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Diurnal Fish Density in Relation to Seagrass and Drift Algae Cover in Tampa Bay, Florida

DAVID A. RYDENE AND RICHARD E. MATHESON JR.

To assess the relationship between fish density and seagrass and drift algae cover on a small geographic scale, we collected quantitative data on fish and vegetation communities during daylight hours near the mouth of the Little Manatee River, Tampa Bay, Florida. In 1991, fish were collected with two types of sampling gear, a 120-m long-haul seine and 1-m² roving dropnets. Seagrass and drift algae cover in each sampled area was categorized as none, sparse, moderate, or dense. Despite evident gear bias, sampling with both types of gear produced similar overall fish densities. Anchoa mitchilli, Lagodon rhomboides, and Syngnathus scovelli were the most abundant or frequently collected species, regardless of gear type. Densities of 12 of the 20 most abundant species were significantly related to either seagrass or drift algae cover or both. When fish density-vegetation cover relationships were significant, the greatest fish densities always occurred in either dense or moderate covers of seagrass or drift algae. Densities of L. rhomboides and Orthopristis chrysoptera were positively related to the level of seagrass and drift algae cover in samples collected with both types of gear, but significant relationships between the densities of other species and the level of vegetation cover generally varied by vegetation or gear type (or both). Density of Eucinostomus gula peaked in moderate seagrass and declined at higher and lower levels of cover. Total fish density was similar at sites dominated by either drift algae or seagrass but was significantly reduced at sites with little cover from either vegetation type. We conclude that both seagrass and drift algae are essential habitats for juvenile and small adult fish in Tampa Bay and that fish density on a small geographic scale is strongly related to vegetation cover. Drift algae may form an important alternate habitat for fish during winter months, when levels of seagrass cover are lowest and those of drift algae are highest.

E stuarine seagrass beds are recognized as highly productive habitats and are especially important as nursery areas for postlarval and juvenile fish, many of which support important recreational or commercial fisheries (Pollard, 1984). Unattached clumps of macroalgae (drift algae) have received less attention, but studies indicate that algae may also be important fish habitat (e.g., Kulczycki et al., 1981). Under the Magnuson-Stevens Fishery Conservation and Management Act of 1996, the essential habitat for all fishery species must be identified, but studies of the relationships between habitat type and abundance of nonfishery species also have important management implications because many of these animals compose the forage base necessary to sustain populations of fishery species (Minello, 1999).

Many studies have compared fish densities in seagrass with those over bare substrate (e.g., Briggs and O'Connor, 1971; Weinstein et al., 1977; Orth and Heck, 1980; Heck and Thoman, 1984; Snodgrass, 1992; Fonseca et al., 1996; Duffy and Baltz, 1998), but from a man-

agement perspective, simply characterizing estuarine habitats as either vegetated or unvegetated may not be sufficient for determining their value to fish. Generally, fish are more abundant in submerged vegetation than over bare substrate (e.g., Orth and Heck, 1980; Rozas and Odum, 1987; Duffy and Baltz, 1998), but there are exceptions (e.g., Heck and Thoman, 1984; Sheridan, 1992). Studies relating fish densities to vegetation cover on a per-sample basis (i.e., microhabitat studies) have shown that total fish density and various measures of seagrass cover may (Bell and Westoby, 1986a; Sogard et al., 1987) or may not (Sheridan, 1992) be correlated. Also, the effect of vegetation cover on fish density may be species specific or even sex specific within a species (Bell and Westoby, 1986a; Steffe et al., 1989), and for species that react to plant cover, there may be threshold values of plant cover above which their abundance does not change (Worthington et al., 1991; Fonseca et al., 1996). Finally, several studies have shown that relationships that exist at a small geographic scale, such as in a particular region within an estuary,

may not exist at larger scales, such as within an entire estuary or among estuaries (Bell and Westoby, 1986b; Worthington et al., 1992).

The importance of drift algae as fish habitat has been studied by relatively few authors. Gore et al. (1981; Indian River Lagoon, Florida), Kulczycki et al. (1981; Indian River Lagoon, Florida), Wright (1989; Kuwait), Kingsford (1992; New Zealand), Holmquist (1994; Florida Bay, Florida), and Langtry and Jacoby (1996; Australia) have examined the relationships between fish and drift algae. Kingsford (1992) and Holmquist (1994) emphasized the potential value of this mobile habitat as a faunal dispersal mechanism, particularly for species such as pipefish that do not have planktonic larval stages or for other small fish that must traverse areas of open water. Gore et al. (1981) and Kulczycki et al. (1981) emphasized the importance of drift algae as both a dispersal mechanism and an alternate habitat for seagrass-associated fish and macroinvertebrates. The latter authors mentioned that winter defoliation of seagrasses did not lead to abundance declines in two seagrass-associated fish, Gobiosoma robustum and Syngnathus scovelli, both of which also make extensive use of drift algae. However, Langtry and Jacoby (1996) found that algal biomass was not a good predictor of faunal abundance and that the fauna of drift algae was a subset of that found in nearby seagrass beds.

Several studies have described the ichthyofaunas of seagrass beds on the Gulf of Mexico coast of the Florida Peninsula (Reid, 1954; Springer and Woodburn, 1960; Carr and Adams, 1973; Szedlmayer, 1991), but to our knowledge only Sheridan (1992; Rookery Bay) and Fonseca et al. (1996; Tampa Bay) have documented the relationship between seagrass cover and fish density (on a microhabitat-persample basis), with the latter study including few species-specific comparisons.

In this study, we document fish density in vegetated and unvegetated habitats near the mouth of the Little Manatee River (LMR) in the Tampa Bay estuary, Florida. We examined the relationships between fish density and seagrass or drift algae (or both) cover based on visual and volumetric determination of vegetation cover in microhabitats sampled by two gear types, a 120-m long-haul seine (LHS) and a 1-m^2 roving dropnet (RDN). We made detailed comparisons for all fish combined and for the 20 most abundant species. In doing so, we are following the advice of Bell and Westoby (1986a), who commented that "The best way to assess effects of seagrass leaf height and density on fish and decapods is by examining responses of individual species."

MATERIALS AND METHODS

Study area.—The mouth of the LMR is located at ca. 27°43'N 82°29'W in eastern Tampa Bay, and submerged habitat consists of seagrass-covered flats, sandy patches, and several small boating channels. The three major seagrass species are Halodule wrightii, Thalassia testudinum, and Syringodium filiforme, with much smaller amounts of Halophila englemanii. Our observations indicate maximum development of seagrass beds from late spring to mid fall, and this agrees with the pattern generally observed in Tampa Bay (Lewis et al., 1985). From winter through late spring, large quantities of drift algae (principally Gracilaria spp., with lesser amounts of Acanthophora spp., Chaetomorpha spp., and Hypnea spp.) become entangled in the seagrass.

Field and laboratory methods.—Diurnal sampling was conducted monthly from Jan. through Dec. 1991 at five sites distributed across the mouth of the LMR (Fig. 1). Sampling gear included paired RDNs and an LHS (Kushlan, 1974, 1981; Kjelson and Johnson, 1975), each made of 3.2-mm–stretched mesh nylon netting. Sampling with the two gear types was conducted on different days, ca. 2 wk apart, during each month of the study.

Roving dropnets were deployed from a boom system extending over the bow of a moving (ca. 2 knots) 5.2-m skiff. To eliminate interobserver variability, the first author always inspected the area enclosed by the RDN and assigned a seagrass and drift algae cover category to each collection. All fish were removed from the RDNs using 1-m², 3.2-mm-mesh bar seines. The bar seines were swept through the enclosed area at least 10 times, continuing until no fish were obtained on two consecutive passes. Earlier testing showed that this protocol removed nearly 100% of the fish trapped in the RDNs (R. McMichael, unpubl. data). All drift algae were removed from the RDNs and returned to the laboratory for determination of volume displacement. Sampling was conducted with the RDN during all but 2 mo (June and Dec. 1991) for a total of 200 drops (20 samples/mo).

The LHS was deployed in a circular to elliptical pattern from a 7-m "mullet" skiff (a flatbottomed boat with an outboard engine mounted through the center of the hull). The leading edge of the net was then pulled beRYDENE AND MATHESON—FISH IN SEAGRASS AND DRIFT ALGAE



Fig. 1. Sampling locations near the mouth of the Little Manatee River, Tampa Bay, Florida.

tween two vertical poles held stationary near the bag or terminal end of the net. The area enclosed by the net was continually decreased until only the bag portion remained. The bag was then pursed and hauled onto the skiff, where fish were removed and processed. During net deployment, four weighted floats were thrown from the boat to demarcate two perpendicular transects through the area sampled. After the completion of each set, the first author swam the two transects and assigned seagrass and drift algae cover categories to the entire area sampled. Areas with less than 40% vegetation coverage were considered unvegetated. Drift algae collected in the seine were included in the overall estimate of drift algae cover for each set. The area covered by each LHS sample was estimated using the formula for the area of a circle, with the only variable parameter being the circumference (if less than the entire 120 m was deployed). This procedure tends to overestimate the area sampled (and thus underestimate fish density) if the set is elliptical. Sampling with the LHS was conducted during all months for a total of 59 hauls (four samples in April and five in all other months).

Air and water temperatures, pH, dissolved oxygen (DO), conductivity, and salinity were measured with a Hydrolab Surveyor II on each sampling date. Water-quality data were generally recorded for each LHS sample and for each pair of RDN samples, but separate data were not generally recorded for sites in close proximity to one another if the samples were collected sequentially within a short time period. During Feb. 1991, pH and DO were not recorded for RDN samples.

Each fish sample was placed on ice in the field, returned to the laboratory, and frozen. Later, fish were thawed, sorted to the lowest practical taxonomic level, and counted. Length was recorded for up to 40 individuals of each species in each sample. For samples containing more than 40 individuals of a species, the measured subsample included specimens selected to cover the entire size range present: all specimens were arrayed from smallest to largest, and the 40 individuals to be measured were selected from this size gradient (e.g., every third specimen would be selected from a sample containing 120 individuals). This procedure retains both the mode(s) and the range of the size data. Standard length (SL) was measured for most species, maximum disk width was measured in batoid fish, and tip of tail (straightened) to top of head was measured in seahorses (Hippocampus zosterae). Some large, readily identifiable fish were counted, measured, and released in the field.

From each sample, at least two individuals of each species were kept as voucher specimens. All voucher specimens were reexamined to verify the initial identifications.

Identification of some species was problematic. For two abundant genera in our samples, Eucinostomus and Menidia, species-level identification of all specimens was not practical, but one species predominated in subsamples identified to species. Of 980 Eucinostomus examined, 921 (94%) were Eucinostomus gula, 44 (4.5%) were Eucinostomus argenteus, and 15 (1.5%) were Eucinostomus harengulus (based on diagnostic characters in Matheson and Mc-Eachran, 1984). Of 51 Menidia examined, 49 (96%) were Menidia peninsulae and two (4%) were Menidia beryllina (based on diagnostic characters in Chernoff et al., 1981). Both these findings agree with other studies of the distribution of these species in Tampa Bay (R. E. Matheson, unpubl. data). Because of these results, we treat all Eucinostomus as E. gula and all Menidia as M. peninsulae in analyses. All specimens in the genus Hyporhamphus were identified as Hyporhamphus unifasciatus before the description of Hyporhamphus meeki by Banford and Collette (1993), and the vouchers were discarded. In this document, we report our specimens as H. meeki because identifications of numerous specimens collected from Tampa Bay indicate that H. meeki is the dominant species in this area (B. Collette, pers. comm.; R. E. Matheson, unpubl. data).

Because the seagrass cover categories used in this study were based on the perception of one observer, our results are not readily comparable with those of other studies. During 1992 and 1993, the first author quantified his perception by assigning cover categories to 0.10-m² plots and then calculating several seagrass community metrics for vegetation removed from these plots. Methods for this study were modified from those of Livingston et al. (1976), and details can be obtained from the first author. Dry weight best defined the seagrass cover categories. Significant overall differences in dry weight, blade density, and blade length were detected among the cover categories, but between seagrass beds characterized as moderate and dense only dry weight was significantly different (Table 1). Because of the small sample sizes and to make the seagrass cover characterization more comparable with that of drift algae, the "very sparse" and "sparse" categories are combined in our analyses of the relationships between fish density and habitat.

We visually assigned a drift algae cover cat-

TABLE 1. Quantification of dry interquartile range, and sample	weight, blade density, and bladt size (in parentheses). Median Dunn	c length in four categories of visu: values followed by the same lett i's test for paired comparisons; P	ally determined seagrass cover. Val ter are not significantly different > < 0.05).	ues for each category are median, (Kruskal–Wallace test followed by
Parameter	Very sparse	Sparse	Moderate	Dense
Dry weight $(g/0.10 \text{ m}^2)$	0.15 D, 0.09-0.23 (20)	1.45 c, 1.05–2.78 (30)	5.13 B, 3.55-6.14 (26)	8.63 A, 5.82–10.00 (30)
Blade density (no./0.10 m ²)	41.5 c, 31.5–63.0 (20)	151.0 B, 108.3–268.3 (31)	503.0 A, 170.0-868.0 (30)	782.0 A, 198.0–1224.0 (30)
Blade length (mm)	46.8 c, 37.0–52.4 (20)	72.6 в, 51.9–95.7 (31)	100.4 A, 79.8–120.9 (30)	107.7 A, 100.6–131.8 (30)

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Species	Total specimens	Species	Occurrences
Roving dropnet (200 collection	ıs)		
Anchoa mitchilli	210	Lagodon rhomboides	33
Lagodon rhomboides	142	Syngnathus scovelli	31
Syngnathus scovelli	52	Bairdiella chrysoura	20
Bairdiella chrysoura	44	Eucinostomus gula	15
Orthopristis chrysoptera	32	Microgobius gulosus	15
Gobiosoma robustum	30	Orthopristis chrysoptera	14
Eucinostomus gula	22	Gobiosoma robustum	13
Microgobius gulosus	19	Anchoa mitchilli	11
Hippocampus zosterae	9	Hippocampus zosterae	8
Symphurus plagiusa	9	Symphurus plagiusa	8
Long-haul seine (59 collections	5)		
Anchoa mitchilli	65,623	Syngnathus scovelli	49
Lagodon rhomboides	55,076	Lagodon rhomboides	45
Bairdiella chrysoura	21,373	Eucinostomus gula	41
Orthopristis chrysoptera	18,739	Cynoscion nebulosus	38
Eucinostomus gula	8,280	Bairdiella chrysoura	33
Harengula jaguana	1,686	Orthopristis chrysoptera	33
Syngnathus scovelli	1,654	Gobiosoma robustum	33
Cynoscion nebulosus	1,128	Microgobius gulosus	29
Microgobius gulosus	716	Anchoa mitchilli	26
Gobiosoma robustum	558	Syngnathus louisianae	25

 TABLE 2.
 Ten most abundant or frequently collected species in roving dropnet and long-haul seine collections near the mouth of the Little Manatee River in 1991.

egory to all RDN samples, but displacement volume was also determined for drift algae removed from each RDN. In our analyses, drift algae in RDN samples are characterized by volume as follows: none (0 ml), sparse (1–20 ml), moderate (21–99 ml), and dense (\geq 100 ml). We attempted to approximate these categories in the visual characterization of LHS sampling areas.

Statistical analyses.—Detailed analyses were conducted for the 20 most abundant species as well as for all species combined. These 20 species were present for 6 mo or more and had overall densities of >0.05 fish/10 m² based on at least one gear type. Data from the entire study were used in analyses of species that either occurred in most months (e.g., *S. scovelli*) or occurred sporadically throughout the year (e.g., *Hippocampus zosterae*); in analyses of species with obvious seasonal abundance patterns, months in which these species were absent or rare in samples collected with either gear were not included.

Three separate sets of analyses were conducted: 1) fish density in relation to seagrass cover, 2) fish density in relation to drift algae cover, and 3) fish density in relation to combined seagrass and drift algae cover. Because of sample size constraints, the latter analyses were conducted using only RDN data and were based on two combined vegetation cover categories: low cover (none or sparse) and high cover (moderate or dense). Before these analyses, all RDN samples were assigned to one of four categories: 1) low drift algae cover and low seagrass cover, 2) high drift algae cover and low seagrass cover, 3) low drift algae cover and high seagrass cover, and 4) high drift algae cover and high seagrass cover.

Statistical tests included nonparametric Kruskal-Wallace tests, with Dunn's test for multiple comparisons (Neave and Worthington, 1988; Glantz, 1992; Fox et al., 1994), and parametric analyses of variance using the leastsquares means option in the Statistical Analysis Systems general linear model (GLM) procedure (SAS Institute Inc., 1988). Nonparametric tests were used in the quantification of the seagrass cover categories (Table 1). Parametric comparisons (GLMs) (using log + 1-transformed fish density data) were used in analyses of fish density in relation to vegetation cover. All GLMs were conducted beginning with a full model and then sequentially removing nonsignificant terms until only significant terms remained. Salinity and water temperature were used as covariates in all comparisons, drift al-

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TABLE 3. Species collected with both long-haul seine (LHS) and roving dropnets (RDN) near the mouth of the Little Manatee River in 1991. Length^a is given as an interquartile range; numbers in parentheses are number of fish measured; and asterisks indicate probabilities from Kolmogorov–Smirnov tests (*, P < 0.05; **, P < 0.01; ***, P < 0.001). Data are based on 59 hauls with the LHS and 200 drops with the RDN. Letters following species names indicate ecological or morphological groupings as follows: B, benthic; D, demersal percoids; P, pelagic, schooling planktivores; S, syngnathids (seahorse and pipefish); and T, tetrao-dontids (puffers).

	Density (fis	h/10 m ²)	· · · ·	Lengt	h (mm)	
	LHS	RDN	LHS	5	RE	Ň
Achirus lineatus (B)	$0.01 \pm < 0.01$	0.30 ± 0.12	13-22	(64)	19-25	(6)
Anchoa mitchilli (P)	9.52 ± 4.18	10.50 ± 5.11	25 - 36	(882)	20-32	(156)***
Archosargus probatocephalus (D)	0.04 ± 0.02	0.10 ± 0.07	15 - 22	(160)	14 - 170	(2)
Bairdiella chrysoura (D)	3.36 ± 0.89	2.20 ± 0.64	21 - 45	(903)	19 - 30	(44) * * *
Chasmodes saburrae (B)	0.01 ± 0.01	0.15 ± 0.11	18 - 35	(48)	20 - 35	(3)
Chilomycterus schoepfi (T)	$0.01~\pm~<0.01$	0.10 ± 0.07	17-47	(69)	25 - 150	(2)
Cynoscion arenarius (D)	$<\!0.01~\pm~<\!0.01$	0.05 ± 0.05	25-192	(20)	16	(1)
Cynoscion nebulosus (D)	$0.17~\pm~0.04$	0.10 ± 0.07	25 - 45	(705)	14-29	(2)
Eucinostomus gula (D)	1.24 ± 0.27	1.10 ± 0.31	18–53	(1,160)	19 - 30	(22)*
Gobiosoma robustum (B)	0.08 ± 0.03	1.50 ± 0.48	16 - 21	(260)	16 - 22	(30)
Hippocampus zosteraeª (S)	$0.01~\pm < 0.01$	0.45 ± 0.16	25-30	(61)	26-31	(9)
Lagodon rhomboides (D)	8.21 ± 2.87	7.25 ± 1.63	20-70	(1,295)	16 - 25	(145)***
Menidia peninsulae (P)	0.07 ± 0.04	0.05 ± 0.05	74–81	(100)		(1) ^b
Microgobius gulosus (B)	$0.11~\pm~0.04$	0.95 ± 0.26	25–37	(325)	19 - 31	(19)**
Mugil gyrans (P)	$<\!0.01~\pm~<\!0.01$	0.05 ± 0.05	153 - 234	(15)	12	(1)
Orthopristis chrysoptera (D)	2.99 ± 1.03	1.60 ± 0.50	18 - 48	(969)	17 - 26	(32)**
Prionotus scitulus (B)	$< 0.01 \pm < 0.01$	0.05 ± 0.05	20-40	(5)	22	(1)
Sciaenops ocellatus (D)	0.03 ± 0.03	0.05 ± 0.05	14-26	(52)	20	(1)
Sphoeroides nephelus (T)	$0.01~\pm~<0.01$	0.05 ± 0.05	26 - 52	(48)	14	(1)
Symphurus plagiusa (B)	0.01 ± 0.01	0.45 ± 0.16	23–52	(63)	23-32	(9)
Syngnathus louisianae (S)	$0.02~\pm~<0.01$	0.15 ± 0.09	103 - 135	(118)	100 - 114	(3)
Syngnathus scovelli (S)	0.25 ± 0.05	2.60 ± 0.52	67–90	(880)	50 - 74	(52)***
Synodus foetens (B)	$0.01~\pm < 0.01$	0.25 ± 0.11	42-96	(43)	45 - 48	(5)*
Total fish	26.65 ± 5.67	30.30 ± 5.58	_			

^a Hippocampus zosterae measurements are total length (see methods); values for all other species are standard length.

^b The one specimen collected was not measured.

gae volume was used as a covariate in comparisons involving RDN data, and percentage of sampled area covered by seagrass was used as a covariate in comparisons involving LHS data. Because data were missing for some samples, pH and DO were not used as covariates. Only vegetation cover by gear categories with sample sizes of five or greater were included in comparisons. Finally, Kolmogorov–Smirnov tests were used in comparisons of fish length distributions between gear types. In all statistical tests, probabilities <0.05 were considered significant.

RESULTS

Physical variables.—Water-quality data associated with LHS and RDN collections were similar (Fig. 2). Water temperature ranged from 14.2 C to 32.3 C, with a marked increase during May–Sep. (LHS) and April–Sep. (RDN). Salinity ranged from 11.5 to 30.3 ppt for LHS samples and from 5.5 to 32.0 ppt for RDN samples. Salinity values in the sampling area were generally between 24 and 31 ppt, except for a sharp decline in Aug.–Sep. Dissolved oxygen concentrations ranged from 3.3 to 11.1 ppm and declined from April or May through Sep. The patterns of monthly variation observed for temperature and DO were nearly mirror images. Hydrogen ion concentrations (pH) ranged from 6.9 to 8.4; most values were between 7.3 and 8.1.

Sampling depths were similar for both gear types but averaged slightly greater for LHS samples (mean \pm SE = 0.78 \pm 0.04 m for LHS vs 0.72 \pm 0.02 m for RDN). Overall sampling depths ranged from 0.2 to 1.4 m, and average sampling depths were somewhat greater from April through July (mean \pm SE = 0.97 \pm 0.02 m vs 0.63 \pm 0.01 m for other months).

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Vegetation communities.—Maximum development of seagrass beds and maximum drift algae cover occurred in different seasons (Fig. 3). Dense to moderate seagrass coverage was most often encountered during April through Aug., whereas dense to moderate drift algae were most often encountered from Jan. through May and in Oct. and Nov.

Halodule wrightii was the dominant seagrass in the study area. Among the 59 LHS samples, the dominant seagrasses were H. wrightii in 58%, T. testudinum in 14%, and S. filiforme in 7%. Eight percent of the LHS samples were characterized as mixed seagrasses with no clearly dominant species, and 14% were dominated by bare substrate. Fifty-two percent of the 200 RDN samples were dominated by H. wrightii, 13% were T. testudinum, and 10% were S. filiforme. Three percent of the RDN samples were characterized as mixed seagrasses, and 23% were bare substrate. The dominance of H. wrightii along with the small sample sizes precluded the analysis of fish density in relation to seagrass species.

Gear comparison .- The most abundant and most frequently collected species were similar for both types of gear (Table 2). The 200 RDN collections (covering 200 m²) produced 606 fish in 23 species. The numerical dominants were Anchoa mitchilli and L. rhomboides: these two species represented 58% of the total number of specimens collected. Lagodon rhomboides and S. scovelli were the most frequently collected species, each occurring in more than 15% of the RDN samples. The 59 LHS collections (covering ca. 64,470 m²) produced 177,803 fish in 63 species. The numerical dominants were again A. mitchilli and L. rhomboides: these two species represented 68% of the total number of specimens collected. The most frequently collected species were again S. scovelli and L. rhomboides, each occurring in more than 75% of the LHS samples.

Twenty-three species were collected with both types of gear (Table 3). Densities of syngnathids and benthic species were generally one or two orders of magnitude higher in RDN collections than in LHS collections, whereas densities of demersal percoids, the most abundant planktivore (*A. mitchilli*), and all fish combined were comparable for the two gear types.

The RDN generally collected smaller fish than did the LHS, but this trend varied depending on species. Syngnathids and benthic species (e.g., *G. robustum* and *Symphurus plagiusa*) were often collected at similar sizes by both gear types, but the LHS did capture significantly larger specimens of some species (e.g., *S. scovelli* and *Microgobius gulosus*). The more abundant demersal percoids (*Bairdiella chrysoura, E. gula, L. rhomboides,* and *Orthopristis chrysoptera*) were significantly smaller in RDN collections than in LHS collections (75th percentiles, 25- to 30-mm SL for RDN collections vs 45- to 70-mm SL for LHS collections).

Forty species were collected only with the LHS. Thirty-five of these species were rare (<0.01 fish/10 m²; 1–52 individuals collected), and 13 of these rare species were relatively large (25th percentile, >100-mm SL). Among the more abundant taxa collected only with the LHS, two [*Elops saurus* (0.02 fish/10 m²) and *H. meeki* (0.03 fish/10 m²)] were relatively large (25th percentile, >179-mm SL) pelagic species, whereas three [*Anchoa hepsetus* (0.08 fish/10 m²), *Harengula jaguana* (0.24 fish/10 m²), and *Membras martinica* (0.04 fish/10 m²)] were relatively small (75th percentile, <95-mm SL) schooling planktivores.

Relationships between fish density and seagrass or drift algae cover.--Densities of nine of the 20 species selected for these comparisons had statistically significant relationships with seagrass cover (Figs. 4, 5; Table 4): maximum abundance of all nine species was found in either dense or moderate seagrass. Significant differences were detected in both LHS and RDN data for B. chrysoura, E. gula, L. rhomboides, O. chrysoptera, and S. scovelli; in only LHS data for Archosargus probatocephalus, Chasmodes saburrae, and Syngnathus louisianae (<4 individuals of each of these three species captured in RDN); and in only RDN data for G. robustum. Eucinostomus gula was the only species with a significant preference for moderate seagrass cover vs either lower or higher categories (Fig. 4); a similar but nonsignificant trend was also observed for O. chrysoptera.

Fish (all species combined) were more frequently collected and most abundant in either dense or moderate seagrass and least abundant in either sparse or no seagrass (Fig. 5; Table 4). All LHS collections contained fish, regardless of bottom vegetation, but only 13% of RDN collections in unvegetated areas contained fish. Sparse seagrass harbored the fewest fish in LHS samples, whereas areas with no seagrass harbored the fewest fish in RDN samples.

Densities of 10 of the 20 selected species had statistically significant relationships with drift algae cover (Figs. 6, 7; Table 5): maximum abundance of all 10 species was found in either dense or moderate drift algae cover. Signifi-

TABLE 4. Frequency of occurrence and density in relation to seagrass cover for selected species of fish collected near the mouth of the Little Manatee River in 1991. Months in parentheses below species names are the months used in statistical comparisons (see text). Statistics for each species are as follows: f = frequency of occurrence (%), m = mean density per 10 m², and e = standard error of mean density. Entries in bold indicate significant relationships between fish density and seagrass cover (Figs. 4, 5).

n na manan an			Long-hau	ıl seine			Rovin	g dropnet	
		None	Sparse	Moderate	Dense	None	Sparse	Moderate	Dense
Achirus lineatus (June–Nov.)	f	20	40	45	0	0	7	0	15
_	m	< 0.01	0.02	0.03	0.00	0.00	0.65	0.00	1.50
	e	< 0.01	0.01	0.01	0.00	0.00	0.37	0.00	0.82
Anchoa hepsetus (May–Oct.)	f	50	56	40	57	0	0	0	0
	m	0.08	0.31	0.11	0.04	0.00	0.00	0.00	0.00
	e	0.05	0.30	0.07	0.02	0.00	0.00	0.00	0.00
Anchoa mitchilli (May–Oct.)	f	100	67	90	71	5	17	8	9
	m	34.20	5.33	32.31	7.69	5.00	35.56	0.83	22.19
	e	20.50	3.86	21.58	5.41	5.00	22.99	0.83	18.07
Archosargus probatocephalus (JanOct.)	f	50	12	31	70	3	0	3	0
	m	0.01	<0.01	0.02	0.17	0.27	0.00	0.30	0.00
	e	<0.01	< 0.01	0.01	0.10	0.27	0.00	0.30	0.00
Bairdiella chrysoura (April–Sep.)	f	100	88	100	100	0	6	19	47
	m	0.14	3.38	6.29	12.61	0.00	1.56	2.50	10.94
	e	0.05	2.90	2.25	3.07	0.00	1.11	1.44	3.43
Chasmodes saburrae (Jan.–Dec.)	f	0	14	32	73	0	0	3	2
	m	0.00	< 0.01	0.01	0.06	0.00	0.00	0.30	0.49
	e	0.00	< 0.01	<0.01	0.03	0.00	0.00	0.30	0.49
Chilomycterus schoepfi (March–Sep.)	f	33	40	46	63	0	0	0	6
	m	< 0.01	0.01	0.02	0.03	0.00	0.00	0.00	0.63
	e	< 0.01	< 0.01	0.01	0.01	0.00	0.00	0.00	0.43
Cynoscion nebulosus (May–Oct.)	f	100	100	100	100	0	3	0	3
	m	0.17	0.22	0.50	0.33	0.00	0.28	0.00	0.31
	e	0.07	0.13	0.14	0.07	0.00	0.28	0.00	0.31
Eucinostomus gula (May-Dec.)	f	100	77	100	100	0	15	50	6
	m	0.51	0.98	3.23	1.91	0.00	1.70	8.33	1.25
	e	0.30	0.40	0.84	0.54	0.00	0.63	2.97	0.98
Gobiosoma robustum (JanSep.)	f	50	67	80	70	0	5	3	23
	m	0.04	0.10	0.19	0.04	0.00	0.70	1.33	5.64
	e	0.03	0.09	0.07	0.02	0.00	0.42	1.33	2.04

TABLE 4. Continued.

		Long-haul seine					Rovin	g dropnet	
		None	Sparse	Moderate	Dense	None	Sparse	Moderate	Dense
Harengula jaguana (May–Oct.)	f	50	22	60	100	0	0	0	0
3 3 3 4 7 7	m	0.32	0.12	0.88	0.26	0.00	0.00	0.00	0.00
	e	0.28	0.11	0.40	0.10	0.00	0.00	0.00	0.00
Hippocampus zosterae (Jan.–Dec.)	f	0	0	32	36	0	8	6	0
	m	0.00	0.00	0.02	< 0.01	0.00	0.75	0.91	0.00
	e	0.00	0.00	0.01	< 0.01	0.00	0.30	0.67	0.00
Lagodon rhomboides (Jan.–June)	f	100	90	100	100	0	24	52	52
	m	3.93	1.13	38.08	14.46	0.00	6.47	24.40	29.05
	e	3.87	0.54	15.23	3.27	0.00	2.60	7.28	10.16
Menidia peninsulae (Jan.–Oct.)	f	17	24	25	30	0	1	0	0
	m	0.01	0.06	0.15	0.06	0.00	0.14	0.00	0.00
	e	0.01	0.06	0.11	0.04	0.00	0.14	0.00	0.00
Microgobius gulosus (Jan.–Aug.)	f	75	33	80	70	0	14	13	8
	m	0.05	0.07	0.23	0.17	0.00	2.29	0.71	0.83
	е	0.05	0.04	0.14	0.12	0.00	0.91	0.50	0.47
Orthopristis chrysoptera (Jan.–June)	f	50	70	100	100	0	9	28	14
	m	1.03	0.38	10.05	9.92	0.00	2.35	7.60	1.90
	e	1.03	0.15	4.97	3.39	0.00	1.34	3.18	1.12
Symphurus plagiusa (Feb.–Sep.)	\mathbf{f}	33	42	33	22	0	9	4	8
	m	0.01	0.02	0.04	0.01	0.00	0.85	0.38	1.11
	e	0.01	0.02	0.02	0.01	0.00	0.41	0.38	0.66
Syngnathus louisianae (Jan.–Dec.)	f	25	14	53	91	2	3	0	0
	m	<0.01	0.01	0.02	0.06	0.22	0.25	0.00	0.00
	e	<0.01	<0.01	<0.01	0.02	0.22	0.18	0.00	0.00
Syngnathus scovelli (Jan.–Dec.)	f	25	86	95	100	0	10	18	41
	m	0.03	0.05	0.44	0.48	0.00	1.13	2.73	8.29
	e	0.03	0.02	0.10	0.15	0.00	0.40	1.17	2.00
Synodus foetens (Jan.–Dec.)	f	25	19	26	27	7	3	0	0
	m	< 0.01	0.01	< 0.01	0.01	0.65	0.25	0.00	0.00
	e	< 0.01	0.01	< 0.01	0.01	0.37	0.18	0.00	0.00
Total fish (Jan.–Dec.)	f	100	100	100	100	13	45	67	80
	m	20.04	5.61	47.88	34.96	3.48	28.00	36.06	60.24
	е	11.14	2.53	15.02	6.12	2.41	10.58	7.96	15.27

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TABLE 5. Frequency of occurrence and density in relation to drift algae cover for selected species of fish collected near the mouth of the Little Manatee River in 1991. Months in parentheses below species names are the months used in statistical comparisons (see text). Statistics for each species are as follows: f = frequency of occurrence (%), m = mean density per 10 m², and e = standard error of mean density. Entries in bold indicate significant relationships between fish density and drift algae cover (Figs. 6, 7).

and a second			Long-hai	ıl seine			Rovin	g dropnet	
		None	Sparse	Moderate	Dense	None	Sparse	Moderate	Dense
Achirus lineatus (June–Nov.)	f	35	29	33		5	7	6	0
C A	m	0.02	< 0.01	0.01		0.51	0.73	0.56	0.00
	e	0.01	< 0.01	0.01	a	0.36	0.41	0.56	0.00
Anchoa hepsetus (May-Oct.)	f	45	50	80	0	0	0	0	0
	m	0.21	0.02	0.06	0.00	0.00	0.00	0.00	0.00
	e	0.14	0.01	0.02	b	0.00	0.00	0.00	0.00
Anchoa mitchilli (May–Oct.)	f	80	100	60	100	14	11	0	0
	m	24.83	11.00	4.22	0.20	17.96	32.97	0.00	0.00
	e	11.57	9.30	3.55	p	11.91	22.46	0.00	0.00
Archosargus probatocephalus (Jan.–Oct.)	f	38	0	36	71	2	0	0	6
	m	0.01	0.00	0.15	0.02	0.15	0.00	0.00	0.59
	e	0.01	0.00	0.09	0.01	0.15	0.00	0.00	0.59
Bairdiella chrysoura (April–Sep.)	f	100	80	100	100	13	32	18	0
	m	6.17	4.57	12.40	4.64	2.29	6.05	9.09	0.00
	e	2.11	2.70	5.30	2.41	1.16	1.79	8.14	0.00
Chasmodes saburrae (Jan.–Dec.)	f	27	7	50	43	0	0	3	6
	m	<0.01	< 0.01	0.02	0.07	0.00	0.00	0.50	0.59
	e	< 0.01	<0.01	0.01	0.05	0.00	0.00	0.50	0.59
Chilomycterus schoepfi (March–Sep.)	f	56	43	50	0	4	0	0	0
	m	0.02	0.01	0.03	0.00	0.38	0.00	0.00	0.00
	е	0.01	0.01	0.01	0.00	0.27	0.00	0.00	0.00
Cynoscion nebulosus (May–Oct.)	f	100	100	100	100	4	0	0	0
	m	0.31	0.52	0.26	0.33	0.41	0.00	0.00	0.00
	e	0.07	0.32	0.09	b	0.29	0.00	0.00	0.00
Eucinostomus gula (May-Dec.)	f	92	88	100	100	13	9	22	0
	m	1.95	1.35	1.60	3.841	1.85	1.52	2.78	0.00
	e	0.48	0.68	0.94	<u> </u>	0.75	0.82	1.35	0.00
Gobiosoma robustum (Jan.–Sep.)	f	76	70	60	71	3	9	8	27
~ ^	m	0.18	0.03	0.08	0.10	0.49	1.89	3.20	5.33
	е	0.09	0.01	0.05	0.05	0.36	0.90	2.50	2.91

TABLE 5. Continued.

and and and a second			Long-haul seine				Rovin	g dropnet	
		None	Sparse	Moderate	Dense	None	Sparse	Moderate	Dense
Harengula jaguana (May–Oct.)	f	50	50	80	100	0	0	0	0
8 9 8 4 9 7	m	0.32	0.25	0.81	0.33	0.00	0.00	0.00	0.00
	e	0.16	0.25	0.64	b	0.00	0.00	0.00	0.00
Hippocampus zosterae (Jan.–Dec.)	f	19	14	25	0	3	4	5	6
	m	0.02	< 0.01	0.01	0.00	0.42	0.42	0.50	0.59
	e	0.01	< 0.01	< 0.01	0.00	0.31	0.24	0.35	0.59
Lagodon rhomboides (Jan.–June)	f	100	83	100	100	6	17	59	73
	m	1.55	1.25	17.04	41.48	0.94	6.00	15.45	57.33
	e	0.58	0.88	4.15	19.25	0.69	2.98	3.53	14.85
Menidia peninsulae (JanOct.)	f	10	10	45	57	0	0	3	0
	m	< 0.01	0.10	0.02	0.41	0.00	0.00	0.29	0.00
	e	< 0.01	0.10	0.01	0.25	0.00	0.00	0.29	0.00
Microgobius gulosus (Jan.–Aug.)	f	76	30	60	71	7	7	16	20
	m	0.09	0.05	0.06	0.56	1.32	0.42	1.74	2.00
	e	0.03	0.03	0.02	0.31	0.71	0.29	1.02	1.07
Orthopristis chrysoptera (Jan.–June)	f	83	67	90	100	3	13	32	7
······································	m	0.95	0.19	6.57	14.73	0.31	2.33	8.64	2.67
	e	0.37	0.12	2.79	5.91	0.31	1.24	3.44	2.67
Symphurus plagiusa (Feb.–Sep.)	f	44	38	11	33	2	8	16	0
	m	0.03	< 0.01	< 0.01	0.05	0.17	0.98	1.58	0.00
	e	0.02	< 0.01	< 0.01	0.04	0.17	0.51	0.86	0.00
Syngnathus louisianae (Jan.–Dec.)	f	35	36	75	29	0	3	3	0
	m	0.01	0.01	0.05	0.02	0.00	0.28	0.25	0.00
	e	<0.01	<0.01	0.02	0.01	0.00	0.20	0.25	0.00
Syngnathus scovelli (Jan.–Dec.)	f	73	86	100	86	6	15	30	24
	m	0.22	0.13	0.38	0.41	0.85	3.66	3.25	4.12
	e	0.07	0.08	0.09	0.24	0.48	1.19	0.83	2.11
Synodus foetens (Jan.–Dec.)	f	27	14	33	14	3	3	3	0
	m	0.01	< 0.01	0.01	0.01	0.28	0.28	0.25	0.00
	e	< 0.01	< 0.01	< 0.01	0.01	0.20	0.20	0.25	0.00
Total fish (Jan.–Dec.)	f	100	100	100	100	34	46	68	71
	m	27.17	6.82	28.77	60.72	20.42	33.10	27.75	65.88
	e	10.40	3.61	6.90	20.30	8.71	11.93	5.77	16.61

^a No samples were collected in dense drift algae during this period. ^b Only one sample was collected in dense drift algae during this period. Published by The Aquila Digital Community, 2003

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Fig. 2. Water-quality data collected at the time of long-haul seine and roving dropnet sampling near the mouth of the Little Manatee River. Error bars represent one standard error.

cant differences were detected in both LHS and RDN data for *C. saburrae, L. rhomboides,* and *O. chrysoptera;* in only LHS data for *A. probatocephalus, M. peninsulae, M. gulosus,* and *S. louisianae;* and in only RDN data for *G. robustum, S. plagiusa,* and *S. scovelli.* Gear differences (except in the case of *M. gulosus*) may be related to overall abundance (*A. probatocephalus*, *M. peninsulae*, and *S. louisianae* were rare in RDN samples) or gear efficiency (densities of *G. robustum*, *S. plagiusa*, and *S. scovelli* were at least an order of magnitude higher in RDN



Fig. 3. Seagrass and drift algae cover categories represented each month in long-haul seine and roving dropnet samples taken near the mouth of the Little Manatee River.

collections). Orthopristis chrysoptera was unique in its significant preference for moderate drift algae cover in RDN collections.

Fish (all species combined) were more frequently collected and more abundant in dense to moderate drift algae than in sparse to no drift algae (Fig. 7; Table 5). All LHS collections contained fish, but only 34% of RDN collections from areas with no drift algae contained fish. The relationship between total fish density and drift algae cover was similar based on either gear.

Relationships between fish density and combined seagrass and drift algae cover.—Densities of five of the 20 most abundant species and of all fish combined were significantly different among combined seagrass and drift algae cover categories in RDN collections (Fig. 8). In all these cases, the low algae and low seagrass cover category had the lowest or among the lowest fish densities, whereas the highest fish densities were distributed among the other three categories. The high algae and high seagrass cover category harbored significantly more individuals than did any other category in only one species, *G. robustum*, although the trend was similar for *L. rhomboides*. For *S. scovelli* and all species combined, all categories with high levels of either seagrass or drift algae cover harbored similar numbers of individuals. Drift algae cover appeared to have a stronger relationship with the density of *S. plagiusa* than did seagrass cover. Seagrass cover may have had a stronger influence on *B. chrysoura* density than did drift algae cover, but too few samples were available in the high algae and low seagrass category for it to be included in the analysis.

DISCUSSION

The seagrass beds near the mouth of the LMR harbored an ichthyofauna comparable with that observed in seagrass beds in other Florida estuaries. Anchoa mitchilli, L. rhomboides, S. scovelli, B. chrysoura, O. chrysoptera, and E. gula were among the five most abundant species in collections made with one or both of our gear types (Table 2). Of these species, only B. chrysoura is not among the five most abundant species reported in other studies con-

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Fig. 4. Geometric mean densities of six species of fish in relation to seagrass cover in roving dropnet (RDN) and long-haul seine (LHS) collections taken near the mouth of the Little Manatee River in 1991. Bars capped by different letters represent means that are significantly different [P < 0.05; general linear model (GLM) procedure with least-squares means option (SAS Institute Inc., 1988)]. Numbers in parentheses are sample sizes. Letters after "model" indicate significant terms in the GLM as follows: GC, grass cover; TE, water temperature; SA, salinity; and AL, algae volume. Refer to Table 4 for months included in analyses for each species.

ducted with similar sampling gear in Florida waters [i.e., Brook, 1975 (Card Sound); Schooley, 1977 (Banana River); Schooley, 1980 (Mosquito Lagoon); Gilmore, 1988 (Indian River Lagoon); and Brown-Peterson et al., 1993 (Indian River Lagoon)]. *Bairdiella chrysoura* was, however, among the 10 most abundant species collected by Gilmore (1988). Our fish density values, ca. 27 and 30 fish/10 m² for LHS and RDN, respectively, are within the lower portion of the range of values recorded in the above-mentioned studies. These values (in fish/10 m²) have ranged from 19 (Brown-Peterson et al., 1993) to 203 (Gilmore, 1988) in studies using seines and from 26 (Brook, 1975) to 76 (Gilmore, 1988) in studies using enclosure gear.

Similar results were obtained in this study with both large (LHS) and small (RDN) sampling gears (Table 3). Most gear-associated differences in either density or occurrence of fish species can be attributed to species- or size-related biases (or both) or to the huge difference in total area sampled with the two gears: 200 m² for the RDN vs ca. 64,470 m² for the LHS. The LHS was biased toward larger, more mobile or surface-oriented species (e.g., *H. jaguana, H. meeki*, and *E. saurus*) and against



Fig. 5. Geometric mean densities of three species of fish and of all fish combined in relation to seagrass cover in roving dropnet (RDN) and long-haul seine (LHS) collections taken near the mouth of the Little Manatee River in 1991. Bars capped by different letters represent means that are significantly different [P < 0.05; general linear model (GLM) procedure with least-squares means option (SAS Institute Inc., 1988)]. Numbers in parentheses are sample sizes. Letters after "model" indicate significant terms in the GLM as follows: GC, grass cover; TE, water temperature; SA, salinity; and AL, algae volume. Refer to Table 4 for months included in analyses for each species.

smaller, less mobile or benthic species (e.g., gobiids and syngnathids); the opposite trends were observed in RDN collections. Densities of demersal percoids, represented mostly by juveniles, were similar in collections made with either gear type. The observed size bias may be due to the positive relationship between fish size and swimming speed (Helfman et al., 1997): faster animals would be able to escape the smaller gear (i.e., the RDN). Among percoids, smaller individuals may have a greater tendency to seek shelter in seagrass when frightened (Wyda, 1998) and would therefore be more vulnerable to the RDN. The bias against less mobile or benthic species in LHS collections is probably due to the lead line of the LHS being forced off the bottom in dense vegetation (Rozas and Minello, 1997). This would allow escapement of small benthic fish and syngnathids that either lie on the bottom or intermingle with the vegetation; thus, our overall results based on data from the LHS collections (i.e., more animals in denser vegetation) should be considered conservative.

Few fish were collected over bare substrate in the RDN, which may be explained by the absence of *A. mitchilli* over bare substrate in the RDN samples. Also, some of the more abun-



Fig. 6. Geometric mean densities of seven species of fish in relation to drift algae cover in roving dropnet (RDN) and long-haul seine (LHS) collections taken near the mouth of the Little Manatee River in 1991. Bars capped by different letters represent means that are significantly different [P < 0.05; general linear model (GLM) procedure with least-squares means option (SAS Institute Inc., 1988)]. Numbers in parentheses are sample sizes. Letters after "model" indicate significant terms in the GLM as follows: AC, drift algae cover; TE, water temperature; and SA, salinity. Refer to Table 4 for months included in analyses for each species.

dant species collected over bare substrate in the LHS (e.g., *H. jaguana* and *E. saurus*) were larger, more mobile species that were never collected in the RDN. Another factor contributing to this difference may be the location of our sampling area: most of the bare areas sampled with the RDN were near seagrass beds. We suspect that some fish briefly foraging over the open substrate escaped into the seagrass bed when the boat approached. Shulman (1985) and Bell and Westoby (1986a) observed that when small fish are frightened, they typically move ca. 1 m and then hide in foliage, and Wyda (1998) observed similar behavior in *E. gula.*

Schooling, pelagic planktivores exhibited the least dependence on vegetated habitats. Of the four abundant pelagic planktivores, densities of three (A. hepsetus, A. mitchilli, and H. jaguana) were not significantly related to either seagrass or drift algae cover. Density of the fourth species, M. peninsulae, was greater in samples with greater drift algae cover (LHS only) but showed no relationship to seagrass cover. We might expect the distributions of schooling, pelagic planktivores to depend less



Fig. 7. Geometric mean densities of four species of fish and of all species combined vs drift algae cover in roving dropnet (RDN) and long-haul seine (LHS) collections taken near the mouth of the Little Manatee River in 1991. Bars capped by different letters represent means that are significantly different [P < 0.05; general linear model (GLM) procedure with least-squares means option (SAS Institute Inc., 1988)]. Numbers in parentheses are sample sizes. Letters after "model" indicate significant terms in the GLM as follows: AC, drift algae cover; TE, water temperature; SA, salinity; and GP, grass coverage (%). Refer to Table 4 for months included in analyses for each species.

on bottom cover than on the distribution of their planktonic prey (Motta et al., 1995), and previous studies of these species generally indicate either no association or a negative association with vegetation cover (e.g., Orth and Heck, 1980; Sogard et al., 1987; Sheridan, 1992; Zengel, 1993; Duffy and Baltz, 1998; Rozas and Minello, 1998; Raposa and Oviatt, 2000). The significant increase in density of *M. peninsulae* in areas with denser drift algae may indicate selection of drift algae as the spawning habitat: many of our specimens were adults (Table 3; Middaugh et al., 1986), and *Menidia* spp. are known to deposit adhesive eggs in vegetation, including algae (Martin and Drewry, 1978; Middaugh et al., 1986). Ross and Epperly (1985) speculated that seagrass habitats may be important to *Menidia menidia* for this same reason.

Among the benthic species collected in this study, *Achirus lineatus* and *Synodus foetens* often use the substrate as a refuge by partially burying themselves (Anderson et al., 1966; Topp and Hoff, 1972) and generally show little preference for, or avoidance of, dense vegetation (Reid, 1954; Springer and Woodburn, 1960; Thayer et al., 1987; Rakocinski et al., 1992; Sheridan, 1992; this study). Although we have



Combined Drift Algae and Seagrass Cover

Fig. 8. Geometric mean densities of five species of fish and of all species combined in relation to combined seagrass and drift algae cover in roving dropnet (RDN) collections taken near the mouth of the Little Manatee River in 1991. Bars capped by different letters represent means that are significantly different [P < 0.05; general linear model (GLM) procedure with least-squares means option (SAS Institute Inc., 1988)]. Numbers in parentheses are sample sizes. Low cover represents sparse or no drift algae or seagrass, and high cover represents moderate or dense drift algae or seagrass. Letters after "model" indicate significant terms in the GLM as follows: AS, combined drift algae and seagrass cover; TE, water temperature; and SA, salinity. Refer to Table 4 for months included in analyses for each species.

found no reference to burying behavior in S. plagiusa, it is a cryptic species that may have little need for vegetation as a refuge from predation. Studies of the habitat preferences of S. *plagiusa* have produced conflicting results: greater abundance in unvegetated areas or areas with little plant cover (Clark, 1974; Rakocinski et al., 1992; Rozas and Zimmerman, 2000), greater abundance in seagrass than over unvegetated substrate (Sheridan, 1992), or greater abundance in higher levels of drift algae cover (this study). Microgobius gulosus is a burrowing species, but it also spends time resting on or hovering above the substrate in a variety of habitats (Baird, 1965; Birdsong, 1981; Provancha and Hall, 1991). Previous studies have generally documented weak or negative relationships between the density of this species and the level of seagrass cover (Clark, 1974; Sogard et al., 1987; Provancha and Hall, 1991; Sheridan, 1992; Sheridan et al., 1997), but Duffy and Baltz (1998) did find this species to be more abundant in seagrass areas than over bare substrate. A significant positive relationship between the density of this species and the dense drift algae cover (this study) has not been reported previously.

The two benthic species with the strongest relationship to vegetative cover in our study, *G. robustum* and *C. saburrae*, are often observed resting on the substrate (pers. obs.), and both are generally associated with some type of cover (e.g., vegetation, oyster shell, or rocks) (Reid, 1954; Joseph and Yerger, 1956; Springer and Woodburn, 1960; Springer and McErlean, 1961; Tabb and Manning, 1961; Tabb et al., 1962; Dawson, 1969; Clark, 1974; Bass and Guillory, 1979; Mulligan and Snelson, 1983; J.

C. S. Wang and E. C. Raney, unpubl.). As in our study, a significant relationship between the abundance of G. robustum and the drift algae cover was reported by Kulczycki et al. (1981), and these authors indicated that a seagrass decline in winter, when drift algae were abundant, did not coincide with a decline in the abundance of G. robustum. In contrast to our results, Sheridan (1992) found this species to be significantly more abundant over bare substrate than over seagrass, Stoner (1983) found it to be most abundant in areas with lower seagrass biomass, and Sheridan et al. (1997) found no difference in its abundance among Thalassia, Halodule, and algae covers and unvegetated mud-bottomed habitats.

Demersal percoids were principally represented by small juveniles in our samples (Table 3), and the densities of most species were positively related to vegetation cover. Of the six demersal percoid species included in detailed analyses, densities of A. probatocephalus, L. rhomboides, and O. chrysoptera were positively related to both seagrass and drift algae cover; densities of B. chrysoura and E. gula were significantly related to seagrass cover; and density of Cynoscion nebulosus was not significantly related to cover of either vegetation type. References supporting a preference for vegetated habitats and, in some cases, preferences for specific levels of vegetation cover exist for all these percoid species (e.g., Springer and Woodburn, 1960; Briggs and O'Connor, 1971; Odum and Heald, 1972; Clark, 1974; Weinstein et al., 1977; Orth and Heck, 1980; Mulligan and Snelson, 1983; Stoner, 1983; Heck and Thoman, 1984; Campos, 1985; McMichael and Peters, 1989; Rutherford et al., 1989; Thayer and Chester, 1989; Chester and Thayer, 1990; Zengel, 1993; Sheridan et al., 1997; Nelson, 1998; Rooker et al., 1998; Rozas and Minello, 1998; Wyda, 1998; Arrivellaga and Baltz, 1999). Vegetation may only be the preferred habitat for juveniles [e.g., A. probatocephalus (Odum and Heald, 1972) and O. chrysoptera (Reid, 1954)], and these species can be common in unvegetated habitats [e.g., B. chrysoura (Thomas, 1971), C. nebulosus (McMichael and Peters, 1989), E. gula (Weinstein et al., 1977; Bass and Guillory, 1979)]. Documented reactions of these percoids to variations in seagrass cover include 1) no response to plant surface area [L. rhomboides (Duffy and Baltz, 1998)], 2) increased abundance in areas with higher shoot density and standing crop [B. chrysoura, C. nebulosus, E. gula, L. rhomboides, and O. chrysoptera (Thayer and Chester, 1989)], and 3) increased abundance in areas with intermediate levels of

seagrass coverage [E. gula (Wyda, 1998)] or biomass [O. chrysoptera (Stoner, 1983)]. The last trend is also seen in our RDN data (significant in E. gula and similar but not significant in O. chrysoptera; Figs. 4, 5).

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Apparent preferences for intermediate vegetation density may result from the dual roles of seagrass beds as shelter and feeding areas (Heck et al., 1997) or from a preference for seagrass coupled with a behavioral change at higher seagrass densities. Savino and Stein (1989) observed that Lepomis macrochirus switched from schooling to dispersion as habitat structure increased, and this could lead to a decrease in observed abundance, especially in collections made with a relatively small sampling gear such as the RDN. Finally, we believe that the strong association between the densities of some percoid species and the drift algae cover indicates the potential value of drift algae as an alternate habitat for structure-associated species during winter, when the amount of seagrass cover is relatively low and that of drift algae is relatively high (Gore et al., 1981; Kulczycki et al., 1981). This could be particularly important for species that recruit to the estuary during winter (e.g., A. probatocephalus, L. rhomboides, and O. chrysoptera).

The absence of a significant relationship between the density of C. nebulosus and the vegetation cover in this study conflicts with the results of previous studies, which indicate a strong association between this species and seagrass (Springer and Woodburn, 1960; Mc-Michael and Peters, 1989; Rutherford et al., 1989; Chester and Thayer, 1990; Rooker et al., 1998). All collections made with the LHS during the period used in our analyses (May-Oct.) contained this species, and mean density was similar for all seagrass cover categories. Despite the literature mentioned above, few studies have provided quantitative data regarding the abundance of this species in relation to vegetation cover. Stoner (1983) indicated that abundance of C. nebulosus was nearly equal at all levels of seagrass biomass in Apalachee Bay, Rutherford et al. (1989) found greater abundance in Halodule or Thalassia than in other vegetation or unvegetated areas in Florida Bay, Rooker et al. (1998) found much greater abundance of small juveniles in Halodule than in Thalassia in Texas, and Rozas and Minello (1998) found greater abundance in either emergent vegetation or seagrass than in unvegetated areas in Texas. If the results of Rooker et al. (1998) are applicable to Tampa Bay, then our conclusions may be compromised by the mixed nature of the seagrass beds at the

mouth of the LMR. If this is not the explanation, then *C. nebulosus* may be an example of a species that frequently uses seagrass flats as feeding areas but is not dependent on dense seagrass for cover.

Pollard (1984) listed Syngnathidae among the 10 most important seagrass-associated fish families on a global basis, and S. scovelli and S. louisianae are not exceptions to this rule. Most of the quantitative data referring to the abundance of these two species in different habitats refer to S. scovelli. Clark (1974), Sheridan (1992), Zengel (1993), Sheridan et al. (1997), Tolan et al. (1997), Duffy and Baltz (1998), and Rozas and Minello (1998) found this species to be more abundant in vegetated than in unvegetated habitats. We found significantly greater densities of S. scovelli in moderate to dense seagrass, regardless of the sampling gear used. Using only data from collections made with the RDN, because of the apparent inefficiency of the LHS at capturing this species, the density of this species increases sharply and significantly in dense seagrass (Fig. 4). If the refuge function is the dominant factor driving the use of seagrass microhabitats by S. scovelli, then our results may be evidence of a threshold level or step function relationship between the effectiveness of predators of S. scovelli and the grass cover (Nelson, 1979; Heck and Thoman, 1981; Orth et al., 1984; Sogard et al., 1987). We have found no other references to a preferred seagrass cover threshold in S. scovelli, although Thayer and Chester (1989) did find a positive association between the abundance of this species and the seagrass abundance. Kulczycki et al. (1981) documented a significant positive relationship between drift algae biomass and abundance of S. scovelli, and we found significantly more individuals of this species when drift algae cover was present (Fig. 7).

Because of the inherent difficulties in quantifying habitat in the area actually swept by a sampling gear, researchers have used various surrogate methods. For larger gears, such as seines and trawls, the approach has often been to take a limited number of small seagrass cores in or near the area covered by the sampling gear and to use the data from these cores to characterize the entire sampled area. In some studies, these data have been compared with animal abundances on a per-sample basis (e.g., Duffy and Baltz, 1998). In other studies, these data have been used to derive an average condition for a fixed site during an entire study period, and the latter value has been compared with animal abundances (e.g., Adams, 1976; Orth and Heck, 1980). For smaller

gears, such as dropnets and throw traps, cores have often been taken from just outside the trap (to eliminate the effects of sweep nets or internal seines on seagrass blades and drift algae and to avoid producing holes in the substrate inside the trap where animals might congregate) (e.g., Matheson et al., 1999), and the data derived from the these cores are assumed to be representative of conditions within the trap. With any of the above methods, the patch of habitat on which habitat characterization is based may be from zero to many meters away from the habitat patch (es) from which animals were collected. Because of the small size and limited vagility of many seagrass-associated fish, we believe that this may be a significant bias in the results of most previous studies. Habitats need to be quantified in the area actually swept by the net in order to accurately assess relationships between animal abundance and habitat. We accomplished this by having one observer characterize the entire area swept by both the RDN and the LHS.

Both seagrass and drift algae were important habitats for fish near the mouth of the LMR, and the level of cover by both vegetation types was often a more important determinant of fish density than was the mere presence or absence of vegetation. At least 40% of the substrate in areas included in our sparse vegetation category was covered by either seagrass or drift algae; yet, densities of many species continued to increase as vegetation cover increased, at least through the category of moderate vegetation and often up to that of dense vegetation. At small geographic scales, other studies (e.g., Bell and Westoby, 1986a) have shown that fish abundance is related to plant density and that radical changes in seagrass density may be associated with radical changes in faunal species composition and relative abundance (Matheson et al., 1999).

In summary, our results indicate that it is a gross oversimplification to classify habitat value on the basis of the presence or absence of bottom vegetation. All models of habitat suitability and all delineations of essential fish habitat should include some measure of the amount of vegetation cover. The effects of vegetation cover should be determined from the relationships between fish density and vegetation cover in the area swept by the sampling gear to account for microhabitat effects, and these relationships should be determined separately for each species of fish. We also recommend that future studies use the distance to the nearest seagrass bed as a covariate in their analyses and that they consider gear efficiency in relation to fish behavior and morphology.

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