelines along the river's mainstem. Although extensive beds of the submerged grass *Vallisneria americana* were present in the river prior to 2000, the beds have been largely absent from the river during the past decade (only 2% of the sampling sites in the present study contained submerged aquatic vegetation). The scarcity of this grass is attributed to drought conditions and high salinities in the upper river that are intolerable to this freshwater species (Doering personal communication). Low light availability can also limit growth (Hunt and Doering 2005). The Caloosahatchee River ultimately drains into the southern portion of the Charlotte Harbor estuarine system.

Comparisons of water conditions and fish assemblages were made in three river sections (lower, middle, and upper) to account for differences in river morphology (e.g., oxbows in the upper river vs. tidal tributaries and embayments in the lower river) and likely differences in fish assemblages along the environmental gradient of the river. The upper section was defined as the area from the Franklin Lock to the confluence of the Orange River, where a distinct change in river morphology occurs. The middle section was the area from the Orange River downstream to the urban centers of Ft. Myers and Cape Coral, and the lower section extended from the urban centers to the river mouth.

Field Sampling

Monthly stratified-random sampling for fishes and selected invertebrates was conducted in the tidal Caloosahatchee River using a small center-bag seine (21.3 m long× 1.8 m deep, 3-mm-stretch mesh) from November 2003 to December 2007. For the purposes of site selection, the river was divided into seven mainstem zones and three backwater zones, and the number of sites sampled in each zone was proportional to zone area to ensure adequate coverage along the environmental gradient of the river. The sampling locations were chosen randomly each month from

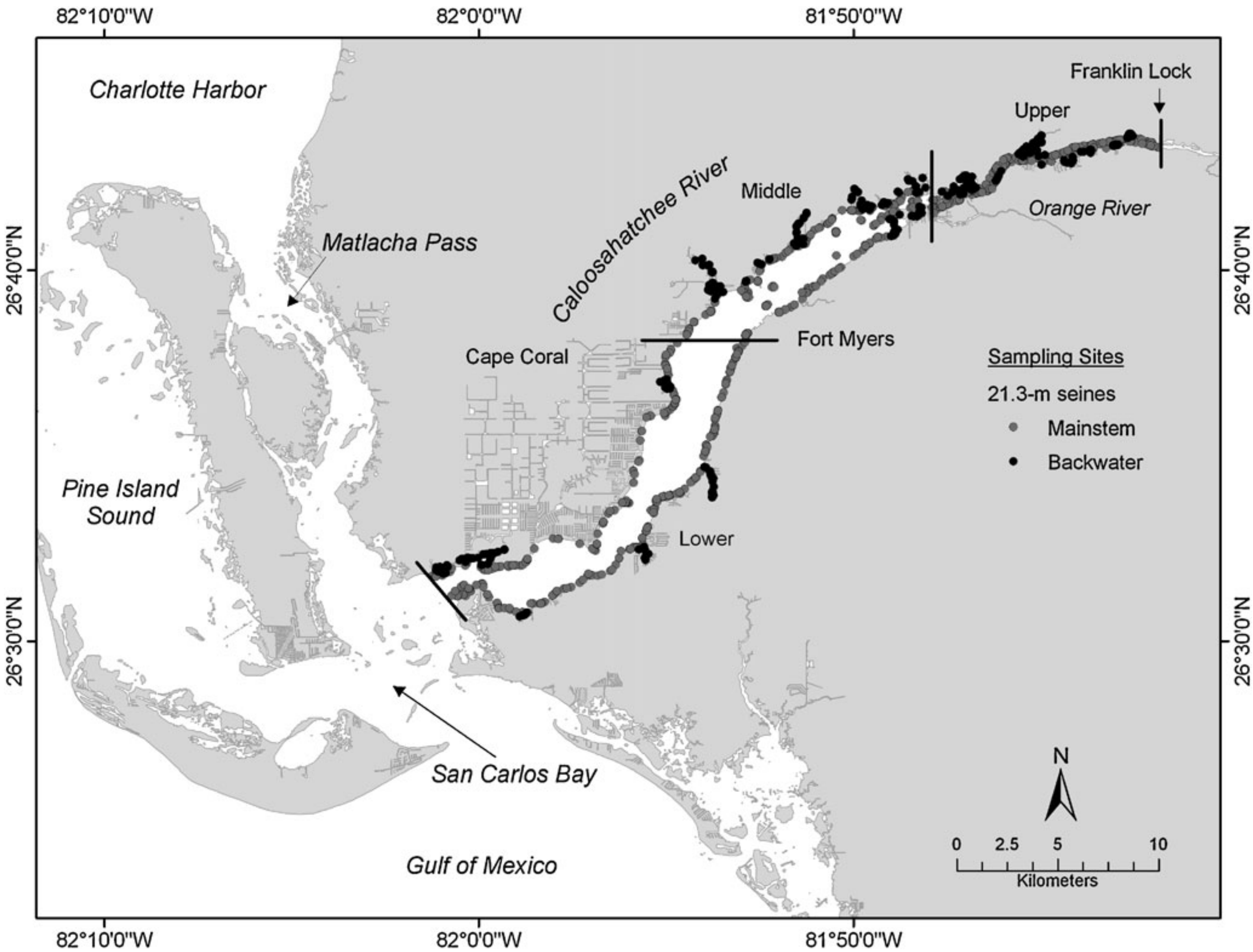

Fig. 1 Mainstem and backwater sampling sites in the Caloosahatchee River, Florida. River sections (lower, middle, upper) used in the analysis are delineated by vectors

a universe of 0.2×0.2 km grids that contained shoreline. A total of 16 sites were selected along the mainstem of the river, and seven sites were selected in the river's backwaters. The upper reaches of the tributaries considered for site selection corresponded to those areas that could be reached by shallow-draft skiffs and coincided well with the uppermost extent of the tributaries depicted on National Oceanic and Atmospheric Administration nautical charts.

Upon arrival at a sampling site, the seine was deployed from a boat in a shallow arc along the shore in depths suitable for the gear (0.3–1.8 m at the center bag). The two ends of the seine were pulled together while keeping the net along the shore type (e.g., mangrove, leatherfern, seawall), sampling an area of ~68 m^2. During each net deployment, water conditions—including temperature (°C), salinity, and dissolved oxygen ($mg l^{-1}$)—were profiled with a water quality datasonde (measurements taken at 0.2 m, 1.0 m if applicable, and at the bottom). Fishes and select invertebrates collected in each sample were identified to the lowest practical taxonomic level (nomenclature for fishes follows Nelson et al. 2004), measured, enumerated, and released in the field. Representative subsamples of organisms were retained for laboratory verification. To avoid introducing additional taxonomic terms throughout this paper, we include two swimming invertebrates, blue crab *Callinectes sapidus* and pink shrimp *Farfantepenaeus duorarum*, in the term fish assemblage.

Due to frequent hybridization and extreme difficulty in the identification of smaller individuals, members of several species complexes were either not identified to species or were treated as one functional group. Species complexes included menhaden species of the genus *Brevoortia* (*Brevoortia patronus*, *Brevoortia smithi*, and hybrids), silverside species of the genus *Menidia* (*Menidia peninsulae*, *Menidia beryllina*, and hybrids), and small individuals of the mojarra genus *Eucinostomus* (<40 mm standard length), the goby genus *Gobiosoma* (<20 mm standard length), and the sunfish genus *Lepomis* (<20 mm standard length). These species complexes were included and treated as individual species in subsequent analyses because of their high abundance in the study area, but caution should be used in the interpretation of these results because members of the species complexes may have different habitat and physiochemical affinities. Further details of site selection, sampling techniques, and taxonomic groupings can be found in Idelberger and Greenwood (2005).

Data Analyses

Water conditions measured during fish sampling were compared among river section (lower, middle, upper) and stratum (mainstem, backwater) using analysis of variance. The physiochemical variables were ln-transformed to improve normality and better satisfy the assumptions of the statistical test. Comparisons were deemed significant at $p<0.05$. Significant differences were analyzed further using Tukey's pairwise comparisons.

Spatial patterns in fish assemblage structure were analyzed using multivariate techniques. Sample abundance indices for each species (fish 100 m^{-2}) were square-root transformed to reduce the influence of highly abundant species. To determine if any observed spatial patterns in fish assemblage structure vary temporally, analyses were conducted separately for two seasons that roughly correspond to those used by south Florida water managers: wet (May–October) and dry (November–April). Analyses were also conducted separately using three seasons established for fish assemblages in nearby rivers (Idelberger and Greenwood 2005), but this approach did not add any additional information than for two seasons. Nonmetric multidimensional scaling (MDS; Clarke and Warwick 2001) was used to graphically depict relative differences in fish assemblages, after calculating Bray–Curtis similarity (Bray and Curtis 1957) matrices on data averaged by river section and stratum. A two-way analysis of similarity (ANOSIM; Clarke and Warwick 2001) was used to formally compare fish assemblages found in the mainstem and backwaters of each of the three river sections. Prior to performing ANOSIM, Bray–Curtis similarity matrices were calculated for data averaged by river section, stratum, and month. All multivariate analyses were conducted with PRIMER v.6 (PRIMER-E Ltd., Plymouth, UK).

Although similarity percentage analysis (SIMPER; Clarke and Warwick 2001) is often used to identify species representative of dissimilarities between groups determined from MDS and ANOSIM, this procedure was not performed because a more powerful species-specific comparison using a generalized linear model approach (PROC GLIMMIX in SAS v.9.1; SAS Institute, Inc., Cary, NC) was used to compare differences in species' abundance between river section and stratum. For each species, differences in adjusted (least-squares) mean abundance indices (fish 100 m^{-2}) between stratum, river section, and their interaction were tested. A negative binomial distribution with log link function and an offset of 0.68 (to convert count data to density estimates) was chosen to best represent the data. Adjusted mean abundance indices and associated standard errors were back-transformed following analysis. Species chosen for comparison were those that occurred in at least 5% of the samples and that had sample sizes of least 200 individuals. For species with distinct recruitment periods, only the months in which the species occurred in relatively high abundance were included in the analysis.

Results

Water conditions varied along the longitudinal axis of the river, but conditions were similar between the river's mainstem and its backwaters (Table 1). Analysis of variance revealed that water temperature differed among river sections ($p=0.002$), but not stratum. Pairwise comparisons showed that water temperature in the upper river was about 1°C warmer than in the lower river ($p<0.001$; the middle section of the river did not differ from the other two sections). Salinity also differed among river sections ($p<0.001$), but not stratum. Pairwise comparisons showed that salinity differed in each of the river sections (p values<0.001). The greatest difference between adjacent sections (up to 9.8 PSU) occurred between the lower and middle sections of the river. Comparisons of dissolved oxygen among river sections and stratum revealed a significant interaction ($p=0.02$). In general, dissolved oxygen was lower in the river's backwaters, but differences in mean values were never greater than 1.3 mgl^{-1}.

Fish assemblages differed by river section as expected and by stratum to a lesser degree. Lower, middle, and upper river fish assemblages on the MDS plots clearly separated from one another (Fig. 2). The mainstem and backwater fish assemblages within each river section also separated from one another, and the distances of these separations were of similar magnitude to distances between river sections. The spatial patterns of fish assemblage structure were similar for both wet and dry seasons. The results of ANOSIM support the relationships depicted in the MDS plots, although differences between mainstem and backwater fish assemblages were weaker ($R=0.11$ and 0.34; low values indicating that fish assemblages were barely distinguishable) than for river section ($R=0.44$ and 0.62; moderate values indicating that fish assemblages were fairly well separated).

Species-specific comparisons of mainstem and backwater abundances showed significant differences (Table 2,

Table 1 Mean (±SE) water temperature, salinity, and dissolved oxygen measured during fish sampling in the Caloosahatchee River, Florida

Habitat	Temperature (°C)			Salinity (PSU)			Dissolved oxygen ($mg l^{-1}$)		
	River section			River section			River section		
	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Mainstem	25.1±0.2	25.9±0.3	26.7±0.3	13.7±0.5	6.2±0.6	3.6±0.6	7.9±0.1	7.7±0.1	7.0±0.1
Backwater	25.4±0.4	25.8±0.4	26.5±0.4	14.8±0.8	5.0±0.7	3.6±0.8	6.6±0.2	6.4±0.2	6.8±0.2

Fig. 3): 14 of the species tested were significantly more abundant in the river backwaters. These included species tested in the families Fundulidae, Poeciliidae, Cyprinodontidae, Cichlidae, and Gobiidae, and three economically important fishes: bluegill *L. macrochirus*, striped mojarra *Eugerres plumieri*, and common snook *Centropomus undecimalis*. The magnitude of difference (mean backwater abundance divided by mean mainstem abundance) ranged from 1.5 to 20.5. These species tended to be more abundant in the middle and upper sections of the river.

The remaining species tested were either significantly more abundant along the mainstem of the river or showed no difference in abundance between the mainstem and backwaters. Several of these species are highly abundant,

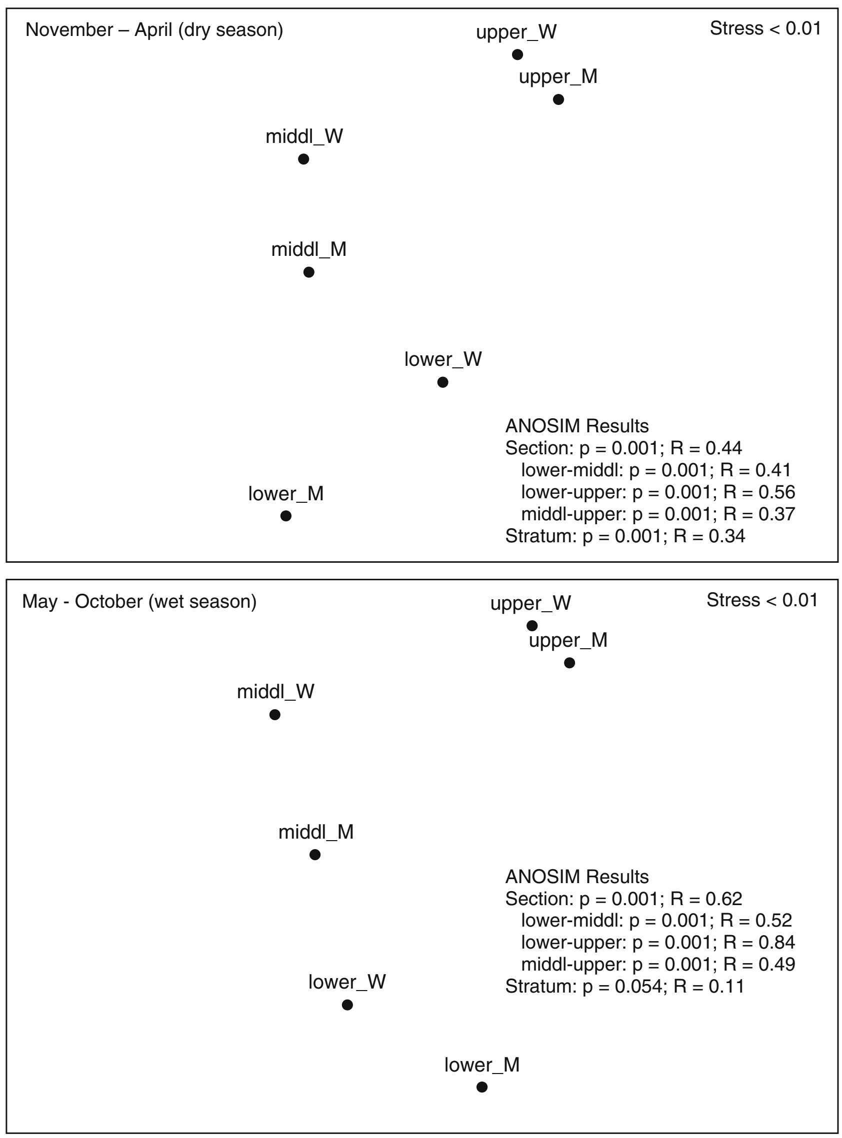

Fig. 2 Two-dimensional non-metric scaling ordination (MDS) of fish assemblages collected in 21.3-m seines along the mainstem (*M*) and in backwaters (*W*) of the lower, middle, and upper sections of the Caloosahatchee River during November 2003–December 2007. Plots are shown separately by season (November–May, dry season; May–October; wet season). The results of two-way ANOSIM comparing river sections and habitat for each season are given

Table 2 Summary of generalized linear model analyses comparing the mainstem and backwater abundance of common species in the Caloosahatchee River, Florida

Species	Common name	Adjusted mean (fish·100m^{-2})		Magnitude of difference	River section with highest abundance	River section× stratum interaction
		Mainstem	Backwater			
Species more abundant in backwaters						
Poecilia latipinna	Sailfin molly	0.1	2.9	20.5	Middle and upper	A
Tilapia mariae	Spotted tilapia	0.1	0.8	12.8	Middle and upper	A
Cichlasoma urophthalmus	Mayan cichlid	0.2	1.7	11.1		
Lucania parva	Rainwater killifish	0.2	2.1	10.4	Middle	
Gambusia holbrooki	Eastern mosquitofish	3.4	24.2	7.1	Upper	A
Centropomus undecimalis	Common snook	0.2	1.2	6.5		A
Lepomis macrochirus	Bluegill	0.1	0.5	4.0	Upper	
Eugerres plumieri	Striped mojarra	0.5	2.0	3.7		
Fundulus seminolis	Seminole killifish	0.2	0.6	3.5	Upper	B
Cyprinodon variegatus	Sheepshead minnow	0.1	0.3	3.2	Upper	
Trinectes maculatus	Hogchoker	1.5	4.6	3.1	Upper	B
Gobiosoma bosc	Naked goby	0.5	0.8	1.7	Upper	
Gobiosoma spp.	Gobies	0.5	0.8	1.6	Upper	
Microgobious gulosus	Clown goby	3.6	5.4	1.5	Upper	B
Species more abundant along mainstem						
Anchoa hepsetus	Striped anchovy	0.3	< 0.1	695.8	Lower and middle	C
Leiostomus xanthurus	Spot	2.9	< 0.1	386.0	Lower and middle	C
Opisthonema oglinum	Atlantic thread herring	1.0	0.1	16.7		
Eucinostomus gula	Silver jenny	3.2	0.2	13.3	Lower	C
Mugil cephalus	Striped mullet	22.6	1.8	12.8	Middle and upper	C
Brevoortia spp.	Menhadens	2.9	0.3	10.3	Lower	
Bairdiella chrysoura	Silver perch	0.9	0.1	8.4	Lower	
Oligoplites saurus	Leatherjack	2.4	0.8	2.9		C
Lagodon rhomboides	Pinfish	4.4	2.0	2.3	Middle	
Species showing no difference						
All species	Total catch	501.7	553.7		Middle	
Anchoa mitchilli	Bay anchovy	220.5	323.3		Middle	
Menidia spp.	Silversides	85.5	78.7		Upper	
Eucinostomus spp.	Mojarras	25.8	35.7			
Eucinostomus harengulus	Tidewater mojarra	10.1	12.0			
Sciaenops ocellatus	Red drum	3.1	1.7		Middle	
Lepomis spp.	Sunfishes	2.0	2.8			
Elops saurus	Ladyfish	1.4	2.7			
Callinectes sapidus	Blue crab	0.8	0.7		Middle	
Farfantepenaeus duorarum	Pink shrimp	0.6	0.4		Lower	
Strongylura notata	Redfin needlefish	0.1	0.2		Lower	

Also shown are any significant differences in mean abundance by river section and any significant river section-stratum interactions

A general trend of greater mean backwater abundance in each of the river sections, *B* greater mean backwater abundance in lower and middle river sections, but mean mainstem abundance was greater in upper section, *C* general trend of greater mean mainstem abundance in each of the river sections

including bay anchovy *Anchoa mitchilli*, silverside species of the genus *Menidia* spp., and mojarra species of the genus *Eucinostomus*. Others are economically important, including striped mullet *Mugil cephalus*, red drum *Sciaenops ocellatus*, blue crab *C. sapidus*, and pink shrimp *F. duorarum*. The species in these groups were generally more abundant in the lower and middle sections of the river.

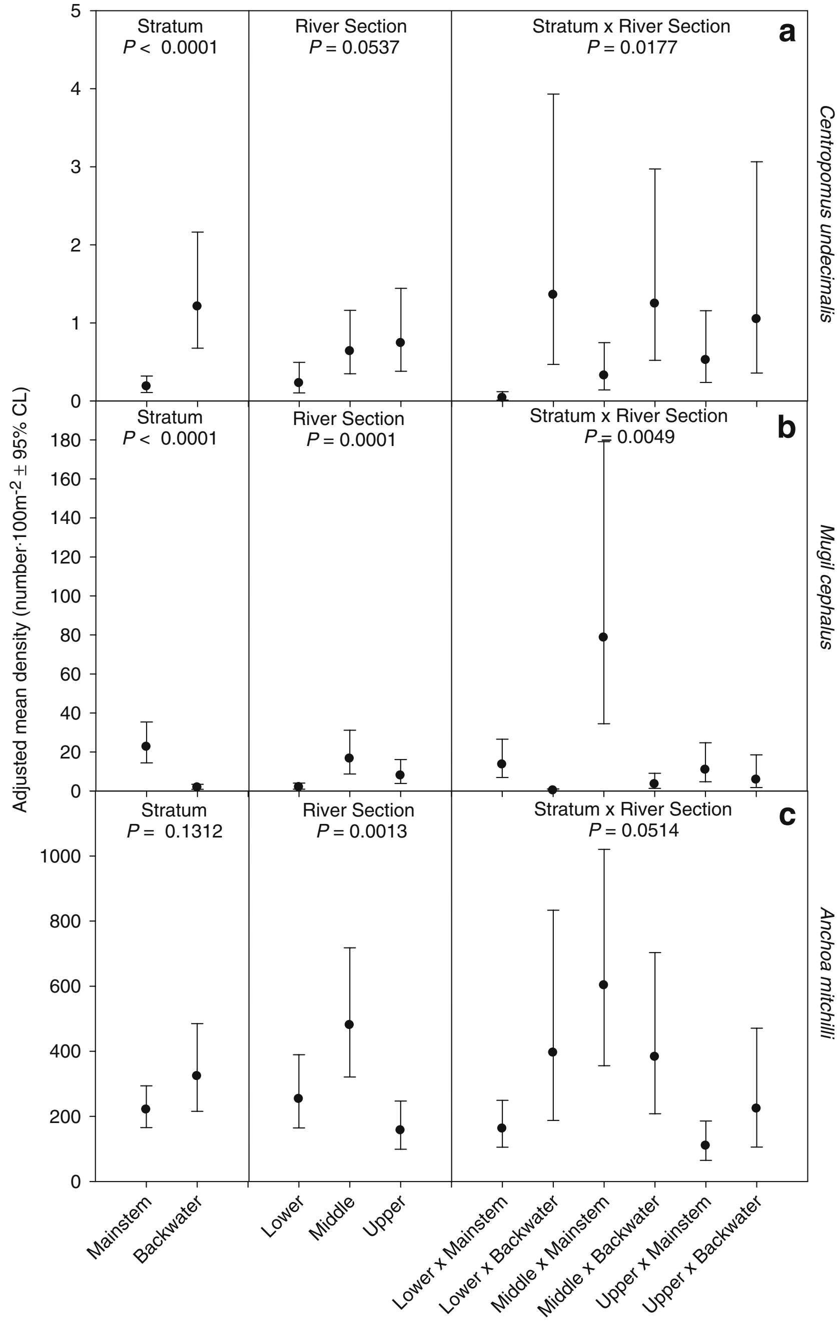

Fig. 3 Examples of species that **a** were more abundant in the backwaters, **b** were more abundant along the mainstem, and **c** did not differ in abundance between the mainstem and backwaters of the Caloosahatchee River, as assessed with generalized linear models

Discussion

Understanding how river geomorphology influences habitat for both estuarine and freshwater fishes is a critical first step in addressing how fishes respond to variable inflow. River geomorphology and associated habitat were nearly as important in structuring the fish assemblages as were relatively major changes in the physiochemical variables (differences in salinity up to 9.8, for example) along the mainstem of the river. Differences in mainstem and backwater fish assemblages persisted even when evaluated separately by season. Because water conditions did not significantly differ between the mainstem and backwaters within each river section, the differences in fish assemblages likely result from differences in vegetation, stream morphology, current velocity, wind exposure, food resources, and a myriad of other factors that characterize these two habitats. Although catch efficiency of seines can vary when used in different habitats (Rozas and Minello 1997), the spatial differences observed in this study are unlikely to occur due to sampling bias alone. Substrates sampled were comprised of either sand/mud or mud only; submerged aquatic vegetation was largely absent in both habitats during the study period; sampling depths in the two habitats were comparable; the sampling technique (pulling the net along the shore type) ensured that the net was not fouled in shoreline vegetation, and the species reported to be different between the habitats were predominately mid-water, not benthic.

For those species that were more abundant along the mainstem of the river or showed no difference, analyses that measure changes in the distribution and abundance with varying inflow along the mainstem of the river are appropriate. As withdrawals increase to meet demands for potable water, upstream movement of fishes in response to changing physiochemical conditions and prey abundance may place these fishes in areas of the river that are small in area and volume (Estevez 2002). The displacement of fish from optimal static habitat (e.g., emergent vegetation) in response to shifts in dynamic habitat (e.g., salinity) has been hypothesized to decrease fish productivity (Browder and Moore 1981; Sklar and Browder 1998). Thus, information about the position of fishes along the river under specific flow regimes is critical to resource managers developing minimum flows for the river (Flannery et al. 2002; Greenwood et al. 2007b).

The majority of the species that were more abundant in the river's backwaters could be classified as river residents (species that complete their life cycle within the river). The species in the families Fundulidae, Poeciliidae, and Cyprinodontidae are adapted to living in saltmarsh and mangrove habitats (Nordlie 2006). These species have broad tolerances for temperature and salinity, are capable of respiring at the water's surface to cope with low oxygen, and have reproductive strategies adapted for living in coastal wetlands. Saltmarsh and mangrove fishes are important in the flow of energy through estuarine ecosystems. They convert marsh production (e.g., detritus) to high-quality, vagile biomass (fishes concentrate energy, protein, and nutrients as body mass), which can then be consumed by estuarine predators. In a seasonally flooded saltmarsh in east-central Florida, at least 20% of the fish production was estimated to have been consumed by piscivorous fishes and birds (Stevens et al. 2006).

Two of the river residents that were found to be more abundant in the river's backwaters are targeted by recreational anglers: *E. plumieri* and *L. macrochirus*. *E. plumieri* is a subtropical, estuarine species that inhabits mangrove-lined creeks and tidal rivers. In studies correlating species abundance with physiochemical and habitat conditions, *E. plumieri* was shown to associate with mangroves, unvegetated bottoms, and low salinity (Kupschus and Tremain 2001; Greenwood et al. 2007a; Whaley et al. 2007), characteristics associated with the river backwaters of the present study. The greater abundance of the freshwater *L. macrochirus* in backwater oxbows and tributaries has been reported in previous studies conducted in channel border and backwater areas of major rivers (Scott and Nielson 1989; Lehtinen et al. 1997). Because *L. macrochirus* prefers structured habitat and is a nest-builder, quiescent waters that enable nest building and have dense habitat structure (overhanging vegetation and snags) were thought to explain the high abundance of this species in backwaters. Similar life-history characteristics (nest building and associations with quiescent waters and highly structured habitats) have been described for the exotic *Cichlasoma urophthalmus* and spotted tilapia *Tilapia mariae* (Shafland 1994; Faunce and Lorenz 2000) and likely explain their greater abundance in the backwaters of the Caloosahatchee River relative to the mainstem.

C. undecimalis, one of the most important sport fish in southwest Florida, is a river transient (a species that uses the river during only a portion of its life cycle) found to be more abundant in the backwaters. Relatively few *C. undecimalis* nurseries in the Charlotte Harbor estuary have been identified (Adams et al. 2006; Stevens et al. 2007). Those that have been identified are located in coastal wetland ponds, creeks, and island networks, many of which are so remote they are inaccessible to sampling by boat. The close proximity of the Caloosahatchee River to ocean passes used as spawning sites and the availability of coastal wetland habitat in its backwaters are factors that likely explain the presence of juvenile *C. undecimalis* in the river. The abundances of juvenile *C. undecimalis* in the backwaters of the Caloosahatchee River are of the same magnitude (~1 fish 100 m^{-2}) as those described for the few juvenile *C. undecimalis* habitats found elsewhere in the Charlotte Harbor estuary. Because the river's backwaters provide juvenile habitat for *E. plumieri*, *L. macrochirus*, and *C. undecimalis*, these morphologically distinct areas of the river should be of prime importance to programs targeting lands for acquisition, management, and conservation.

In conclusion, river geomorphology and associated habitat were important factors influencing fish assemblage structure and species-specific abundance. Evaluating the influence of river geomorphology is an important first step in assessing factors affecting fish use of habitats along salinity and other environmental gradients. The mainstem assemblages may be more relevant to managers wishing to apply quantitative relationships between fishes and freshwater inflow, for example as distribution responses. The river backwaters, however, are of considerable importance because of their value as habitat for resident and transient species. In the Caloosahatchee River, the shorelines of backwater habitats are composed of native vegetation, which differs from the hardened shorelines along many portions of the river's mainstem. It is possible that these striking habitat differences were as important as river geomorphology in shaping the fish assemblages. A similar sampling design should be implemented in tidal rivers with less anthropogenic alteration to corroborate this study's findings.

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