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The Effects of Season and Proximity to Fringing Mangroves on Seagrass-Associated Fish Communities in Charlotte Harbor, Florida

GREGG R. POULAKIS, DAVID A. BLEWETT, AND MICHAEL E. MITCHELL

Little has been published on habitat use by fishes in Charlotte Harbor, one of Florida's largest—and still relatively pristine—estuaries. Multivariate analyses of data from 21.3-m-seine samples (1996–2000) were used to examine spatiotemporal patterns of seagrass habitat use by Charlotte Harbor fishes. Two habitats (mangrove-associated seagrass shorelines and offshore seagrass flats) were examined. Throughout the year, the mangrove–seagrass habitat was distinguished by *Menidia* spp., *Mugil gyrans*, *Eucinostomus harengulus*, and *Floridichthys carpio*, and the offshore seagrass flats habitat was distinguished by *Bairdiella chrysoura*, *Orthopristis chrysoptera*, and *Cynoscion nebulosus*. The dry season (Dec.–May) was distinguished by *Lagodon rhomboides*, *Leiostomus xanthurus*, and *O. chrysoptera* in both habitats and by *Mugil cephalus* in the mangrove–seagrass habitat. The wet season (June–Nov.) was distinguished by *Lucania parva*, *F. carpio*, and *Fundulus grandis* in the mangrove–seagrass habitat and by *Eucinostomus gula*, *Microgobius gulosus*, *C. nebulosus*, and *E. harengulus* in the offshore seagrass flats habitat. *Eucinostomus* spp., *Anchoa mitchilli*, and *Strongylura notata* were abundant in both habitats during the wet season. In general, many species were collected in both habitats and were widely distributed in the estuary. Various combinations of four environmental variables (i.e., water temperature, salinity, dissolved oxygen, water depth) and their coefficients of variation were well correlated with the biotic community patterns. These results show that different fish communities use different seagrass habitats in Charlotte Harbor, depending on the season and the proximity of the seagrasses to fringing mangroves.

The importance of seagrasses as habitat for estuarine fishes, especially during their early life stages, is well documented (e.g., Weinstein et al., 1977; Livingston, 1982; Ziemann, 1982; Comp and Seaman, 1985). Various methods were used in these studies, and many of them implicated species-specific larval availability and distribution, seagrass bed size, leaf height, or leaf density as determinants of species composition and abundance of fishes in seagrass habitats (e.g., Bell and Westoby, 1986a, 1986b; Bell et al., 1987, 1988; Savino and Stein, 1989). Comparatively, only a few studies have considered the effect that seagrass bed location within an estuary has on the associated fish community (e.g., Bell and Westoby, 1986a; Bell et al., 1988; Gilmore, 1988), and none of these studies was conducted in southwest Florida.

Even though extensive estuarine research throughout the world has shown that the composition of subtropical estuarine fish assemblages typically varies both spatially and temporally and is affected by various abiotic and biotic factors (e.g., Comp and Seaman, 1985), it is important to characterize a given estuary in sufficient detail for the extent of inevitable anthropogenic effects (e.g., freshwater with-

drawals, development) to be determined. Within a particular zoogeographic province, the species composition of estuarine ichthyofaunas may be similar; however, spatiotemporal aspects of habitat use are likely to have system-specific variability for a variety of reasons (e.g., amount and timing of freshwater input). The spatial organization of fish species within an estuary is related to the habitat characteristics in the system (Livingston et al., 1976; Blaber and Blaber, 1980; Comp and Seaman, 1985), whereas the temporal structure of the fish community is frequently related to the predictable life-history patterns of the component species (Tremain and Adams, 1995; Jackson and Jones, 1999).

Charlotte Harbor is one of the largest and least studied estuarine systems in Florida. Early descriptions of the fish community were generally limited to qualitative surveys (e.g., Henshall, 1891; Woolman, 1892; Lönnberg, 1894) and observations made after local fish-kills (e.g., Willcox, 1887; Storey and Gudger, 1936; Gilmore et al., 1978). Other studies provided more detailed information (e.g., Phillips and Springer, 1960; Clark and von Schmidt, 1965; Gunter and Hall, 1965; Wang and Raney, 1971; Champeau, 1990; Fraser, 1997; Nelson and Lef-

fler, 2001; Seitz and Poulakis, 2002) although many were of limited duration and geographic coverage or remain unpublished. The purpose of this study was to describe the spatial and seasonal patterns of habitat use by fishes in two of the most common habitats found in Charlotte Harbor: mangrove-seagrass shorelines and offshore seagrass flats.

STUDY LOCATION

Charlotte Harbor is a 700-km² coastal plain estuarine system located on the southwest coast of Florida and is the second largest estuarine system in the state (Hammett, 1990; Fig. 1). Tidal water exchange occurs between the estuary and the Gulf of Mexico through Boca Grande Pass, San Carlos Bay, and three smaller inlets. Considerable freshwater input (ca. 13,250 million liter d⁻¹) is received from the Peace, Myakka, and Caloosahatchee rivers, and together, these rivers drain a basin whose extent exceeds 12,000 km² (Hammett, 1990). The modal depth of the estuary is 3–4 m (Brooks, 1973), with a maximum depth of 15.5 m in Boca Grande Pass (Huang, 1966). Seasonal mean water temperatures range from 12 C to 36 C, and annual rainfall averages about 127 cm (Stoker, 1986).

Charlotte Harbor supports a variety of habitats (Taylor, 1974; Harris et al., 1983). Among the predominant habitats are seagrass flats (262 km²; Sargent et al., 1995) and mangrove fringe (143 km²; L. Kish, unpubl. data). Seagrass beds consisting primarily of *Thalassia testudinum* and *Halodule wrightii* are most prevalent in the southern portion of the harbor, and if present in the northern portion, typically occur as thin bands of *H. wrightii* near the shore (Stoker, 1986). Mangrove fringe consists primarily of *Rhizophora mangle* and includes *Avicennia germinans* and *Laguncularia racemosa*. Although Charlotte Harbor remains one of the least-impacted water bodies in Florida, rapid population growth and development surrounding the harbor and within the watershed have resulted in increased stress on the ecosystem (Hammett, 1990; Stoker, 1992; Charlotte Harbor National Estuary Program, 1999).

MATERIALS AND METHODS

Sample collection.—We examined data collected by the Florida Fish and Wildlife Conservation Commission (FWC) Florida Marine Research Institute's Fisheries-Independent Monitoring program. Sampling was conducted on a monthly basis during the day (23–32 samples

mo⁻¹) from 1996 to 2000. A stratified random design was used for sample-sight selection. Charlotte Harbor was divided into 1 × 1 cartographic grids (1 nm²), and grids with appropriate water depths for seine sampling (up to 1.5 m) were selected as the sampling universe. This universe was then subdivided into five sections to facilitate sampling logistics and to ensure adequate sampling coverage of the estuary. Grids to be sampled during each month were randomly selected from within each section. Each selected grid was then subdivided into microgrids by using a 10 × 10 cell overlay, and sample sites were randomly selected from among these microgrids. Samples were collected with center-bag seines (21.3 × 1.8 m, 3.2-mm stretch mesh) along mangrove shorelines and on offshore flats (>5 m from shore) inside the estuary. Seines were pulled over a distance of 9.1 m, and a separation of 15.5 m was maintained between the opposite ends of the net during the haul. Seines were pulled into the current and were landed either on shore or retrieved by collapsing the seine around a pivot pole to close the wings and force the sample into the bag.

Fishes were identified to the lowest practical taxon, measured (standard length for teleosts, disk width for rays), and enumerated in the field. Representative subsamples of fishes were retained for taxonomic verification and as voucher specimens, and the remainder of the catch was released. Nomenclature follows Robins et al. (1991) unless otherwise noted. Because of taxonomic difficulties in the field, *Brevoortia* spp. (includes *Brevoortia patronus* and *B. smithi*), *Menidia* spp. (includes *Menidia beryllina* and *M. peninsulæ*), and small (<ca. 40 mm standard length) *Eucinostomus* spp. (includes primarily *Eucinostomus gula* and *E. harengulus*) were identified to genus (Matheson, 1983; Rogers and Van Den Avyle, 1983; Middaugh et al., 1986). Several specimens belonging to the genera *Hyporhamphus* and *Gobionellus* could not be identified to species with certainty, so these taxa were also identified to genus for this analysis. Hydrologic data, including water temperature (C), salinity (‰), and dissolved oxygen (ppm), were recorded at each sample site using a Hydrolab®. Data regarding environmental parameters such as water depth, seagrass coverage, and shoreline characteristics (e.g., percent coverage and type of vegetation) were qualitatively assessed and recorded at each site.

Statistical analysis.—Samples were grouped by habitat type, geographic location, and season. Two habitat types were examined: (1) man-

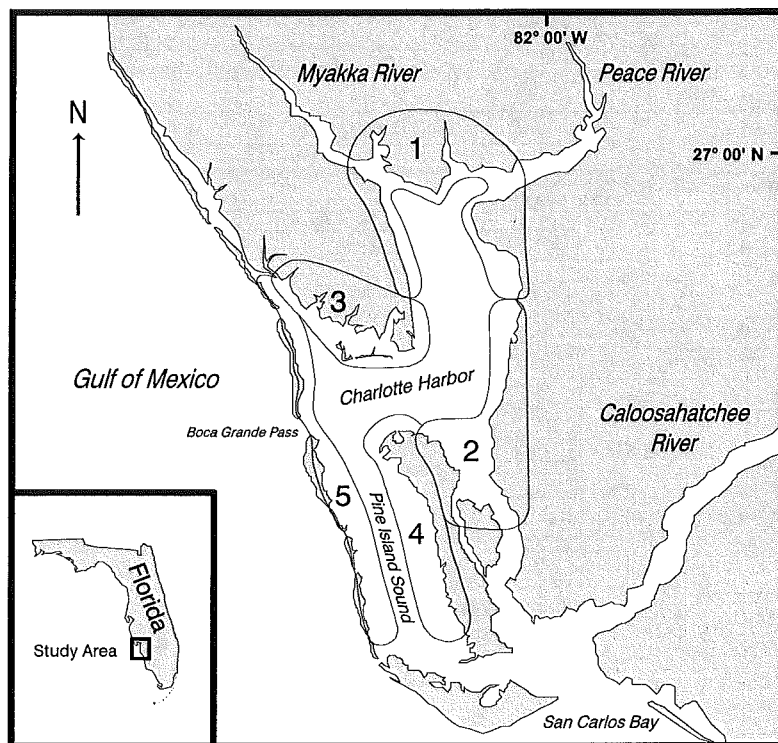


Fig. 1. Location of the Charlotte Harbor estuarine system in Florida and the geographic zones used for the analysis. To date, no areas in the extreme southern end of the system have been included in the regular sampling program.

grove shorelines ($\geq 50\%$ *R. mangle*) with $\geq 50\%$ seagrass coverage (visual estimate) and (2) off-shore flats (> 5 m from shore) with $\geq 50\%$ seagrass coverage. On the basis of previously identified areas of similar hydrologic influence (Alberts et al., 1969, 1970; Stoker, 1992; Goodwin, 1996), we created five geographic zones that encompassed all the shoreline and flats areas we sample (Fig. 1). Two seasons (dry season: Dec.–May; wet season: June–Nov.) were defined on the basis of historical monthly rainfall levels (Charlotte Harbor National Estuary Program, 1999).

Multivariate analyses were used to examine habitat use by fishes. Catch data for all years combined were converted to an abundance index (mean number of fish 100 m^{-2}) for each species in each combination of habitat type, zone, and season (e.g., mangrove–seagrass habitat/zone 1/dry season = MID). To emphasize the contribution of the less abundant species, we double–square–root transformed the catch data before calculating similarities. Nonmetric multidimensional scaling (MDS) was used to ordinate habitat groups from biotic similarity matrices that were created using a

group-average linkage method based on Bray–Curtis similarities (Bray and Curtis, 1957). Analysis of similarity (ANOSIM) was used to compare species compositions between the two habitats and between the two seasons within each habitat (Clarke, 1993). The contributions of individual species to within-group similarities and among-group dissimilarities were determined by similarity percentages analysis (SIMPER; Clarke, 1993). Taxa that distinguished a given habitat (or season) had high dissimilarity ratios (d_{avg}/SDd) and large differences between average abundance when compared with the same taxa in the other habitat (see Clarke and Warwick, 1994).

The biotic ordination was linked to environmental variables by using the BIO-ENV procedure of Clarke and Ainsworth (1993). We calculated the similarity matrices for environmental data by using Euclidean distance on the basis of the following eight abiotic variables: water temperature, salinity, dissolved oxygen, water depth, and each of their coefficients of variation (CV). The CV was used to incorporate the variability of the chosen parameters. All possible combinations of environmental

TABLE 1. List of taxa collected between 1996 and 2000 (abundance index = number of fish 100 m⁻²) in the mangrove-seagrass habitat (mangrove) and the offshore seagrass flats habitat (flats) during the two seasons. Nomenclature follows Robins et al. (1991) unless otherwise noted.

	Mangrove		Flats	
	Dry ^a	Wet	Dry	Wet
Dasyatidae				
<i>Dasyatis sabina</i>	0.03	0.02	0.01	0.02
<i>Dasyatis say</i>	0	0	0	<0.01
Elopidae				
<i>Elops saurus</i>	0	0	0.01	0
Albulidae				
<i>Albula vulpes</i>	0	0	<0.01	0
Clupeidae				
<i>Brevoortia</i> spp. ^b	0	0	0.01	0
<i>Harengula jaguana</i>	4.55	2.22	0.53	8.85
<i>Opisthonema oglinum</i>	0	0.01	0.01	0.42
<i>Sardinella aurita</i>	0	0.20	0	0.62
Engraulidae				
<i>Anchoa hepsetus</i>	22.01	0.33	1.72	0.73
<i>Anchoa mitchilli</i>	17.74	76.89	19.19	47.67
Ariidae				
<i>Arius felis</i>	0	0.01	0	0.01
Synodontidae				
<i>Synodus foetens</i>	0.28	0.21	0.36	0.17
Gadidae				
<i>Urophycis floridana</i>	0.01	0	0.01	0
Batrachoididae				
<i>Opsanus beta</i>	0.06	0.11	0.03	0.09
Gobiesocidae				
<i>Gobiesox strumosus</i>	0.02	<0.01	0.01	0
Exocoetidae				
<i>Hyporhamphus</i> spp. ^c	0	0	0.03	<0.01
Belontiidae				
<i>Strongylura marina</i>	0	0	0	<0.01
<i>Strongylura notata</i>	0.53	1.82	0.09	0.30
<i>Strongylura timucu</i>	0.08	0.06	0.01	0.01
Cyprinodontidae				
<i>Adinia xenica</i>	0.03	0.01	0	0
<i>Cyprinodon variegatus</i>	0.89	0.38	0.04	0.27
<i>Floridichthys carpio</i>	5.69	13.50	1.24	2.11
<i>Fundulus confluentus</i>	0	0.01	0.01	0
<i>Fundulus grandis</i>	0.26	1.20	0.03	0.03
<i>Fundulus majalis</i>	0.04	0.50	0	0.01
<i>Lucania parva</i>	37.70	97.70	53.58	62.05
Poeciliidae				
<i>Gambusia holbrooki</i>	0.24	0.02	<0.01	0
<i>Poecilia latipinna</i>	0.57	0.99	0	0
Atherinidae				
<i>Membras martinica</i>	0.09	0.59	0	0.02
<i>Menidia</i> spp. ^d	84.29	22.44	0.84	1.70

TABLE 1. Continued.

	Mangrove		Flats	
	Dry ^a	Wet	Dry	Wet
Syngnathidae				
<i>Anarchopterus criniger</i>	0.01	<0.01	0.01	0.01
<i>Hippocampus erectus</i>	0	0.01	0.03	<0.01
<i>Hippocampus zosterae</i>	0.37	0.27	0.44	0.20
<i>Syngnathus floridae</i>	0.06	0.07	0.34	0.59
<i>Syngnathus louisianae</i>	0.18	0.19	0.40	0.47
<i>Syngnathus scovelli</i>	2.98	5.53	4.22	6.36
Scorpaenidae				
<i>Scorpaena brasiliensis</i>	0	0	0	0.02
Triglidae				
<i>Prionotus scitulus</i>	0.03	0.03	0.03	0.02
<i>Prionotus tribulus</i>	0.04	0.10	0.01	0.02
Centropomidae				
<i>Centropomus undecimalis</i>	0.02	0.01	<0.01	0
Serranidae				
<i>Centropristis striata</i>	0	0	0.01	0.02
<i>Diplectrum formosum</i>	0	0	<0.01	<0.01
<i>Mycteroperca microlepis</i>	<0.01	0.01	0.01	0.03
<i>Serranus subligarius</i>	0	0.01	<0.01	0.01
Carangidae				
<i>Caranx hippos</i>	0.01	0.01	0	0.01
<i>Chloroscombrus chrysurus</i>	0	0	0	0.23
<i>Hemicaranx amblyrhynchus</i>	0	0	0	<0.01
<i>Oligoplites saurus</i>	0.01	0.87	0.01	0.18
<i>Selene vomer</i>	0	0	0	0.01
<i>Trachinotus falcatus</i>	0	0.02	<0.01	0
Lutjanidae				
<i>Lutjanus analis</i>	0	0.01	0	0
<i>Lutjanus griseus</i>	0.05	0.44	0.06	0.34
<i>Lutjanus synagris</i>	0.01	0.13	0.04	0.31
Gerreidae				
<i>Diapterus plumieri</i>	0.08	2.01	0	0.04
<i>Eucinostomus gula</i>	19.25	30.46	6.44	23.71
<i>Eucinostomus havengulus</i>	6.65	6.03	0.29	1.52
<i>Eucinostomus</i> spp. ^c	16.63	37.39	9.16	35.70
Haemulidae				
<i>Haemulon plumieri</i>	<0.01	0.04	0.15	0.45
<i>Orthopristis chrysoptera</i>	3.12	0.29	8.64	0.62
Sparidae				
<i>Archosargus probatocephalus</i>	0.12	0.25	0.40	0.16
<i>Calamus arctifrons</i>	0.02	<0.01	0.08	0
<i>Diplodus holbrookii</i>	0.01	0	0.05	0
<i>Lagodon rhomboides</i>	139.22	27.54	166.00	19.37
Sciaenidae				
<i>Bairdiella chrysoura</i>	3.21	8.21	10.40	17.57
<i>Cynoscion arenarius</i>	0	0.05	0	0.09
<i>Cynoscion nebulosus</i>	0.30	1.22	0.56	2.61
<i>Leiostomus xanthurus</i>	2.57	0.07	1.62	0.03
<i>Menticirrhus americanus</i>	0.01	0.03	0	0.23

TABLE 1. Continued.

	Mangrove		Flats	
	Dry ^a	Wet	Dry	Wet
<i>Menticirrhus saxatilis</i>	0.05	0	0.04	<0.01
<i>Sciaenops ocellatus</i>	0.80	0.37	0.09	0.19
Ephippidae				
<i>Chaetodipterus faber</i>	0	0.02	0	0.04
Mugilidae				
<i>Mugil cephalus</i>	1.18	0.15	0.01	0
<i>Mugil curema</i>	0.01	<0.01	0	0
<i>Mugil gyrans</i>	3.13	3.05	0.31	0.08
Sphyraenidae				
<i>Sphyraena barracuda</i>	0	0.01	0	0
<i>Sphyraena picudilla</i>	0	0	0.05	<0.01
Labridae				
<i>Halichoeres bivittatus</i>	0	0	<0.01	<0.01
Scaridae				
<i>Nicholsina usta</i>	0.01	0.01	0.18	0.01
Uranoscopidae				
<i>Astroscopus y-graecum</i>	0	0	0.01	0
Clinidae				
<i>Paraclinus marmoratus</i>	0.01	0.03	0.01	0.02
Blenniidae				
<i>Chasmodes saburrae</i>	0.56	0.54	0.63	0.85
<i>Hypsoblennius hentz</i>	0	0	0.02	0.01
Eleotridae				
<i>Dormitator maculatus</i>	0.01	<0.01	0	0
Gobiidae				
<i>Bathygobius soporator</i>	0	0.01	0	0
<i>Gobionellus</i> spp. ^f	0.10	0	<0.01	0
<i>Gobiosoma bosc</i>	0.01	<0.01	0.01	<0.01
<i>Gobiosoma robustum</i>	4.63	1.93	3.95	1.95
<i>Microgobius gulosus</i>	4.44	5.20	2.44	4.85
<i>Microgobius thalassinus</i>	0	0	0	0.06
Bothidae				
<i>Citharichthys macrops</i>	0	0	<0.01	0
<i>Paralichthys albigutta</i>	0.01	0.01	0.05	0.02
Soleidae				
<i>Achirus lineatus</i>	0.11	0.20	0.05	0.06
<i>Symphurus plagiusa</i>	0.04	0.08	0.03	0.06
<i>Trinectes maculatus</i>	0.01	0.04	0	0.02
Balistidae				
<i>Aluterus schoepfi</i>	0	0	<0.01	<0.01
<i>Monacanthus ciliatus</i>	0	0	<0.01	0.02
<i>Monacanthus hispidus</i>	0.13	0.12	0.56	0.30
Ostraciidae				
<i>Lactophrys quadricornis</i>	0.01	0	0.01	0.01

TABLE 2. Summary of similarity percentages analysis comparing the mangrove–seagrass habitat (mangrove) and the offshore seagrass flats habitat (flats). In terms of similarity, 10 taxa accounted for >50% of the total similarity within each group, and eight of these taxa were common to both groups. The percent contribution of each taxon to the total similarity is listed in parentheses after the average abundances (number of fish 100 m⁻²). In terms of dissimilarity, the most abundant taxa with the highest ratios (d_{avg}/SDd) and the largest difference between average abundance in both groups are listed as consistent distinguishing taxa (Clarke and Warwick, 1994). The percent contribution of each taxon to the total dissimilarity is listed in parentheses after the ratio. d_{avg} is the mean contribution of a taxon to the dissimilarity between the two groups, and d_{avg}/SDd is the ratio between the mean contribution of a taxon and the standard deviation of the values for that taxon. The cutoff for cumulative dissimilarity was 55%.

	Similarity		Dissimilarity	
	Mangrove	Flats	Mangrove vs Flats	
<i>Lagodon rhomboides</i>	79.3 (7.2)	89.6 (7.8)	Distinguishing taxa from mangrove group:	
<i>Lucania parva</i>	62.5 (6.8)	52.1 (7.1)		
<i>Menidia</i> spp.	53.8 (6.4)	^a	<i>Menidia</i> spp.	1.9 (4.3)
<i>Anchoa mitchilli</i>	53.2 (6.1)	42.2 (6.4)	<i>Mugil gyrans</i>	1.4 (2.4)
<i>Eucinostomus</i> spp.	24.9 (6.0)	20.6 (5.0)	<i>E. harengulus</i>	1.3 (2.1)
<i>Eucinostomus gula</i>	23.3 (6.0)	14.4 (4.8)	<i>Floridichthys carpio</i>	1.2 (2.4)
<i>Eucinostomus harengulus</i>	5.7 (3.6)	^a	Distinguishing taxa from flats group:	
<i>Microgobius gulosus</i>	5.1 (3.8)	4.1 (3.5)		
<i>Syngnathus scovelli</i>	3.9 (3.8)	5.6 (4.7)	<i>B. chrysoura</i>	1.5 (2.7)
<i>Gobiosoma robustum</i>	3.2 (3.6)	2.9 (3.7)	<i>Orthopristis chrysoptera</i>	1.3 (2.2)
<i>Bairdiella chrysoura</i>	^a	15.7 (5.3)	<i>C. nebulosus</i>	1.2 (1.4)
<i>Cynoscion nebulosus</i>	^a	1.7 (3.0)		

^a Average abundances were given only for taxa that contributed to >50% of the total similarity in each group.

gulosus, *Sphaeroides nepheus*, *Syngnathus louisianae*, and *S. scovelli* were also encountered throughout the year and throughout the estuary. Abundance indices in the 20 habitat type–zone–season combinations ranged from 185 to 574 fish 100 m⁻² and were generally lowest near the mouths of the Peace and Myakka rivers (zone 1) during the dry season.

Fish communities differed between habitat types (ANOSIM: $R = 0.351$, $P = 0.0\%$; Fig. 2). Ten taxa accounted for >50% of the total similarity within both the mangrove–seagrass habitat and the offshore seagrass flats habitat (Table 2). Although some taxa (e.g., *L. rhomboides*, *L. parva*, *A. mitchilli*) were abundant in both habitats (average dissimilarity = 34%), several taxa consistently distinguished one habitat or the other (high d_{avg}/SDd and large difference in average abundance; Table 2). Throughout the year, *Menidia* spp., *Mugil gyrans*, *E. harengulus*, and *Floridichthys carpio* distinguished the mangrove–seagrass habitat, and *Bairdiella chrysoura*, *Orthopristis chrysoptera*, and *Cynoscion nebulosus* distinguished the offshore seagrass flats habitat.

Numerous taxa varied in abundance seasonally in each habitat (Table 3). Species composition was significantly different between seasons in the mangrove–seagrass habitat (ANOSIM: $R = 0.412$, $P = 0.8\%$) and in the offshore

seagrass flats habitat (ANOSIM: $R = 0.672$, $P = 0.8\%$). The dry season was distinguished by *L. rhomboides*, *Leiostomus xanthurus*, and *O. chrysoptera* in both habitats and by *Mugil cephalus* in the mangrove–seagrass habitat. The wet season was distinguished by *L. parva*, *F. carpio*, and *Fundulus grandis* in the mangrove–seagrass habitat and by *E. gula*, *M. gulosus*, *C. nebulosus*, and *E. harengulus* in the offshore seagrass flats habitat. The wet season was distinguished by *Eucinostomus* spp., *A. mitchilli*, *Strongylura notata*, and *Oligoplites saurus* in both habitats. Numerous rare taxa (e.g., *Lutjanus synagris*, *Nicholsina usta*) were found only seasonally in each habitat.

On the basis of the zones created for this analysis, habitat use by fishes was very similar throughout Charlotte Harbor, but some species were found in higher abundances seasonally in mangrove–seagrass habitats in the river-influenced areas of the upper harbor (zone 1). For example, *Cyprinodon variegatus* and *L. xanthurus* were more abundant in upper-harbor mangrove–seagrass habitats during the dry season, and *Diapterus plumieri* and *M. gulosus* were more abundant in this habitat during the wet season.

Observed patterns of habitat use by fishes were best explained by a combination of environmental variables (Table 4). The highest

TABLE 3. Summary of similarity percentages analysis between seasons in the mangrove-seagrass habitat (mangrove) and the offshore seagrass flats habitat (flats). Taxa in three abundance categories with the highest ratios (d_{avg}/SDd) and the largest difference between average abundance are listed as consistent distinguishing taxa in each season (Clarke and Warwick, 1994). The percent contribution of each taxon to the total dissimilarity is listed in parentheses after the ratio. d_{avg} is the mean contribution of a taxon to the dissimilarity between the two seasons, and d_{avg}/SDd is the ratio between the mean contribution of a taxon and the standard deviation of the values for that taxon. The cutoff for cumulative dissimilarity was 55%.

		Dissimilarity			
		Mangrove		Flats	
		Dry season ^a	Wet season	Dry season	Wet season
Abundant taxa (average abundance ≥ 10 fish 100 m⁻²):					
<i>Lagodon rhomboides</i> 2.2 (4.2)	<i>Eucinostomus</i> spp. 1.6 (1.7)	<i>L. rhomboides</i> 3.7 (5.3)	<i>Eucinostomus</i> spp. 1.5 (3.3)		
	<i>Lucania parva</i> 1.5 (3.0)		<i>Eucinostomus gula</i> 1.5 (3.0)		
	<i>Floridichthys carpio</i> 1.5 (2.3)		<i>A. mitchilli</i> 1.5 (2.8)		
	<i>Anchoa mitchilli</i> 1.5 (3.7)				
Common taxa (1 \leq average abundance <10 fish 100 m⁻²):					
<i>Mugil cephalus</i> 2.0 (2.5)	<i>Fundulus grandis</i> 2.5 (1.8)	<i>L. xanthurus</i> 2.4 (3.1)	<i>Microgobius gulosus</i> 2.3 (1.9)		
<i>Leiostomus xanthurus</i> 1.7 (3.4)	<i>Strongylura notata</i> 2.0 (1.6)	<i>O. chrysoptera</i> 2.2 (3.0)	<i>Cynoscion nebulosus</i> 1.7 (1.3)		
<i>Orthopristis chrysoptera</i> 1.5 (1.9)	<i>Bairdiella chrysoura</i> 1.4 (2.3)		<i>Eucinostomus harengulus</i> 1.5 (2.0)		
Rare taxa (average abundance <1 fish 100 m⁻²):					
	<i>Oligoplites saurus</i> 3.1 (2.7)	<i>Calamus arctifrons</i> 1.9 (1.5)	<i>O. saurus</i> 2.1 (1.7)		
	<i>Fundulus majalis</i> 1.5 (1.8)	<i>Nicholsina usta</i> 1.6 (1.4)	<i>Lutjanus synagris</i> 1.7 (1.4)		
	<i>Membras martinica</i> 1.4 (1.7)		<i>S. notata</i> 1.5 (1.6)		

^a Dry season, Dec.–May; Wet season, June–Nov.

correlation coefficient ($\rho_w = 0.63$) was associated with the four-variable combination of salinity CV, water depth CV, water temperature, and dissolved oxygen. Water temperature was the most common variable in the multivariable combinations, followed by salinity CV and water depth CV. As expected, these variables showed normal seasonal patterns (Table 5). Water temperature and dissolved oxygen levels were highly correlated with season; the lowest dissolved oxygen values were recorded during the warmer wet season, and the highest values were recorded during the cooler dry season. The largest water-depth variations were recorded along the shoreline and the most consistent depths were recorded on flats away from shore. Salinities were lowest (and most variable) in the upper harbor near the Peace and Myakka rivers.

DISCUSSION

Seagrass habitats have been identified as productive (in terms of abundance and bio-

mass) nursery areas for fishes in Florida (Zieman, 1982; Comp and Seaman, 1985; Lewis et al., 1985; Zieman and Zieman, 1989). Seagrass habitats are common along mangrove shorelines as well as on flats away from shore throughout Charlotte Harbor, and we identified two general species groups that regularly use these habitats.

Menidia spp., *E. harengulus*, *M. gyrans*, and *F. carpio* were the taxa that best defined the mangrove-seagrass habitat throughout the year and throughout Charlotte Harbor. *Menidia* spp. (*M. beryllina*, Springer and Woodburn, 1960; *M. peninsulæ*, Thayer et al., 1987) and *F. carpio* (Thayer et al., 1987) have been abundant in shoreline habitats in previous studies conducted in western Florida. *Mugil gyrans* has not been recorded in many studies (perhaps because of historical confusion with *M. curema*) but was collected in mangrove and seagrass habitats in Tampa Bay (Springer and Woodburn, 1960). *Eucinostomus harengulus* has not been listed from mangrove habitats (probably

TABLE 4. Comparison of environmental variables that best explain the biotic ordination (see Fig. 2) produced using fishes collected in Charlotte Harbor, Florida. Combinations of variables were taken k at a time and were compared with the biotic similarity matrices for each k, as measured by the weighted Spearman rank correlation ρ_w (Clarke and Ainsworth, 1993).

k	Best variable combinations (ρ_w) ^a			
1	DO (0.30)	SalCV (0.27)	Temp (0.25)	Sal (0.20)
2	SalCV, Temp; (0.55)	DepthCV, Temp; (0.47)	SalCV, DO; (0.45)	Sal, Temp; (0.44)
3	SalCV, DepthCV, Temp; (0.60)	SalCV, Temp, DO; (0.57)	SalCV, Depth, Temp; (0.56)	Sal, DepthCV, Temp; (0.54)
4	SalCV, DepthCV, Temp, DO; (0.63)	SalCV, Depth, Temp, DO; (0.60)	SalCV, DepthCV, Temp, TempCV; (0.59)	Sal, SalCV, DepthCV, Temp; (0.57)

^a CV, coefficient of variation; Temp, mean water temperature (C); TempCV, water temperature CV; Sal, mean salinity (‰); SalCV, salinity CV; DO, mean dissolved oxygen (ppm); Depth, mean water depth at the bag (m); DepthCV, water depth CV.

TABLE 5. Environmental variables associated with collections in the mangrove-seagrass habitat and the offshore seagrass flats habitat during the two seasons. Temperatures, salinities, and dissolved oxygen values are mean (range); coefficient of variation for surface water values. Water depths are mean (range); coefficient of variation for depths taken at the bag. Dry season, Dec.–May; wet season, June–Nov.; n = number of samples.

Season	Temperature (C)	Salinity (‰)	Dissolved oxygen (ppm)	Water depth (m)
Mangrove-seagrass habitat				
Dry season (n = 119)	22.6 (12.4–31.0); 18.5	29.8 (6.8–37.3); 18.0	8.0 (3.5–12.7); 21.8	0.6 (0.1–1.0); 32.9
Wet season (n = 136)	28.8 (17.6–36.2); 12.3	27.7 (5.0–37.9); 24.2	6.6 (1.0–13.7); 41.5	0.7 (0.2–1.3); 32.1
Offshore seagrass flats habitat				
Dry season (n = 233)	22.4 (12.1–33.4); 19.1	30.1 (5.5–38.7); 20.4	8.2 (4.7–14.8); 19.5	0.7 (0.2–1.2); 27.8
Wet season (n = 234)	28.3 (17.0–34.1); 13.9	26.9 (6.3–37.3); 25.5	7.5 (1.9–16.7); 32.1	0.7 (0.3–1.2); 28.5

because of historical identification as *E. argenteus*; see Matheson, 1983), but *E. gula* and *E. argenteus* have been commonly listed from these areas (Springer and Woodburn, 1960; Wang and Raney, 1971; Thayer et al., 1987; Sheridan, 1992).

Bairdiella chrysoura, *O. chrysoptera*, and *C. nebulosus* were the species that best defined the offshore seagrass flats habitat throughout the year and throughout Charlotte Harbor. These species have been associated with seagrass habitats in western Florida (Springer and Woodburn, 1960; Wang and Raney, 1971; Sogard et al., 1987; Thayer et al., 1987; Nelson and Lefler, 2001). These species were classified as distinguishing species throughout the year in this habitat in part because of their protracted spawning seasons (Lassuy, 1983; Sutter and McIlwain, 1987), although *O. chrysoptera* was comparatively more abundant during the dry season and *C. nebulosus* was comparatively more abundant during the wet season.

Many species used both habitats examined in this study. For example, *L. rhomboides*, *L. parva*, and *Eucinostomus* spp. were abundant in seagrass habitats regardless of their location. *Lagodon rhomboides* and *L. parva* have typically been associated with seagrass communities (e.g., Stoner, 1983; Sogard et al., 1987; Gilmore, 1988), and both species were also commonly found along mangrove-seagrass shorelines in our study. Nelson (1998) suggested that because more shallow-water area with seagrass beds is present in Charlotte Harbor (262 km²) than in Tampa Bay (168 km²) and Choctawhatchee Bay (17 km²), *L. rhomboides* first settled primarily in shallow-water habitats in Charlotte Harbor as opposed to both shallow- and deep-water habitats in the other two systems. Because seagrasses and mangroves are so much more prevalent in Charlotte Harbor (and occur in combination) than they are in other Florida estuaries, species that typically reside in dense seagrass-flat habitats offshore may venture shoreward into mangrove areas (and vice versa), allowing the seagrass beds to act as a corridor for exchange between the two habitats. The broad distribution of seagrasses in Charlotte Harbor may also help explain why many species were widely distributed throughout the estuary and why the overall dissimilarity was low between the two habitats examined.

Although many species were collected in both habitats during the entire year, some species were abundant only seasonally. For example, *L. rhomboides* and *L. xanthurus* were most abundant during the dry season in both habitats, and *M. cephalus* was most abundant during

the dry season in the mangrove-seagrass habitat. *Cynoscion nebulosus* was most abundant on offshore seagrass flats during the wet months. These seasonal patterns of habitat use are commonly observed in estuaries, correspond to well-known spawning and recruitment periods, and ultimately may have evolved in part to reduce interspecific competition (MacPherson, 1981; Comp and Seaman, 1985).

Although not examined in this study, structural complexity, seagrass blade density, predator-prey interactions, interannual variations, and ontogenetic factors have been shown to affect fish abundance and behavior (e.g., Stein, 1979; Zieman, 1982; Stoner, 1983; Savino and Stein, 1989; Sogard and Olla, 1993). For example, encounters with predators in either habitat we examined may cause fish to travel to the other habitat, seeking refuge among the mangrove prop roots or in the more dense seagrass beds. The timing and extent to which these interactions influence fish assemblages is likely to be dependent on predator type and prey-specific behaviors that may change with ontogeny (Savino and Stein, 1989). Future studies in Charlotte Harbor that standardize as many environmental variables as possible (e.g., tidal stage, time of day), quantify detailed aspects of habitat complexity (e.g., seagrass-blade density, seagrass species), and correlate these factors with changes in habitat use would help fine-tune our understanding of the dynamics of habitat use by fishes in the estuary.

Water temperature, salinity, water depth, and dissolved oxygen levels were environmental factors that affected fish abundance in Charlotte Harbor. Various combinations of these variables and their CV were well correlated with observed patterns of habitat use by fishes. Some studies of subtropical fish communities have reported significant correlations between fish abundance and salinity, water temperature, or water depth (e.g., Sogard et al., 1987; Lin and Shao, 1999; Lorenz, 1999), whereas others have not (e.g., Blaber and Blaber, 1980; Bell et al., 1988; Jackson and Jones, 1999). These differences are related to many factors, including study location, study duration, and sampling methodology. The contribution of dissolved oxygen values to some high correlation coefficients in our shallow-water study was most likely related to the fact that temperature was also influential. In Charlotte Harbor, fish habitat use in deeper-water habitats is likely to be affected to an even greater extent by dissolved oxygen levels because large areas of the estuary seasonally become hypoxic (G. R. Poulakis, unpubl. data). The role of sa-

linity CV in explaining the biotic ordination indicates that the mean salinity was not necessarily as important as was the range of salinities experienced by fishes in the estuary. The importance of water depth CV relates in part to tidal influences and may explain why many species were commonly observed in both of the habitats examined. At lower tides for example, fishes that might normally prefer to use habitats along the mangrove-seagrass shoreline are forced into the offshore seagrass habitat.

These results show that different fish communities use different seagrass habitats in Charlotte Harbor depending on the season and on the proximity of the seagrasses to fringing mangroves. These data will be useful to resource managers and will act as a baseline for assessing the extent of future anthropogenic effects on fishes (e.g., freshwater withdrawals, seagrass loss). Future investigations in Charlotte Harbor should address species-specific aspects of fish community structure and habitat use (including ontogenetic changes) as well as habitat use by fishes in riverine habitats during a variety of flow conditions.

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