

## DIEL, LUNAR AND SEASONAL CHANGES IN A MANGROVE FISH ASSEMBLAGE OFF SOUTHWESTERN PUERTO RICO

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### ABSTRACT

Visual censusing was used to investigate diel, lunar, and seasonal variations in abundance and composition of a fish assemblage inhabiting a mangrove key off the southwest coast of Puerto Rico. Forty-one species were visually identified among the mangrove prop-roots during designated census periods: 0700, 1200, 1700, 2200. Statistical analysis indicated distinct trends in diurnal, day versus night, and seasonal abundances. Although diurnal variability was evident, the most pronounced feature was nighttime declines in species abundance. All species present during the day showed marked reduction in numbers or complete absence at night. Unlike coral reef habitats, there was no evidence for a diurnal-nocturnal changeover of species assemblages in the mangroves. Low nighttime abundance was partly due to twilight migrational activities. Movements away from the mangrove prop-root habitat at dusk were observed for a variety of fishes, particularly haemulids. Predictable, well ordered migrations were observed for juvenile French grunts (*Haemulon flavolineatum*) and sub-adult bluestriped grunts (*H. sciurus*). Timing, duration, and pre- and post-migratory behaviors differed among species. Seventy-six % of species examined showed significant ( $P < 0.05$ ) seasonal differences between Oct/Nov 86 (rainy season) and Apr/May 87 (dry season). Lunar periodicity had no obvious effect on species abundance in this mangrove fish assemblage.

Activity patterns within tropical fish assemblages vary prominently. Diurnal and nocturnal differences in activity have been reported in several studies (Hobson, 1965; 1973; Collette and Talbot, 1972; Ebeling and Bray, 1976; Colton and Alevizon, 1981). Most fishes are active mainly during daylight; however, a substantial number of fishes maintain peak activity during nocturnal hours (Hobson, 1965; 1974; Starck and Davis, 1966). Considerable attention has been focused on the events surrounding dawn and dusk transitional periods (Hobson, 1965; 1972; Collette and Talbot, 1972; Domm and Domm, 1973). Twilight transition is characterized by pronounced changes in composition, abundance, and distribution of fish assemblages. A variety of species migrate from daytime habitats to nocturnal feeding grounds (Starck and Davis, 1966; Hobson, 1973; 1974; Ogden and Ehrlich, 1977; Ogden and Zieman, 1977). Certain of these species migrate during twilight on a regular daily basis (Haemulidae (grunts)—Hobson, 1965; 1968; Ogden and Ehrlich, 1977; McFarland et al., 1979; Helfman et al., 1982; Priacanthidae (bigeyes)—Hobson, 1972; Pempheridae (sweepers)—Fishelson et al., 1971; Gladfelter, 1979; Lutjanidae (snappers)—Starck and Davis, 1966; Hobson, 1968; 1972; Atherinidae (silversides)—Hobson and Chess, 1973). Other species undergo a variety of daily movements unrelated to the twilight transitional period (Pomacentridae (damsel-fishes)—Hobson, 1972; Doherty, 1983; Foster, 1987; Scaridae (parrotfishes)—Ogden and Buckman, 1973; Acanthuridae (surgeonfishes)—Hobson, 1972).

Although diurnal-nocturnal changes in abundance have been reported for entire assemblages occupying a particular habitat, few large scale studies have incorporated the effects of lunar and seasonal periodicity. Lunar spawning cycles produce distinct trends in the abundance and distribution of many fishes. Many fish display peak reproductive activity around new or full moon, while other variations in reproductive patterns have also been shown (Munro et al., 1973; Johannes, 1978; Lobel, 1978; Pressley, 1980; Doherty, 1983; Foster, 1987; Colin et al., 1987). Variation in seasonal abundance may be related to changes in environ-

mental parameters (i.e., salinity, temperature, turbidity) that alter habitat characteristics, or to aspects of life history (e.g., reproduction, recruitment) (Williams and Sale, 1981; Williams, 1983).

The vast majority of work to date has concentrated on tropical coral reef habitats (Hobson, 1965; Starck and Davis, 1966; Collette and Talbot, 1972; Domm and Domm, 1973; Sbikin, 1977; Colton and Alevizon, 1981). Information on activity patterns in other habitats is limited (kelp beds—Ebeling and Bray, 1976; rocky coasts—Hobson, 1965; seagrass beds—Robblee and Zieman, 1984).

Mangroves are important areas for growth and development of many marine fishes, but remain a mystery with respect to activity patterns of associated fauna. The majority of mangrove studies have been general ichthyofaunal surveys (Austin, 1971; Austin and Austin, 1971; Valdez Muñoz, 1981; Galzin et al. 1982; Thayer et al., 1987). Due to inherent sampling difficulties, little information is available on mangrove fish community interactions or activity patterns. Extremely low visibility, characteristic of eutrophic waters, has restricted researchers from employing standard visual censusing techniques. Quantitative assessments utilizing poisons have been reported by Galzin et al. (1982) and Thayer et al. (1987). This methodology, however, is inappropriate when repeated sampling of the same locality is required. Many offshore mangrove key formations are located in the backreef portion of fringing coral reefs. Increased water circulation, resulting from reef overwash, provides water sufficiently clear for visual censusing techniques to be employed.

The objectives of this study were to determine activity patterns of fishes occupying an offshore mangrove key prop-root habitat. Emphasis was placed on determining diel periodicity, seasonal and lunar variations in fish abundance, and twilight migrational patterns.

## MATERIALS AND METHODS

*Study Area.*—This study was conducted on the leeward side of the backreef mangrove stand of Cayo Collado located off La Parguera, Puerto Rico (Fig. 1). The forereef is dominated by staghorn coral (*Acropora palmata*) and fire coral (*Millepora alcicornis*). The backreef is comprised of a shallow water lagoonal flat merging with a mangrove fringe dominated by red mangrove, *Rhizophora mangle*. Water depth at the study site was approximately 1 to 1.5 m at the periphery and salinity ranged from 34 to 37‰. Large quantities of green algae (*Ulva fasciata* and *U. lactuca*) covered much of the area immediately adjacent to the prop-root zone; where vegetation was absent the underlying sandy bottom was exposed. Turtle grass (*Thalassia testudinum*) and the green alga (*Codium taylori*) occurred 20 to 30 m away from the prop-roots, with *Thalassia* dominating.

*Census Method.*—Eight 15-m transects were marked off parallel to the prop-root zone using surveyor's tape. Visual censusing was conducted by snorkeling along the transect line. All fish present from the outer edge of the prop-root zone to the innermost point of visibility (approximately 3–5 m) were enumerated. Counts were tabulated on an underwater slate. Some species were subdivided into growth stages (juvenile versus sub-adult/adult) based on size and coloration patterns.

Fish without distinctive coloration or with close morphological resemblance to other species could only be tentatively identified. To avoid errors in identification, species of the genera *Sparisoma* (parrotfishes) and *Eucinostomus* (mojarra) were lumped together into their respective genera and each was treated as a single taxa for statistical purposes. Three species of *Sparisoma* were observed: redband parrotfish (*Sparisoma aurofrenatum*), bucktooth parrotfish (*S. radians*), and redtail parrotfish (*S. chrysopterygum*). Juveniles of all three species possessed extremely similar mottled coloration patterns making visual identification very difficult. More typical distinctive color phases of reef dwelling members of this group are lost in the confines of the mangroves. Highly uniform coloration and general body morphology characterized the genus *Eucinostomus*. The silver jenny (*Eucinostomus gula*), spotfin mojarra (*E. argenteus*), and flagfin mojarra (*E. melanopterus*) all have similar silver body coloration with dusky dorsal fin markings and occur in the La Parguera area. These three species were lumped as accurate identification of small individuals was difficult in the mangroves. Identification difficulties were also experienced for heterotypic schools of juvenile haemulids (<10 cm TL) which ranged in number from 20 to 200 individuals. Although such schools were dominated (over 90%) by French

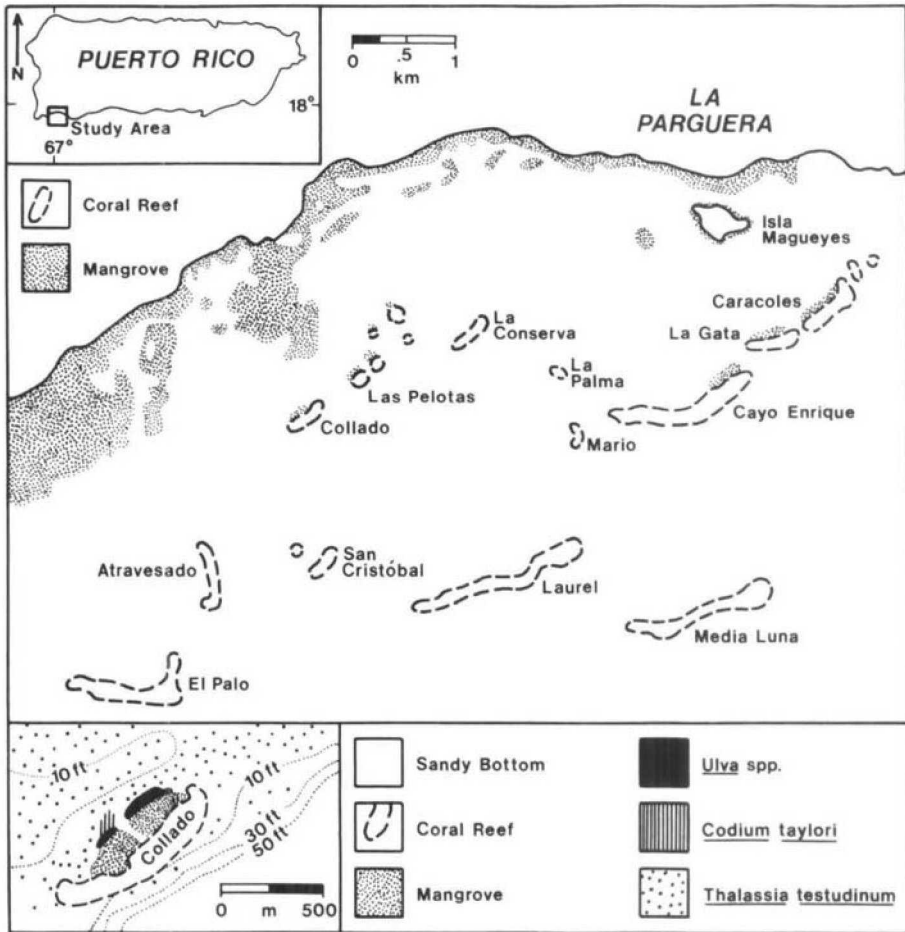


Figure 1. Location of study area off the southwest coast of Puerto Rico. Morphologic features of Cayo Collado are represented.

grunts (*Haemulon flavolineatum*), actual species counts of each haemulid species present was not feasible and thus, this group was treated as a single taxa.

Dwarf herring (*Jenkinsia lamprotaenia*), dusky anchovy (*Anchoa lyolepis*), and hardhead silverside (*Atherinomorus stipes*) occurred in large schools ranging in size from few to thousands of individuals; however, due to obvious censusing difficulties, they were not included in the statistical analyses but were noted as present and their relative abundance estimated.

Aside from these limitations, sources of bias are often inherent with visual census methodology (Sale and Douglas, 1981; Sale and Sharp, 1983). Potential biases in this study result from variations in visibility of fishes in the censused area. Topography, vegetation and water clarity all affect visibility. Certain species, particularly cryptic species, may hide themselves among the prop-roots or substratum leading to underestimations of density. Decreased water clarity (i.e., increased turbidity) often reduces the number of species observed and also leads to underestimation of species abundance. This may have influenced lunar abundances since sampling periods were conducted weekly. Time of day or light level may also influence visibility. Although light levels were fairly constant among diurnal census periods, potential bias may be present in day-night comparisons. Nighttime visibility was limited to some degree, though the dive lit up a section of the prop-roots similar in area to the field of vision observed during diurnal censuses.

There is little seasonal change in water temperature ranging from 27°C (winter) to 30°C (summer) in the La Parguera area. The primary seasonality related to wet and dry periods (Glynn, 1973). Based on historical data sampling was conducted during the rainy season (October–November, 1986) and dry season (April–May, 1987) (Fig. 2).

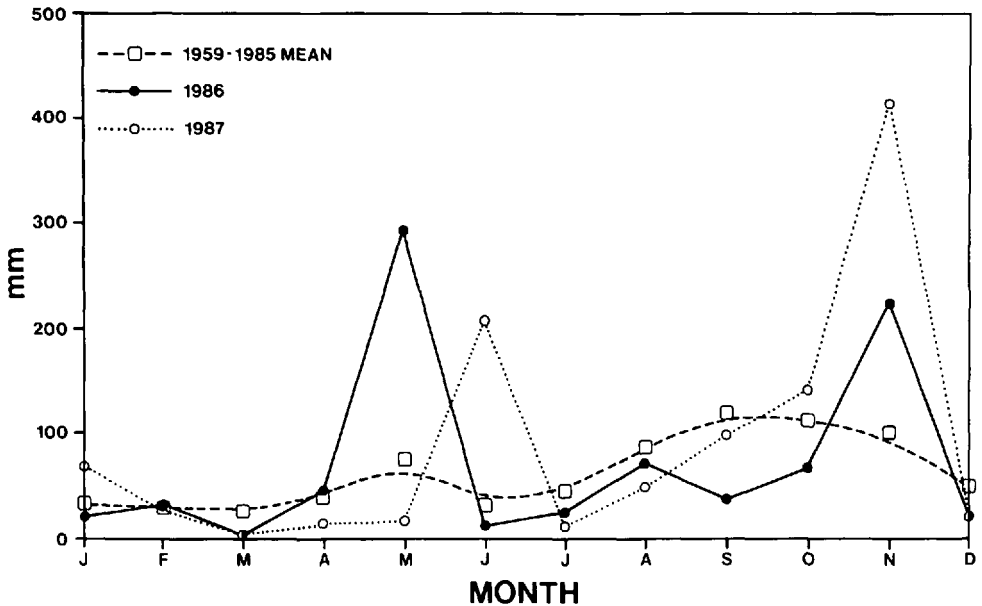


Figure 2. Monthly rainfall data for La Parguera, Puerto Rico.

Sampling periods were spaced at weekly intervals corresponding to moon phases: first quarter, full, last quarter, and on to observe the effects of light on nocturnal fish behavior and did not appear to attract or repel fish to any great extent. Although some unusual behavioral modifications were observed, all fish could still be accurately enumerated.

Twilight activity patterns were observed during seven sunsets from 18 to 30 May 1987. Initial sunset observations were of a preliminary nature, being used to obtain general information such as time frame of migrations, location of twilight departures, and species composition.

Twilight activities were recorded by two or three divers with each diver observing activities at a different locality along the mangrove fringe. In general, each sunset observation was approximately 2 h in duration, starting 1 h before and ending 1 h after sunset. Information recorded during sunset observations included chronological sequence of species present, behavioral activities, departure times, and size classes of fish present.

*Statistical Analysis.*—Species counts collected during diurnal sampling periods were statistically analyzed with either a chi-square “goodness of fit” test (Sokal and Rohlf, 1981) or a repeated-measures analysis of variance test (ANOVA) (Winer, 1971). Species present in low to moderate abundance were analyzed with the chi-square test. The most abundant species were log transformed in order to normalize the counts and then analyzed by two-way repeated measures ANOVA due to the repeated sampling of fixed transects. Moon phase and time period were main effects in this analysis. Significant ANOVA results were further examined with Duncan’s multiple range test (DMRT) (Snedecor and Cochran, 1967) to determine which factor level of the main effect(s) differed from other levels. Day-night and seasonal variations in abundance were analyzed with a chi-square test.

## RESULTS

*Species Composition and Abundance.*—Overall, 38 species were observed during the rainy season and 36 species in the dry season. The dominant taxa were, in order of decreasing abundance: French grunt, schoolmaster (*Lutjanus apodus*), bluestriped grunt (*Haemulon sciurus*), yellowtail snapper (*Ocyurus chrysurus*), and mojarra (*Eucinostomus* spp.).

*Diurnal Variability.*—Distinct trends in diurnal abundance of fishes inhabiting the mangrove prop-root habitat were present. When diurnal counts were pooled over moon phases, 18 species exhibited diel differences in abundance (Table 1).

Fourteen species were present in moderate numbers. Significant variation in diurnal abundance was found in seven species during the rainy season and four species during the dry season (Table 1). Doctorfish (*Acanthurus chirurgus*) showed significant diurnal differences during the rainy season with peak abundance at 1200. The crevalle jack (*Caranx hippos*) displayed high abundance at both 1200 and 1700, and a sharp two-fold decline in abundance at 0700. Due to lack of sufficient numbers the chi-square test could not be employed for the crevalle jack during the dry season. The genus *Eucinostomus* showed consistent diurnal abundance patterns in both seasons with reduced numbers at 1200; however, significant chi-square results were only present during the dry season. The yellowfin mojarra (*Gerres cinereus*) maintained variable abundance patterns among seasons. Yellowfin mojarra were present in significantly lower numbers at 1700 during the rainy season. The sailor's choice (*Haemulon parrai*) revealed significant chi-square values during both sampling seasons with peak abundance levels at 1200. *Sparisoma* spp. showed relatively similar abundance at 0700 and 1700 with midday (1200) abundance approximately double. In both seasons, significant chi-square results and highly similar abundance trends were present for *Sparisoma* spp. Variable abundance levels were observed for yellow goatfish (*Mulloidichthys martinicus*). During the rainy season, high abundance characterized 1200 and relatively low levels occurred at 0700 and 1700, while the dry season showed similar abundance at 1200 and 1700 with a sharp decline at 0700. The timucu (*Strongylura timucu*) showed significantly higher abundance at 1200 only during the rainy season.

Diurnal comparisons for the most abundant species observed, schoolmaster, bluestriped grunt, French grunt, juvenile *Haemulon* spp., and yellowtail snapper, were made with a two-way repeated measures ANOVA with both time period and moon phase as factors. Significant differences in diurnal abundance were observed for schoolmaster, yellowtail snapper, and bluestriped grunt (Tables 2, 3). Significant differences in diurnal abundance were not found for juvenile *Haemulon* spp. and French grunts.

During the rainy season, the abundance of schoolmaster varied significantly with time period (Table 2). Abundance at 0700 was significantly lower than other time periods (DMRT,  $P < 0.05$ ). Peak abundance occurred at 1200 and declined moderately at 1700. During the dry season, no significant time period effects were found; nevertheless, the previously stated trend in abundance was repeated.

Both seasonal sampling periods were characterized by peak bluestriped grunt abundance at 1200, but only the rainy season survey showed significant differences among time periods (Table 2,  $P = 0.020$ ). A reduced ANOVA model with time period as the main factor indicated only marginal significance (Table 2,  $P = 0.052$ ). DMRT showed that the mid-day period (1200) was significantly higher than other times ( $P < 0.05$ ).

The two-way ANOVA for yellowtail snapper abundance suggested that time period might be significant but not moon phase (Table 2). A reduced model with time period only showed significant effects (Table 2,  $P = 0.035$ ). Peak abundance at 1200 was significantly different from other time periods (DMRT,  $P < 0.05$ ). Abundance at 1200 was approximately two times greater than morning or evening.

*Day-Night Changes.*—Nighttime counts were characterized by marked reduction or complete absence of diurnally observed species. No apparent diurnal-nocturnal

Table 1. Chi-square analysis of diurnal, day-night and seasonal variations in abundance of fishes occupying a mangrove prop-root habitat

Time Sample size Species	Oct/Nov 86 (rainy season)						Apr/May 87 (dry season)						Day-night		Seasonal							
	0700		1700		N		0700		1200		1700		2200		N		Diaturnal		Day-night		Seasonal	
	32	32	32	32	96	32	32	32	32	32	32	32	32	32	128	χ <sup>2</sup>	P	χ <sup>2</sup>	P	χ <sup>2</sup>	P	
<i>Abudefduf saxatilis</i>	17	11	10	38	2.26	ns	12	25	14	0	51	5.76	ns	24.59	**	1.90	ns					
<i>Acanthurus bahianus</i>	3	2	3	8	—	—	2	4	4	1	11	—	—	—	—	0.22	ns					
<i>Acanthurus chirurgus</i>	45	94	40	179	29.33	**	19	22	2	1	64	0.28	ns	19.13	**	55.6	**					
<i>Anisotremus virginicus</i>	1	4	1	6	—	—	4	1	2	0	7	—	—	—	—	—	—					
<i>Antennarius</i> sp.	0	0	0	0	—	—	0	0	0	1	1	—	—	—	—	—	—					
<i>Archosargus rhomboidalis</i>	0	1	0	1	—	—	22	28	23	1	74	0.85	ns	23.19	**	70.05	**					
<i>Caranx hippos</i>	20	62	59	141	23.36	**	2	2	0	0	4	—	—	—	—	129.44	**					
<i>Chaetodon capistratus</i>	9	12	3	24	5.25	ns	1	2	4	0	7	—	—	—	—	9.32	**					
<i>Chaetodon striatus</i>	0	1	0	1	—	—	0	0	0	0	0	—	—	—	—	—	—					
<i>Eucinostomus</i> spp.	35	22	36	93	3.94	ns	60	40	65	19	184	6.36	*	28.74	**	20.09	**					
<i>Gerres cinereus</i>	25	28	12	65	6.67	*	6	9	9	0	24	0.75	ns	9.00	*	18.88	**					
<i>Gymnothorax funebris</i>	0	0	0	0	—	—	1	0	0	0	1	—	—	—	—	—	—					
<i>Gymnothorax moringa</i>	0	0	0	0	—	—	0	1	0	0	1	—	—	—	—	—	—					
<i>Haemulon carbonarium</i>	0	1	2	3	—	—	0	1	0	0	1	—	—	—	—	—	—					
<i>Haemulon chrysargyreum</i>	0	0	1	1	—	—	0	0	2	0	2	—	—	—	—	—	—					
<i>Haemulon flavolineatum</i>	211	349	378	938	+	+	119	142	153	55	469	+	+	49.20	**	203.08	**					
<i>Haemulon parrai</i>	16	28	4	48	18.00	**	16	58	12	10	96	45.25	**	65.00	**	10.78	**					
<i>Haemulon plumieri</i>	3	0	2	5	—	—	5	10	2	0	17	5.76	ns	—	—	6.55	*					
<i>Haemulon sciurus</i>	39	206	41	286	+	+	158	465	313	19	936	+	+	467.06	**	330.97	**					
<i>Haemulon</i> spp. (juveniles)	1,040	885	1,142	3,067	+	+	615	1,354	1,100	0	3,069	+	+	1,390.48	**	0.00	ns					
<i>Halichoeres bivittatus</i>	2	3	0	5	—	—	210	462	301	36	1,009	+	+	376.30	**	1.48	ns					
<i>Lujuanus apodus</i>	170	433	317	920	+	+	3	2	3	0	8	—	—	—	—	—	—					
<i>Lujuanus griseus</i>	1	1	1	3	—	—	0	0	0	0	1	—	—	—	—	—	—					
<i>Lujuanus mahogoni</i>	2	7	6	15	2.80	ns	0	0	1	0	1	—	—	—	—	12.25	**					
<i>Lujuanus synagris</i>	0	2	0	2	—	—	0	0	0	0	0	—	—	—	—	—	—					
<i>Mulloidichthys martinicus</i>	22	45	15	82	18.05	**	3	13	19	0	35	11.17	**	26.45	**	18.88	**					
<i>Ocyurus chrysurus</i>	62	194	70	326	+	+	0	0	0	0	0	—	—	—	—	326.00	**					
<i>Ocyurus guacamaia</i>	4	1	0	5	—	—	0	4	2	0	6	—	—	—	—	—	—					
<i>Scorpaena plumieri</i>	0	0	1	1	—	—	0	0	0	0	0	—	—	—	—	—	—					
<i>Sparisoma</i> spp.	35	100	30	165	55.45	**	59	134	58	0	251	45.41	**	145.03	**	17.78	**					
<i>Sphaeroides spengleri</i>	0	0	1	1	—	—	0	0	0	0	0	—	—	—	—	—	—					
<i>Sphyrnaea barracuda</i>	11	18	13	42	1.86	ns	17	14	17	3	51	0.38	ns	10.37	*	0.40	ns					
<i>Stegastes leucostictus</i>	16	11	14	41	0.92	ns	21	27	25	0	73	0.77	ns	25.29	**	8.98	**					
<i>Strongylura timucu</i>	23	59	36	118	16.91	**	23	16	21	5	65	1.30	ns	11.95	*	18.90	**					

\* P < 0.05, \*\* P < 0.01, (—) Insufficient data for statistical testing and (++) Repeated measures ANOVA used. (see Tables 2 and 3).

Table 2. Repeated measures ANOVA results for main effects moon phase (MP) and time period (TP) for five most common taxa during rainy season (Oct/Nov 1986) (Bold numbers indicate factors that are significant at  $P < 0.05$ )

	df	<i>Haemulon flavolineatum</i>		<i>Haemulon sciurus</i>		<i>Haemulon juveniles</i>		<i>Lutjanus apodus</i>		<i>Ocyurus chrysurus</i>	
		F	P	F	P	F	P	F	P	F	P
<b>Full Model (MP and TP)</b>											
Between											
MP	3, 6	0.274	0.842	3.733	0.080	1.100	0.419	2.071	0.206	0.667	0.602
TP	2, 6	1.791	0.246	8.028	<b>0.020</b>	0.816	0.486	9.227	<b>0.015</b>	4.425	0.066
Within											
Transect	7, 42	7.942	< <b>0.001</b>	0.963	0.470	5.251	< <b>0.001</b>	3.938	<b>0.002</b>	9.605	< <b>0.001</b>
by MP	21, 42	0.660	0.846	0.893	0.600	1.487	0.135	1.135	0.353	1.590	0.099
by TP	14, 42	1.231	0.290	1.625	0.112	0.809	0.655	1.483	0.160	1.088	0.396
<b>Reduced Model (TP only)</b>											
Between											
TP	2, 9			4.200	0.052			6.799	<b>0.016</b>	4.977	<b>0.035</b>
Within											
Transect	7, 3			0.892*	0.597			1.397*	0.765	4.533*	0.121
by TP	14, 8			1.345*	0.345			0.59*	0.763	0.919*	0.576
DMRT ( $P = 0.05$ )				1200 High	0700 Low			1200 High	0700 Low	1200 High	1700 Low

\* F-value based on multivariate test using Pillai's Trace.

Table 3. Repeated measures ANOVA results for main effects moon phase (MP) and time period (TP) for five most common taxa during the dry season (Apr/ May 1987) (Bold numbers indicate factors that are significant at  $P < 0.05$ )

	df	<i>Haemulon flavolineatum</i>		<i>Haemulon sciurus</i>		<i>Haemulon juveniles</i>		<i>Lutjanus apodus</i>		<i>Ocyurus chrysurus</i>
		F	P	F	P	F	P	F	P	
<b>Full Model (MP and TP)</b>										
Between										
MP	3, 6	3.907	<b>0.073</b>	16.305	<b>0.003</b>	0.837	0.521	19.792	<b>0.002</b>	None
TP	2, 6	2.554	0.158	2.937	0.129	0.442	0.662	7.282	<b>0.025</b>	observed
Within										
Transect	7, 42	3.038	<b>0.011</b>	8.107	<b>&lt;0.001</b>	9.928	<b>&lt;0.001</b>	19.766	<b>&lt;0.001</b>	
by MP	21, 42	2.386	<b>0.008</b>	2.564	<b>0.005</b>	3.331	<b>&lt;0.001</b>	2.830	<b>0.002</b>	
by TP	14, 42	1.058	0.420	1.186	0.321	1.105	0.382	2.544	<b>0.010</b>	
<b>Reduced Model (MP only)</b>										
Between										
TP	2, 9	2.814	0.108	10.985	<b>0.003</b>			7.700	<b>0.010</b>	
Within										
Transect	7, 3	20.748*	<b>0.047</b>	77.620*	<b>0.013</b>			9.126*	0.102	
by TP	14, 8	1.012*	0.509	2.068*	0.098			1.338*	0.307	
DMRT ( $P = 0.05$ )				$\frac{N+1}{High}$	$\frac{3}{Low}$			$\frac{F+1}{High}$	$\frac{N}{Low}$	

\* F-value based on multivariate test using Pillai's Trace.  
 † N—new moon, 1—1st quarter, ‡ F—full moon, 3—3rd quarter.



changeover of species assemblages, typical of the coral reef habitat (Hobson, 1965; 1968; Starck and Davis, 1966; Collette and Talbot, 1972; Domm and Domm, 1973), occurred in the mangrove prop-root habitat of Cayo Collado.

All 15 species analyzed with chi-square showed significant ( $P < 0.05$ ) results, thirteen being highly significant ( $P < 0.01$ ) (Table 1). Six of the 15 species were completely absent at night: sergeant major (*Abudefduf saxatilis*), yellowfin mojarra, *Haemulon* spp. (juveniles), yellow goatfish, *Sparisoma* spp., and beaugregory (*Stegastes leucostictus*). Four other species were observed in extremely low nocturnal abundance ( $\leq 5$ ): doctorfish, sea bream (*Archosargus rhomboidalis*), barracuda (*Sphyraena barracuda*), and timucu.

Although hardhead silversides, dwarf herring, and dusky anchovy were excluded from statistical analysis, all were exceptionally abundant along the mangrove fringe and exhibited distinctive day-night trends. During the day, hardhead silversides appeared in large schools dispersed throughout the water column. At night, all observed silversides were solitary and found near the surface with nocturnal abundance reduced markedly. Low nocturnal abundance also characterized the dwarf herring and dusky anchovy. Dwarf herring were observed to migrate from the back reef area to the windward side of the cay at dusk as has been observed in Cuba (Radakov and Silva, 1974).

*Twilight Activities.* — Timing of twilight departures was defined for sub-adult bluestriped (12–18 cm TL) and juvenile French grunts (6–10 cm TL) during three consecutive sunsets (Table 4). For bluestriped grunts, timing of initial departures was variable and began up to 54 min before sunset. Twilight migration activity lasted approximately 60 min. Final departures were completed approximately 15 to 20 min after sunset. By contrast, initial departures for juvenile French grunts did not begin until approximately 28 to 30 min after sunset. Duration from initial to final departure was limited and within 4 to 7 min. Final departures were generally completed 35 min after sunset. Twilight migratory behavior also differed among species. Juvenile French grunts were not present at departure sites prior to initial departure. Schools began arriving at departure sites approximately 20 to 25 min after sunset. Schools appeared to emerge laterally from other sections of the prop-root fringe. Arriving schools were heterotypically constructed (Ogden and Ehrlich, 1977) with French grunts dominant (over 90%). Juvenile white grunts (*Haemulon plumieri*), bluestriped grunts, crevalle jacks, and sea breams were intermixed in limited numbers. Heterotypic schools generally consisted of 100 to 160 individuals and twilight migration was completed in two or three subgroup movements during each sunset. Bluestriped grunts were present at departure sites when twilight observations began in heterotypic resting schools with schoolmasters, sailor's choice grunts, and French grunts. However, migrating schools were homotypic with almost exclusively bluestriped grunts (99%). Migrating subgroups ranged in size from a few individuals up to groups of 20 to 30. Migrational schedules of individual subgroups was highly variable, but overall twilight migrational timing was quite consistent (Table 4). The number of subgroup migration per sunset ranged from 2 to 12. For the remaining fish, no obvious twilight migrational patterns existed. As previously mentioned, juvenile crevalle jacks, bluestriped grunts, white grunts, and sea breams were often intermixed in haemulid migrations. However, they expressed no migrational activities of their own. Schoolmaster and other less abundant lutjanids were still present among the prop-roots an hour after sunset, although numbers were reduced. Single individuals or pairs of schoolmasters were occasionally observed moving out of the prop-roots, but no definitive mass migration was observed. Species of the families

Table 4. Timing of sunset migration activities observed on three consecutive days in two locations for juvenile French (6–10 mm TL) and intermediate sized bluestripe grunts (12–18 mm TL). Times are expressed in minutes before (–) and after (+) sunset. Sunset occurred at 1831

	Minutes after sunset				
	28 May 87	29 May 87	30 May 87	Mean	SD
Juvenile French grunts (6–10 mm TL) ( <i>Haemulon flavolineatum</i> )					
First Departure					
Location 1	(+) 28	(+) 31	(+) 26	(+) 28.33	2.51
Location 2	(+) 29	(+) 33	(+) 29	(+) 30.33	2.30
Last Departure					
Location 1	(+) 35	(+) 35	(+) 33	(+) 34.33	1.15
Location 2	(+) 33	(+) 37	(+) 35	(+) 35.00	2.00
Bluestripe grunts (12–18 mm TL) ( <i>Haemulon sciurus</i> )					
First Departure					
Location 1	(–) 35	(–) 48	(–) 54	(–) 45.67	9.71
Location 2	(–) 41	(–) 41	(–) 46	(–) 42.67	2.88
Last Departure					
Location 1	(+) 14	(+) 14	(+) 14	(+) 14.00	0.00
Location 2	(+) 21	(+) 15	(+) 14	(+) 15.00	10.98

Acanthuridae, Scaridae, Chaetodontidae, and Pomacentridae, were present when initial sunset observations began, but as sunset approached, their presence became less detectable until they were no longer observed.

*Lunar Periodicity.*—Significant chi-square results were obtained for five species during each sampling period; rainy season: crevalle jack, yellowfin mojarra, sailor's choice, yellow goatfish, and *Sparisoma* spp.; dry season: sergeant major, doctorfish, beaugregory, sailor's choice, and *Sparisoma* spp. Poor visibility, associated with first quarter (rainy season) and last quarter (dry season) moon phases, affected enumerations considerably. All species displaying significance, except the crevalle jack, showed lowest abundance during periods of poor visibility possibly indicating sampling bias instead of lunar effects. Crevalle jacks were highly abundant during first quarter and last quarter phases, and virtually absent during new and full moon phases.

Schoolmaster and bluestriped grunt were the only abundant species showing significant moon phase effects (Table 3). During the dry season the last quarter was significantly lower than the other three periods (DMRT,  $P < 0.05$ ). Trends were not similar between seasons as the last quarter was characterized by high abundance during the rainy season, and low abundance during the dry season.

Bluestriped grunt rainy season analysis suggested possible moon phase effects but were not significant (Table 2,  $P = 0.080$ ). Examination of the raw counts indicates that highest abundance occurred at the first and new moon phases.

*Seasonal Changes.*—Seasonal variation in composition and abundance of mangrove prop-root fish was observed between the rainy (Oct/Nov 1986) and dry (Apr/May 1987) seasons. Twenty-one species were analyzed for seasonal variations in abundance with the chi-square test; 16 species (76%) showed significant differences in seasonal abundance (Table 1). Highly significant ( $P < 0.01$ ) results were observed for doctorfish, sea bream, crevalle jack, four-eye butterflyfish (*Chae-*

*todon capistratus*), *Eucinostomus* spp., yellowfin mojarra, French grunt, sailor's choice, bluestriped grunt, mahogany snapper (*Lutjanus mahogoni*), yellow goatfish, yellowtail snapper, *Sparisoma* spp., beaugregory, and timucu. Peak abundance for the doctorfish, crevalle jack, four-eye butterflyfish, yellowfin mojarra, French grunt, mahogany snapper, yellow goatfish, yellowtail snapper, and timucu were observed during the rainy season, while the sea bream, *Eucinostomus* spp., sailor's choice, bluestriped grunt, *Sparisoma* spp., and beaugregory showed significantly higher abundance during the dry season. Yellowtail snapper, sea bream, and crevalle jack and were moderately to highly abundant during one season and absent or rare in the other. Significant seasonal differences ( $P < 0.05$ ) were detected in one other species, white grunt, that maintained highest abundance during the dry season.

#### DISCUSSION

Ichthyofauna present in the mangrove prop-root habitat of Cayo Collado was similar to that discussed by Austin (1971) for other fringing mangroves in Puerto Rico. Lutjanids, haemulids, scarids, pomacentrids, and various schooling baitfish were the dominant species.

Quantitative comparison of western Atlantic mangrove ichthyofauna is limited to work conducted by Valdez Muñoz (1981)—Cuba, Galzin et al. (1982)—Guadeloupe, and Thayer et al. (1987)—southern Florida. Primary ichthyofauna reported in Cuban and Guadeloupan mangroves was similar to Puerto Rico. However, ichthyofauna in southern Florida differed greatly. Estuarine fishes such as gerreids (mojarras) and cyprinodontids (killfish) were the primary fishes in the southern Florida mangroves. Common coral reef fishes, typical in Puerto Rican mangroves, were absent or in greatly reduced numbers in south Florida.

Activity patterns displayed by these mangrove fishes during the diel cycle appear to be directly or indirectly related to feeding strategy. Diurnally active herbivores and omnivores in the mangroves include the doctorfish, ocean surgeon, and a variety of parrotfishes. Diurnal movements may be responsible for significant differences in daytime abundance. Highly active foraging groups continuously moved in and out of the mangroves in small species-specific schools. Increased abundance observed at midday (1200) may result from diurnal movements into the mangrove prop-root region. Diurnal migration activities have been reported for certain scarids and acanthurids (Hobson, 1973; Ogden and Buckman, 1973). It is also possible that increased foraging activity enhances species visibility that would increase the number of individuals enumerated during the 1200 census. At night, all daytime omnivores and herbivores are either completely absent, or in greatly reduced numbers. Twilight cover-seeking behavior (Dubin and Baker, 1982) and nocturnal inactivity appear responsible for day-night variation in species abundance.

Secondary consumers, which feed principally on crustaceans, are active primarily at night. Snappers and grunts, typical nocturnal feeders, generally form large inactive schools at their daytime resting sites. At night, they migrate off into seagrass beds and sand flats to feed (Hobson, 1968; 1972; 1975; Sbikin, 1977; McFarland et al., 1979). Similar migrations are present in this mangrove prop-root system. Sharp declines in nocturnal abundance of the schoolmaster, French grunt, bluestriped grunt, and other less abundant snappers and grunts results from nocturnal migration activity. Similar types of foraging movements may also be responsible for low nocturnal abundance observed in the sea bream, yellowfin mojarra, and *Eucinostomus* spp., which are also typical sandflat and seagrass bed

feeders. Aside from distinct day-night differences, diurnal variations in abundance were also present. Diurnal variation in abundance may be indirectly related to dawn and dusk migrations to and from nocturnal feeding grounds. Although migrations generally occur during transitional periods, schoolmasters, French grunts, and bluestriped grunts were occasionally observed either returning after 0700 or leaving before 1700, which may indicate that some migration activities were in progress. Peak abundance observed at 1200, midway between transition periods, may represent a near complete resting assemblage of species.

The predominant planktivores in the prop-roots were of two types: demersal planktivores (e.g., beaugregory, sergeant major) and midwater planktivores (e.g., dwarf herring, hardhead silverside, and dusky anchovy). No significant differences in diel abundance were found for these species. However, day-night changes in abundance were very evident. Although present in moderate abundance during the day, the beaugregory and sergeant major were not observed at night. These demersal planktivores, generally regarded as site feeders (Hobson, 1975), appear to restrict feeding activity to diurnal hours and probably seek cover at night (Domm and Domm, 1973). Alternatively, the dwarf herring, hardhead silverside, and dusky anchovy are strainer-type feeders and do not depend on vision to detect prey. These species were present at night, but highly dispersed and in reduced numbers, which appears related to foraging strategy and predator-prey interactions (Major, 1977).

Factors proposed to account for low nocturnal abundance were further supported with evidence attained through sunset observations. All haemulids, as well as the schoolmaster, yellowfin mojarra, crevalle jack, and sea bream, were observed leaving the mangrove prop-roots at dusk. French and bluestriped grunts displayed definite twilight migrations, while other species were less discrete in their movements. Species believed to seek cover at night (acanthurids, chaetodontids, pomacentrids, and scarids) failed to display any distinguishable migration activities. These species were observed prior to sunset, but as light levels decreased, they seemed to disappear.

Twilight observations on juvenile French grunts found on patch reefs off St. Croix, Virgin Islands, (McFarland et al., 1979; Helfman et al., 1982), showed nearly identical twilight behaviors to those observed in the mangrove prop-roots of Cayo Collado. Munz and McFarland (1973) suggested that the intensity and spectral composition of incident light may serve as physical cues, thus accounting for apparent temporal consistency in migration activity among different areas.

Evidence implying threat of predation as responsible for maintaining timing of twilight events has been reported by Hobson (1968; 1973). Predation on coral reefs is thought to be maximum during twilight (Hobson, 1968; 1972; Munz and McFarland, 1973; Major, 1977; Gladfelter, 1979). Hobson (1972) described an interim period, the "quiet period," characterized by peak predatory activity which begins as light levels decrease to approximately 10 lux and continues for 15–20 min until light levels reach 0.01 lux. This occurs between sunset and the end of civil twilight (approximately 25 to 30 min after sunset). Gladfelter (1979) in the Virgin Islands and Major (1977) in Hawaii indicated peak predatory activities occurred between sunset and the end of civil twilight; thus, this can be used to relatively approximate the quiet period.

The timing of twilight migration activities for both the sub-adult bluestriped grunt and juvenile French grunt avoid peak predatory pressure by migrating before or after the quiet period, but not during. Sub-adult bluestriped grunts actively migrate away from the prop-root protection before peak predation pressure occurs. Migrations proceed up to and during initial peak predatory activity. Bluestriped

grunts, however, remain closely associated with the mangrove habitat for protective measures. The threat of predation by barracudas (or divers) may have initiated returns into the mangroves. On one occasion 97 bluestriped grunts quickly returned into the prop-root habitat as a barracuda approached. The small size of juvenile French grunts and other associated juveniles may increase their susceptibility to predation. By restricting their migrational time schedule they may reduce the chance of predation. Juvenile French grunts, in contrast to sub-adult bluestriped grunts, migrate just after peak predatory activity associated with the quiet period. From approximately 10 to 25 min after sunset no migrational activity occurs. Sub-adult bluestriped grunt migrations are generally completed within 10 min after sunset while juvenile French grunt migrations have yet to begin. This period may correspond with the quiet period. Gladfelter (1979) reported similar findings on predatory activity in St. Croix. Peak predatory activity during twilight migrations of the copper sweeper (*Pempheris schomburgki*) occurred between 10 and 25 min after sunset.

Reproductive activities associated with the lunar cycle, such as spawning aggregations, can have significant effects on temporal variation in species abundance (Johannes, 1978). From quantitative mangrove assessments, it was difficult to determine the effect of lunar related reproductive rhythms on species abundance. Since the majority of mangrove inhabitants are reproductively immature, no reproductive-related activities would be expected. Environmental variability, not associated with lunar periodicity, may account for weekly fish abundance variability. Low visibility characterized the last quarter moon phase during the Apr/May 1987 survey and this may have accounted for the significant moon phase effects observed for the schoolmaster and bluestriped grunt.

Seasonal fluctuations in species abundance and age class structure appear closely associated with life history features, particularly recruitment. Recruitment of juveniles to nursery areas is often variable (Ogden and Ehrlich, 1977); consequently, seasonal fluctuations in species numbers may occur. The offshore mangrove habitat of Cayo Collado appears to be an intermediate staging area for many fish species. Most species inhabiting the system were not small juveniles but rather large juveniles to sub-adult sized fish. Species such as yellowtail snapper, French grunt, bluestriped grunt, white grunt, mahogany snapper, and crevalle jack were all characteristically in the size range 10 to 18 cm TL. Small juveniles of these species are often associated with grassbeds and small patch reefs while the adults typically occupy coral reef or related open-water habitats. When small juveniles reach sufficient size, they may migrate into the mangroves, which then serve as an intermediate life stage habitat. When sufficient size is attained, recruitment into the adult population occurs. This category of fish showed significant seasonal differences in abundance, which may indicate that recruitment activity was occurring. Certain species, however, were present in the mangroves from their initial juvenile stages up to early adult stages. Small juvenile stages (less than 5 cm TL) were observed for the schoolmaster, gray snapper, and barracuda as well as adult size fish (e.g., lutjanids to 25 cm TL). Since a complete range of size classes was present, it appears that recruitment processes in and out of the mangrove habitat may be limited to early adult migrations out to established adult populations on the reef. No species maintaining juvenile to adult size classes in the mangroves showed seasonal variation in abundance.

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