RECRUITMENT PATTERNS IN
YOUNG FRENCH GRUNTS, *HAEMULON FLAVOLINEATUM*
(FAMILY HAEMULIDAE), AT ST. CROIX, VIRGIN ISLANDS[1]

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ABSTRACT

During 1979 and 1980 the settlement of postlarval grunts (mostly French grunts, *Haemulon flavolineatum*) from the plankton to inshore areas in Tague Bay, St. Croix, Virgin Islands, was monitored. Settlement occurred at all times of the year, but showed two distinct maxima during May-June and October-November. Summer settlement rates were approximately one-third the peak rates, whereas winter settlement rates were low but always present. A dominant, semilunar periodicity in the settlement of the postlarvae was clearly present, but smaller interspersed weekly peaks occurred. Calculation of the fertilization dates of recently settled postlarval grunts, derived from otolith ages, also established a dominant 15-day periodicity, but again interspersed with smaller weekly fertilization peaks. The phase of settlement and fertilization is most strongly associated with the quarter moons and/or intermediate daily excursions of the tides; the smaller weekly peaks are more closely associated with new and full moons. The pelagic existence of French grunts is about 15 days, suggesting that fertilizations that lead to successful recruitment to inshore areas precede settlement by 15 days. Two hypotheses—semilunar shifts in spawning versus a more constant daily rate of reproduction—are discussed as possible explanations of the dominant semilunar rhythm observed in the settlement patterns.

Community structure is primarily determined by predation, competition, environment, and patterns of reproduction and recruitment (Ricklefs 1979). In most marine fishes the larval stages are planktonic, a circumstance especially true for tropical reef fishes (Breder and Rosen 1966; Sale 1980; Thresher 1984). In general, larger reef species produce numerous but relatively small eggs, which at spawning are dispersed into the plankton; whereas smaller reef species produce fewer but larger demersal eggs, which are guarded until hatching when the larvae also "escape" into the offshore plankton community (Johannes 1978; Barlow 1981). The potential significance of this widespread reproductive strategy to affect coral reef fish assemblage structure is widely recognized (see Helfman 1978 and Sale 1980 for reviews). Most ecologists have assumed that

planktonic larval fishes provide an extensive reservoir of potential recruits that settle to the reef whenever space becomes available (Sale 1977, 1978; Dale 1978; Smith 1978). Virtually all recent studies, however, emphasize that we know little of the ecology of larval fishes at sea and of their patterns of recruitment to benthic juvenile habitats (McFarland in press; McFarland and Ogden in press). Until more quantitative information on the early life history of a variety of species of reef fishes is available, models that "explain" fish community structure remain, at best, first approximations. Here we describe spatial and temporal patterns of recruitment in the French grunt, *Haemulon flavolineatum*, a dominant western Atlantic tropical reef species.

MATERIALS AND METHODS

Recently settled postlarval French grunts and white grunts, *H. plumieri*, standard length (SL) ca. 8.5 mm, are commonly observed in schools over grass beds or associating with coral clumps and gorgonians in Tague Bay, St. Croix, VI. Single individuals and larger aggregations associate with structure and/or intermix with schools of mysids (McFarland and Kotchian 1982). There is little difficulty in recognizing and counting these very small grunts in the field because they lack the body colora-

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tion patterns of slightly larger postlarvae (see table 1 in McFarland and Kotchian 1982). Postlarval grunts, however, cannot be identified by sight at the species level. We will refer to these smallest postlarvae as PL-1 grunts. These recently settled postlarvae are diurnal plankton feeders (McFarland 1980) as, presumably, is the preceding pelagic larval stage. Although the postlarvae show strong social tendencies to school during daytime, they are solitary at night (Helfman et al. 1982); the same pattern is found in older juveniles and adults (Ogden and Zieman 1977). The typical stereotyped twilight migrations of older juvenile and adult grunts (Hobson 1968; Ogden and Ehrlich 1977; McFarland et al. 1979), however, are not present, nor are the agonistic behaviors typical of all later stages (McFarland and Hillis 1982).

During collateral studies on the population dynamics of grunts, on agonistic behavior in juveniles (McFarland and Hillis 1982), and age determinations of grunts (Brothers and McFarland 1981), we noted that recently settled PL-1's appeared in pulses. To investigate this periodicity, an extensive area of bottom in Tague Bay and a series of shallower discrete reef sites were censused repeatedly for PL-1's. In addition, subsamples of PL-1's were collected throughout the census period for size and age determinations.

Tague Bay Census Measurements

Sixteen flagged iron stakes were set 10 m apart along the bottom of Tague Bay parallel to the bay's barrier reef at a depth of ca. 5m. The bottom was characterized by sandhills produced by the burrowing activity of thalassinid shrimps, with stands of the seagrasses *Thalassia testudinum, Syringodium filiforme*, and *Halodole wrightii* between the mounds. Censuses of the total number of postlarvae were made using scuba, recording the numbers of grunts encountered along a 5 m wide transect. The census included all postlarval grunts observed over an area of 800 m² of bay bottom. Because almost all juvenile grunts in the immediate vicinity were French grunts, we presume the census data mostly represent this species. Of 85 PL-1's collected on this site, all were identified as French grunts. The census began on 25 February 1979, and was continued at variable intervals through 31 August 1980. Although numbers of older grunts were also recorded, here we report only the numbers of the smaller and youngest postlarvae (mean SL = 8.5 mm). This census is hereafter referred to as the "sandhill" site.

Reef Census Measurements

A series of 20 individual sites in a shallow sandy area (1-3 m depth) along a 200 m stretch of the Tague Bay barrier backreef were monitored for postlarval settlement. The sites varied somewhat in size and structure, but were composed of small clumps of *Montastrea annularis* and/or *Porites porites*. Sixteen of the sites were in depths of 1 to 2 m; four were in 2 to 3 m depth. Reef areas varied from 0.1 to 8 m²; vertical relief from 20 cm to 1.5 m. Daily censuses were obtained as often as possible from 25 April 1980 through 25 May 1981. The census schedule was intensified especially from 6 May through 27 December 1980 (172 censuses over 236 d). Counts on each site on each census day included the total numbers of PL-1's, older postlarvae, juvenile grunts (see McFarland and Kotchian 1982), damselfishes (all species lumped), and the common sea urchin, *Diadema antillarum*, within the spines of which the middle-sized juveniles often seek refuge (see Helfman et al. 1982). In this reef area, which is surrounded by coral sand and lacks seagrass beds, juvenile white grunts were never encountered, only French grunts. We conclude therefore that recruits were all French grunts.

Reproductive Activity and Aging of French Grunts

Spawning in grunts has not been observed or reported in the literature (Breder and Rosen 1966; Hobson 1968; Johannes 1978; Lobel 1978; our personal observations and field observations of P. Colin and of E. S. Hobson). An indirect method was used to provide information on whether grunts spawned in some periodic manner, as so many reef fishes do (Johannes 1978; Lobel 1978; Colin 1982).

The age of French grunts can be established in days, for example, by counting the number of microstructural growth increments laid down in the lapillus (Brothers and McFarland 1981). The method is especially useful for aging the younger life history stages (< 100 d). By ascertaining the actual age of an individual grunt in days, it becomes possible to establish the specific date on which it was spawned. The method requires a correction, however, because the first "daily" growth increment deposited in the otolith does not coincide with fertilization of the egg. Our best "estimate" for the age at formation of the first distinct increment in the otoliths of French grunts is the third day after fertilization (for details see Brothers and McFarland 1981; this revised estimate is based on laboratory-reared porkfish, the con-

familial *Anisotremus virginicus*, of known age, supplied by Martin Moe). Thus, to each "otolith age" (= total increments counted) 2 d were added to establish the "absolute" daily age of an individual fish.

This method was applied to postlarval French grunts, collected throughout the year in the vicinity of the 20 discrete census sites. On most census days individual PL-1's were collected with a fine mesh net and fixed and preserved in 95% ethanol. Each postlarva was measured (SL) and the otoliths were removed and placed in immersion oil. The number of growth increments was counted and corrected (+ 2 d) to the actual date of fertilization.

Tides

A tidal gauge (NOAA, Ocean Survey #9751224) operates at the West Indies Laboratory dock, about 0.5 km from our Tague Bay study site. Hourly tidal heights for the year 1980 were obtained from NOAA. Missing, due to malfunction of the gauge, are records from 26 June to 9 September 1980. These missing values were approximated from calculated tidal data for San Juan, Puerto Rico. The phase of the tides in Puerto Rico matched closely the tides at Tague Bay (comparisons of dates before and after the missing records), but the actual excursion of the tides was less at St. Croix than calculated for Puerto Rico.

RESULTS

Tague Bay Sandhill Study Site

During 1979, 27 censuses were executed during 300 possible days of sampling (25 February to 21 December). The mean interval between censuses was 11.2 d ± 6.6 (1 SD), the intervals ranging from 4 to 23 d. Five population peaks were recorded, with the number of PL-1's counted between peaks often declining to < 100 individuals. The 1979 census clearly indicated that settlement was represented by a series of pulses, but the sampling intervals were too long to resolve periodicities of much less than 1 mo. Therefore, in 1980 the sampling resolution was improved by increasing the number of censuses to 47 over a possible 325 sampling days (6 February to 26 December 1980); mean sampling interval was 7.0 d ± 7.7, the shortest interval being 1 d and the longest interval 49 d (i.e., the first interval). Eleven peaks, of which 8 are distinct, establish that the postlarvae settle in pulses, with the population numbers on the bay bottom often decreasing to 0 between pulses (Fig. 1). Although the pulses in population numbers
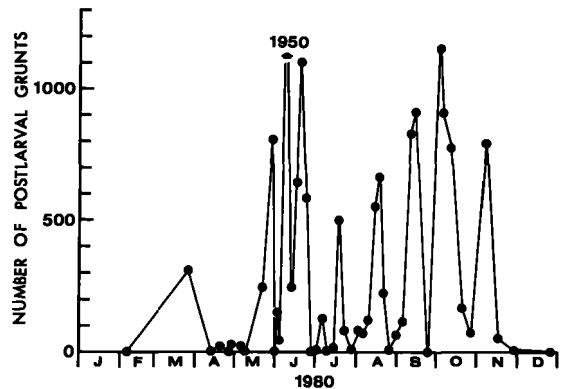

FIGURE 1. – Numbers of recently settled postlarval grunts observed over 800 m² of bottom on the sandhill site area of Tague Bay, St. Croix, V.I.

are suggestive of a semilunar periodicity, the peaks do not coincide more closely with either quarter moons or with the new and full moons than do the population declines.

Individual Barrier Reef Study Sites

The mean sampling interval on the 20 individual census sites from 6 May to 27 December 1980 (possible 236 sampling days) was 1.37 d ± 0.7 (1 SD). This shorter sampling interval vividly reveals the periodicity in the appearance of PL-1's on the sites (Fig. 2). Coincidence between these peaks and the peaks for the sandhill study sites is quite good (compare Figures 1 and 2) and indicates that the timing of the settlement of PL-1's is general over the entire area. Also, as in the sandhill area, the numbers of PL-1's declined to 0 between most pulses. Furthermore, the pooled data for the 20 sites indicate a bimodal seasonal influx of PL-1's, one in late spring and a second increase in fall, as seen also in the sandhill study site (compare Figures. 1 and 2). The summer settlement pulses involved about one-third the number of individuals associated with the bimodal peaks. Winter settlement was very low; only small numbers of PL-1's were observed during January and February 1981.

Age and Reproductive Activity

A total of 2,353 postlarvae from 141 collections spread over 391 d were captured between 20 February 1980 and 16 March 1981 (Fig. 3). From each of these 141 samples 15 PL-1's were measured and aged, or fewer if the collected samples contained
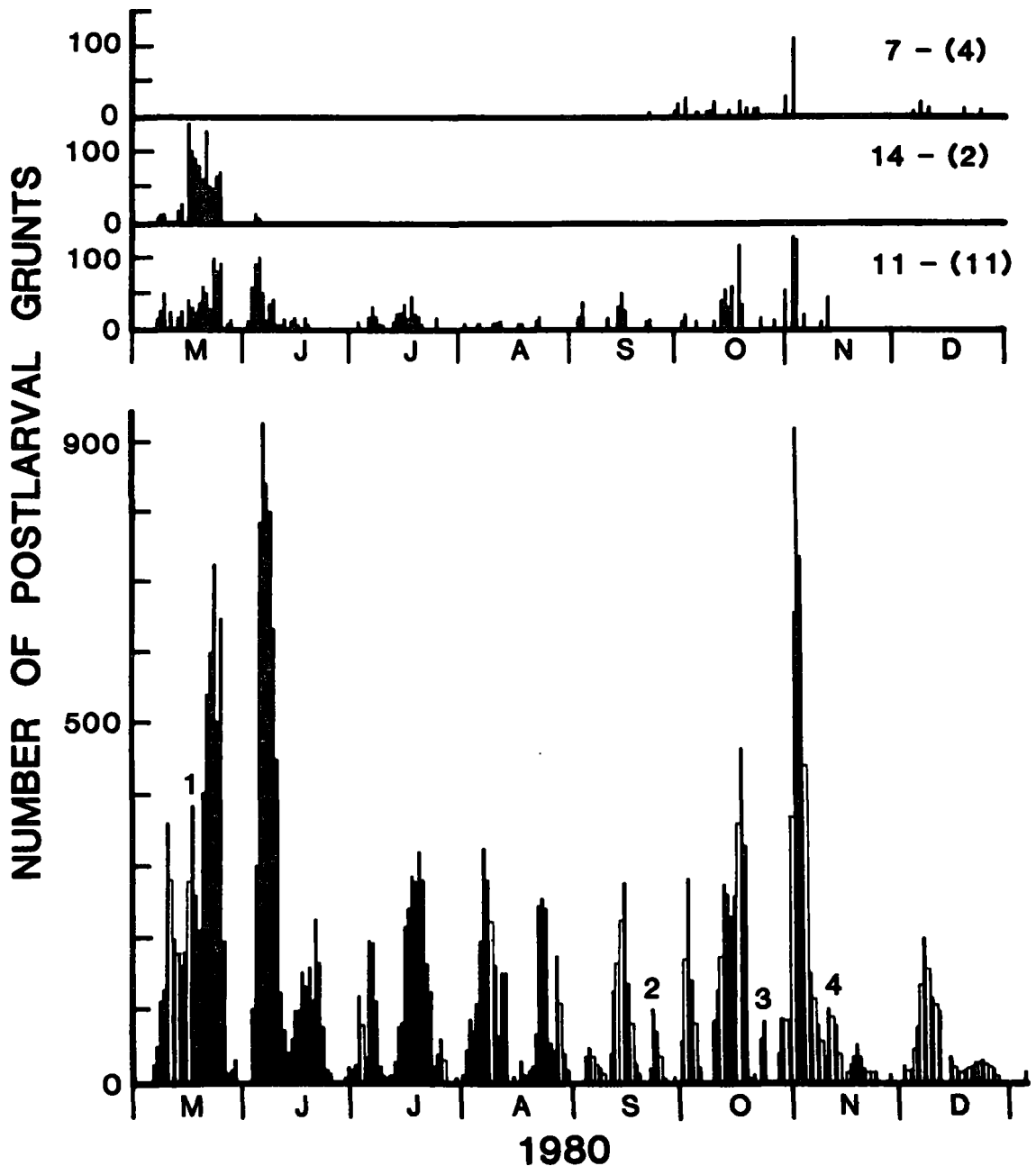
FIGURE 2. – Numbers of recently settled postlarval grunts observed on the individual census sites located in the shallows along the backreef of Tague Bay barrier reef. The three upper graphs represent the recruitment of PL-1's to specific sites 7, 11, and 14. Numbers in parentheses to the right of the hyphens indicate on how many sites a similar seasonal pattern of settlement was observed. Three of the 20 census sites were like 7 or 14, but also recruited grunts in summer (not shown). The lower graph represents the pooled data from all 20 sites. Values for census gaps have been estimated by calculating running averages (open bars). Numbers indicate the weaker but definitive weekly influxes of post-larvae. Additional weekly peaks probably occur but are less certain. Note the bimodal seasonal increase in recruitment during May-June and October-November. This coincides with the modal and bimodal peaks in gonadal development of several Caribbean reef species (Munro et al. 1973).
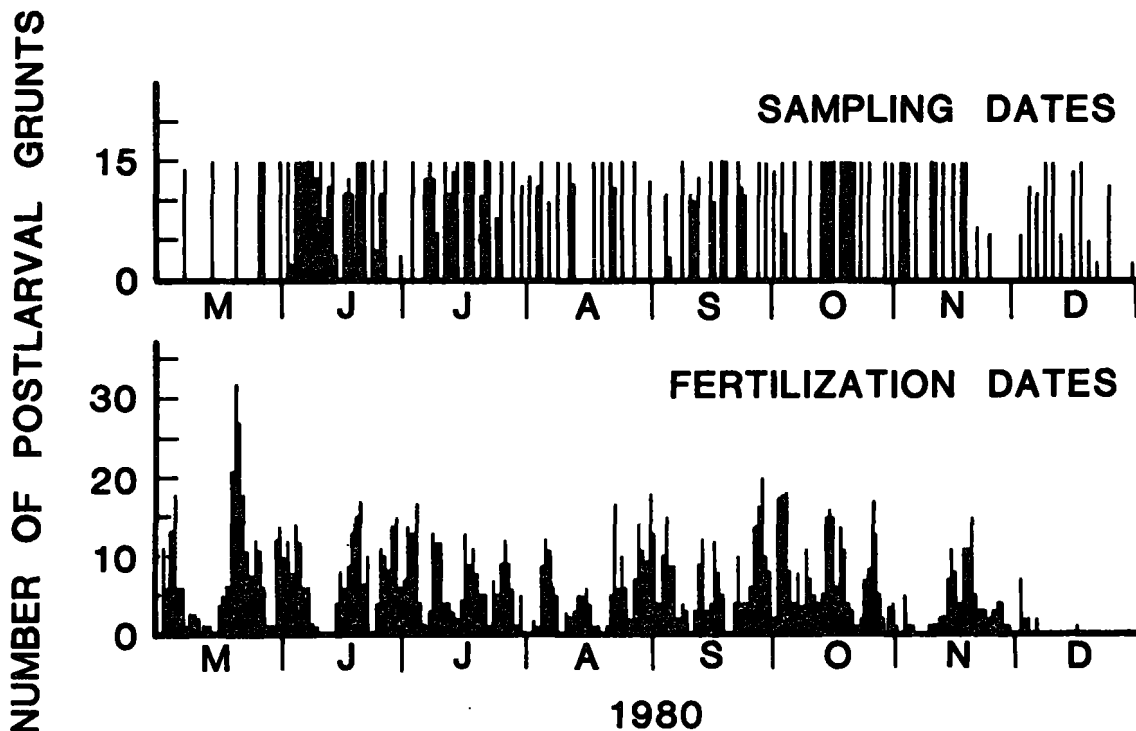
FIGURE 3. – Relationship of fertilization dates of recently settled postlarval grunts to time of the year. Upper graph represents the dates and the numbers of postlarvae collected for aging from the backreef of Tague Bay barrier reef. Lower graph represents the frequencies for back-calculated dates of fertilization of the collected samples in the upper graph.

fewer postlarvae (Fig. 3). The actual day of fertilization for each of these 1,478 French grunts indicates that recently settled individuals were spawned with a consistent periodicity (Fig. 3) that is similar to the settlement periodicity (Fig. 2). These derived spawning data suggest, however, the presence of a more pronounced short cycle.

Periodic Analysis, Times of Settlement and Reproductive Activity, and Patterns of Settlement

Periodic Analysis

To evaluate the periodicity of postlarval settlement and of fertilization times of recently recruited French grunts (Figs. 2, 3), we used a Rayleigh-test (see Batschelet 1965). The method involves a Fourier transform of sequential data (see McFarland and Kotchian 1982 for details). A data set is first sequentially summed for a specified period, and these pooled data are used to evaluate the degree of deviation from a nonperiodic random distribution. By comparing dimensions of the mean vectors obtained for different specified periods, the most dominant period is usually revealed (Fig. 4).

Analysis of the 1980 settlement and fertilization data reveals that a rhythm with a period of about 15 d dominates (Table 1). Examination of the census and fertilization data (Figs. 2, 3) indicates that weak secondary appearances of PL-1's and different fertilization dates may occur. Indeed, their presence (e.g., 4 peaks in Fig. 2) hints at a weekly rhythm superimposed on the semilunar periodicity. It is difficult to assess this possibility with periodic analysis, however, because a natural harmonic of the dominant 15-d rhythm can occur at about 7.5 d, even if a weekly rhythm does not exist (Fig. 4).

With less mathematical elegance the periodicity in the data sets can be estimated by averaging intervals between peaks. Both the 1980 census data for the 20 discrete study sites (Fig. 2) and the fertilization date data (Fig. 3) provide similar estimates of about 13.9 d and 15.1 d (Table 2), which do not differ significantly from the mean semilunar period of 14.64 d that actually occurred. The possible presence of a weekly rhythm often interspersed between the biweekly rhythm is revealed by 5 obvious short-period pulses
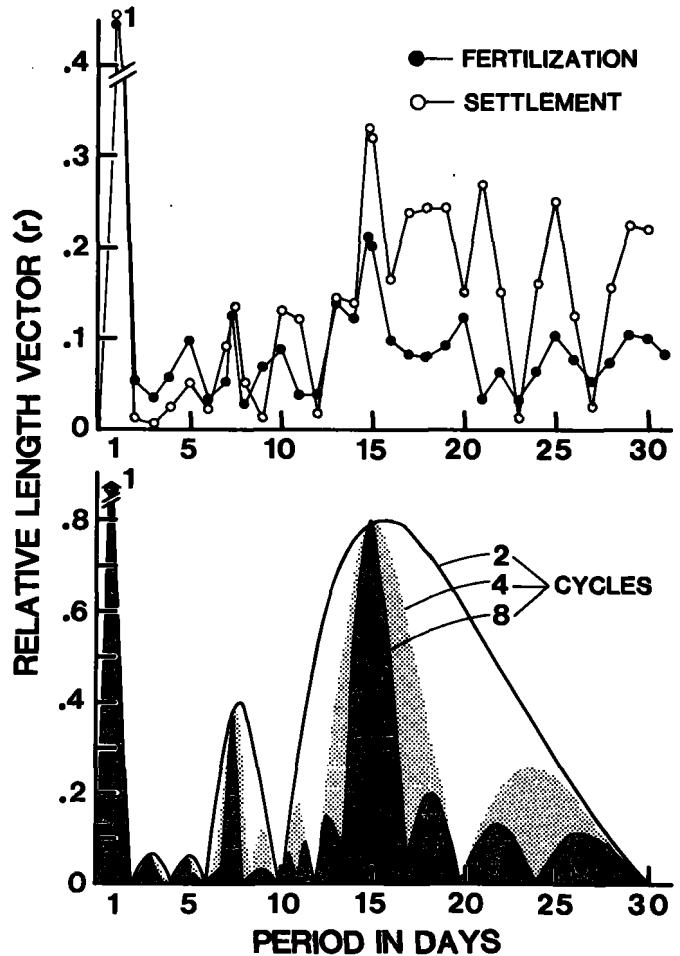
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FIGURE 4.—Variation in the length of vectors derived from a circular distribution test for different periodicities in the settlement and fertilization data presented in Figures 2 and 3 (upper graph). Note that a period of about 15 d provides the largest vector value beyond a 1-d period (Rayleigh test statistic $z = 28.2$ for settlement and 10.8 for fertilization, where $z_{(P=0.01)} = 4.6$). Lower graph is a plot of vector values from artificial data generated by repeating the analysis for 2, 4, and 8 cycles (artificial data were 0, 0, 0, 0, 25, 50, 75, 100, 75, 50, 25, 0, 0, 0, 0). Note how an increased number of cycles or periods narrows the peak for the dominant 15-d period and introduces more harmonics. The settlement and fertilization data (upper graph) represent 16 cycles for a period of 15 d. The height of the harmonics after 15 d probably reflects basic sampling noise and the presence of smaller weekly peaks (see Figs. 2, 3).

TABLE 1.—Dominant periods derived from a circular distribution test of the settlement and fertilization data presented in Figures 2 and 3. Significance symbols are ** = $P < 0.01$; z values are Rayleigh test statistic (Batschelet 1965).

Type of data	Date of samples	Dominant period (days)	z value	No. days	No. cycles analyzed based on dominant period
Settlement	30 Aug.-31 Dec.	14.9	26.5**	244	16.4
	2 May-31 Aug.	15.3	19.2**	122	8.0
	30 Aug.-31 Dec.	17.0	31.6**	124	7.3
Fertilization	2 May-31 Dec.	14.8	10.7**	244	16.5
	2 May-31 Aug.	14.6	8.7**	122	8.4
	30 Aug.-31 Dec.	15.5	2.8 n.s.	124	8.0

for settlement and at least 9 short-period pulses for fertilization (Table 2).

Timing of Settlement and Fertilization

To estimate the phase of settlement and of fertilization to the lunar cycle, the delay in days from the nearest full or new moon was determined for each event (Table 2). The mean phase delay for fertilization was 5.4 d, and for settlement 7.3 d. Clearly both fertilization and settlement are more often associated with the quarter moons than they are with the full or new moons. The overall relation to the lunar cycle is revealed more clearly by matching each in-

TABLE 2.—Comparisons of fertilization and settlement dates for recently recruited postlarval French grunts with the lunar cycle and the state of the tides. F and N are full and new moons; S and N are spring and neap tides; I↑ and I↓ are rising and falling tides of intermediate amplitude between a spring and a neap tide. The peak date for settlement represents the maximum influx of postlarvae, which occurred on average 3 d before the maximum number of French grunts appeared on a site. Values are the sums from all 20 census sites. Rows are aligned so that the most likely fertilization date precedes each settlement date. Vertical lines and summed numbers for days between peaks are best estimates of weekly peaks to yield the dominant biweekly peaks (see mean values at bottom of table).

Fertilization					Settlement				
Peak date	No. PL-1's in peak	No. days between peaks	Moon phase + days	Tidal state	Peak date	Total no. PL-1's in peak	No. days between peaks	Moon phase + days	Tidal state
—	—	—	—	—	4/7	¹18	—	F + 7	I↓
—	—	—	—	—	4/22	¹13	15	N + 8	I↓
—	—	—	—	—	5/7	360	15	F + 7	I↓
—	—	—	—	—	²5/14	383	7 [13]	N + 0	S
5/4	49	—	F + 4	S	5/20	723	6	N + 6	I↓
—	—	—	—	—	²5/26	29	6 [13]	N + 12	I↑
5/19	48	15	N + 5	I↓	6/3	930	7	F + 5	I↓
5/30	18	11	F + 1	S	6/18	224	15	N + 6	I↓
6/19	21	20	N + 7	I↓	7/3	195	15	F + 5	I↓
²6/28	20	9 [14]	F + 0	S	—	—	—	—	—
7/3	34	5	F + 5	I↓	7/17	317	14	N + 5	I↓
²7/7	21	4 [14]	F + 9	I↑	—	—	—	—	—
7/17	19	10	N + 5	I↓	8/4	324	18	F + 10	I↑
²7/25	16	8 [19]	F + 0	S	—	—	—	—	—
8/5	18	11	F + 11	I↑	8/20	255	16	N + 10	I↑
²8/10	8	5 [15]	N + 0	I↓	9/2	45	13	F + 9	I↑
8/20	12	10	N + 10	I↑	—	—	—	—	—
²8/30	24	10	F + 5	S	9/12	226	10	N + 3	N
9/3	15	4 [13]	F + 9	S	²9/20	100	8	N + 11	I↓
²9/12	17	9	N + 3	I↑	—	—	— [18]	—	—
9/16	18	4	N + 7	I↑	9/30	280	10	F + 6	S
²9/21	11	5 [15]	N + 12	I↓	—	—	—	—	—
9/27	20	6	F + 3	I↑	—	—	—	—	—
²10/2	21	6 [11]	F + 8	I	10/15	462	15	N + 7	S
10/8	15	5	N + 0	I	²10/21	82	7 [17]	N + 13	N
²10/14	19	6 [12]	N + 6	S	10/31	917	10	F + 8	I
10/25	17	6	F + 2	I	²11/8	100	8 [16]	N + 1	I
²11/2	5	11	F + 10	N	11/16	50	8	N + 9	I
11/19	17	8 [14]	N + 12	N	12/5	199	19	F + 13	I
²11/25	5	6	N + 3	I	—	—	—	—	—
12/1	6	6	N + 6	N	—	—	—	—	—

Mean days between peaks			
including weekly peaks	7.6 ± 1.4 (2 SE)		11.5 ± 1.8 (2 SE)
excluding weekly peaks	13.9 ± 1.6 (2 SE)		15.1 ± 1.1 (2 SE)
Mean days from F or N moon	5.5 ± 1.5 (2 SE)		7.3 ± 1.5 (2 SE)

¹These two peaks are from sites adjacent to the 20 study sites and were abandoned after April.
²The peaks for these dates approximate weekly fertilization and recruitment pulses interspersed between the biweekly peaks for recruitment (see also Fig. 6).

dividual settlement date and fertilization date to the time of full moon (Fig. 5). Several features stand out: 1) The settlement data are less noisy than the fertilization data; this is explained, in part, by the more strongly expressed weekly patterns in the fertilization data. 2) Although settlement is clearly associated with the quarter moons, it does occur during other periods of the lunar cycle as well (see also Table 2, Fig. 2). 3) Fewer PL-1's are present on the sites during full moons than during new moons.

The relation of settlement pulses to daily tidal excursions (Fig. 6) indicates that settlement was most often associated with rising or falling (intermediate) stages of the tidal cycle than with spring or neap tides. A more extensive evaluation of the results reveals that out of 22 identifiable settlement pulses, 17 occurred during intermediate tides, 3 with spring highs, and 2 during neap tides. Also, out of 26 fertilization periods, 16 occurred during intermediate tides, 7 on spring highs, and 3 during a neap tide.

If a specific state of the moon, such as the quarter moons, is the significant environmental factor that determines the timing of fertilization and/or settlement of French grunts, then the state of the tides
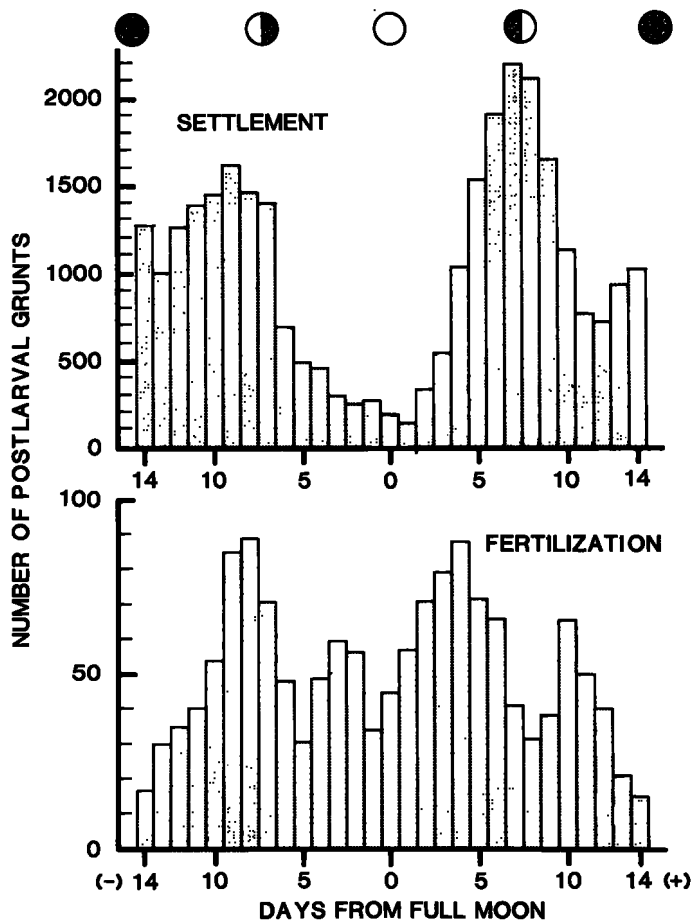
FIGURE 5.—Lunar phase relationships of settlement and fertilization dates for French grunts. Data represent the totals obtained from Figures 2 and 3 summed with reference to the days before and after full moons. The settlement data are the sum of peak numbers of PL-1's on all census sites. Actual settlement rates (maximum rate of influx) were maximal 2 to 3 d before the figured peaks. The fertilization data clearly reveal weaker weekly periods of spawning (see text for details).

should be unimportant. This condition would prevail because the tidal states (springs, neaps, intermediate conditions) change phase relative to the lunar cycle as the year progresses (Fig. 6). In contrast, if a particular state of the tide served as a primary trigger for fertilization and/or settlement then the moon's state would be unimportant. To test for the importance of tidal and lunar state the data were analyzed

using a log likelihood statistic (g-test, Table 3) by grouping the 22 settlement and 26 fertilization peaks into the 9 possible combinations of tidal and lunar state (e.g., spring, neap, and intermediate tides and full, new, and quarter moons). Clearly both the lunar cycle and tidal state have significant effects on settlement and fertilization, but their interaction, although large, is nonsignificant. Because 60 to 80%

TABLE 3.—Summary of comparisons of lunar cycle and tidal state for fertilizations and settlement pulses of French grunts during 1980. Data from Table 2. Log likelihood test from Sokal and Rohlf (1981).

	g-value and associated chi-square			
Category	Settlement data		Fertilization data	
Total G[1]	36.7	$> \chi^2_{.001(8)} = 26.1$	22.5	$> \chi^2_{.01(8)} = 20.1$
Moon alone[2]	11.3	$> \chi^2_{.01(2)} = 9.9$	7.3	$> \chi^2_{.05(2)} = 6.0$
Tide alone[2]	18.0	$> \chi^2_{.001(2)} = 13.8$	10.2	$> \chi^2_{.01(2)} = 9.9$
Moon-tide[3]	7.4 ns	$< \chi^2_{.05(4)} = 9.5$	4.9 ns	$< \chi^2_{.05(4)} = 9.5$

[1]Single classification of all categories.
[2]Single classification of moon or tidal state alone.
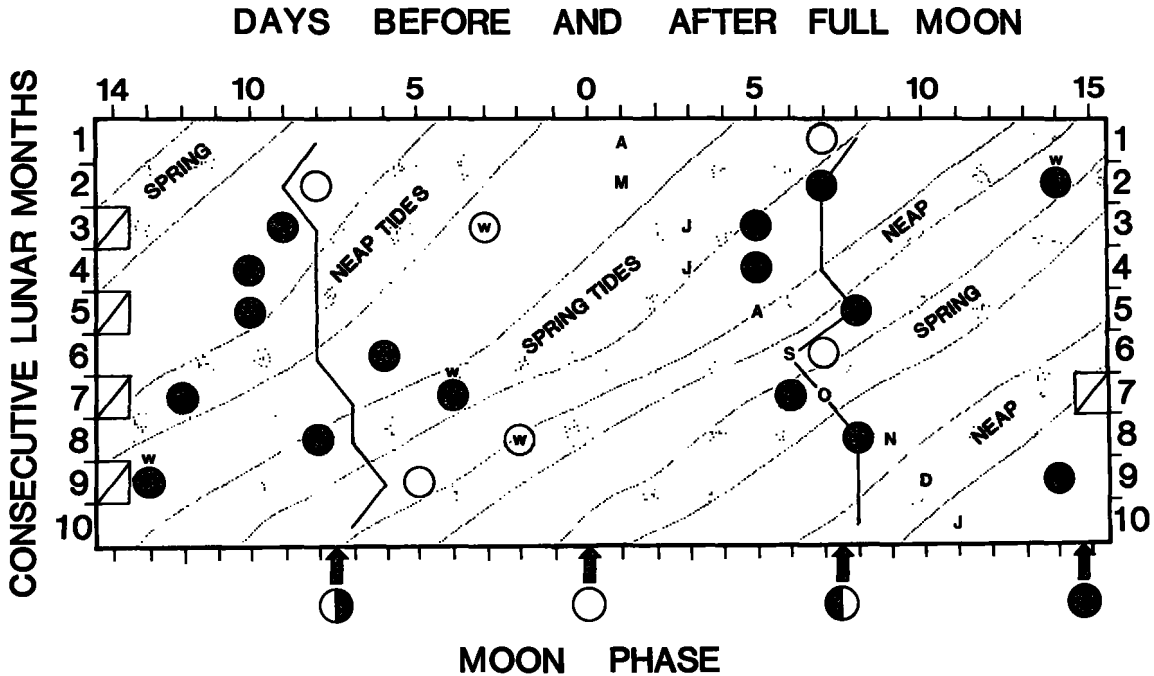[3]Two-way classification, moon phase versus tidal state.

FIGURE 6. – Relation between the periodic settlement pulses of postlarval grunts during 1980, the phases of the moon, and the procession of spring and neap tides. Shaded areas represent relatively uniform series of neap or spring tides; unshaded areas are either increasing or decreasing intermediate tides (see Table 2). The sequence of days reads from left to right across each row. The first day of each calendar month is indicated by the letters, e.g., A at top = April 1980, . . . , J = January 1981. Closed circles represent the large and intermediate-sized pulses (> 100 PL-1's); open circles are settlement pulses with < 100 individuals (see Table 2). Closed and open circles with the letter w are weekly recruitment pulses interspersed between the more common biweekly peaks (see Table 2). The two abruptly changing vertical lines indicate the actual dates of the quarter moons at different times of the year, as determined from the Nautical Almanac for 1980. The mean deviations of those pulses most closely associated in each month with the quarter moons are: first quarter moon = 1.7 d ± 1.9 (SD), third quarter moon = 0.9 d ± 0.8 (SD). Maximum tidal excursions for spring tides occurred in May and June, and in October and November, as did the maximum recruitment of PL-1's to the census sites (Fig. 2, Table 2).

of the settlement pulses and fertilizations were associated with quarter moons and intermediate tides (Table 2), attempts were made to isolate the significant categories by combining the data (springs + neaps versus intermediate tides; full + new moons versus quarter moons). Nonsignificance occurred in all combinations with the exception of tides and settlement (g-test = $9.91 > \chi^2_{.05(1)} = 3.84$).

The relationship between fertilization and settlement of French grunts and the state of the tides and lunar cycle is obviously complex and difficult to unravel without ambiguity. Larger sample sizes (data over several years) would help, but perhaps more important would be specific data on current regimes at actual spawning sites and in the general vicinity of settlement sites. The highly significant but independent effects of moon and tidal state likely point at the importance of favorable currents to successful larval recruitment.

Settlement of Postlarvae in Space and Time

From May through December 1980, when the census frequency was high, there were 16 consecutive quarter-moon periods. On the 20 census sites, therefore, a total of 320 separate pulses (16 × 20) could have been observed if settlement did occur during the quarter moons. During this period 161 pulses were actually observed on the 20 sites during quarter moons. When the number of PL-1's settling was high, most sites recruited fish (90% for May-June, 75% for October-November). In winter, when the number of fish settling was low, recruitment nevertheless occurred on at least 4 or more sites during the quarter moons.

The periodic appearance of PL-1's on 11 of the 20 sites was virtually continuous at each quarter moon, and similar in general pattern to that depicted by the pooled data (e.g., site 11, Fig. 2). On 4 sites,

however, PL-1's settled in spring-summer or in summer-fall. These differences in the pattern of settlement between the census sites are highly significant ($P \ll 0.001$, "distribution-free" nonparametric test; Hollander and Wolfe 1973, p. 139-146). The patterns were so consistent, however, that we were soon able to predict with considerable success not only when, but which sites would attract PL-1's. We can provide no correlations with depth or area of a site, nor with the species of corals and other major residents (fishes, sea urchins, etc.), as to why some sites consistently "attracted" postlarval grunts and others varied, even though it is known that postlarval settlement can be partly governed by priority effects on reefs (Shulman et al. 1983). To understand the characteristics of a site that make it highly "attractive" to settling postlarval grunts will require sophisticated field manipulations.

DISCUSSION

The most conspicuous features concerning the recruitment of French grunts from the plankton are the rhythms in settlement and fertilization dates (Figs. 2-4). The continuing and short 15-d periods of these rhythms over an entire year contrast with other coral reef fishes where settlement, although rhythmic, is concentrated mostly around a particular period of the year (Williams and Sale 1981). Settlement in reef fishes is often episodic; it may show a lunar periodicity (Johannes 1978), it may be monthly but not coupled to a particular phase of the moon (Williams 1983 – mixed guild of pomacentrids), or a rhythm may not be conspicuous (Victor 1982, 1983 – *Thalassoma bifasciatum*).

The short period between fertilization and settlement implies that pelagic existence in French grunts is of short duration (about 2 wk; Brothers and McFarland 1981). To estimate the days spent in the plankton, the average age for the smallest 100 PL-1's was calculated from the sample of 1,478 fish that were used to estimate the actual day of fertilization [mean age = 15.7 d ± 2.1 (SD), range = 13-20; mean length (SL mm) = 6.9 ± 0.67 (SD), range = 5.9-8.5]. If each of these fish had settled from the plankton over the previous day, then pelagic existence (about 15 d) agrees with the periodicity of fertilization and settlement (Table 3, Fig. 4). In contrast, the pelagic existence of most other coral reef fishes investigated exceeds 15 d (Randall 1961; Johannes 1978; Sale 1980; Barlow 1981). This has been verified by results for age at settlement as determined from otoliths (Victor 1982, 1983; Brothers et al. 1983; Brothers and Thresher in press and unpublish-

ed; Thresher and Brothers in press). Most of these fishes settled at various ages: *Thalassoma bifasciatum*, 40-72 d; *Paragobiodon melanosoma*, 39-47 d; *Gobiodon* sp., 27-38 d; several unidentified scarids, 34-58 d; and labrids, 21-56 d. Direct aging of new recruits or otolith counts to presumed settlement marks rarely yield ages as low as found for the French grunt. Examples of species with pelagic phases of 20 d or less include the angel fish, *Holacanthus paru* (Brothers and Thresher in press); several damselfishes, *Glyphidodontops rollandi*, *Pomacentrus amboinensis*, *P. popei*, and *P. wardii*; the blenny *Petroscirtes mitratus*; the nemipterid *Scolopsis dubiosus* (Brothers et al. 1983); and the goby *Gobiosoma prochilos* (Brothers, unpubl. data). These may be exceptional cases; all or at least most of these species represent families characterized by having larval durations moderately to considerably longer than found in grunts. At the family level, therefore, only the haemulids, and perhaps the lutjanids, provide evidence of a short pelagic existence. In support of this conclusion is the lack of haemulids or lutjanids amongst the larval fishes collected offshore throughout the Caribbean (Richards 1981, footnote 8). Are haemulids programmed for short larval lives? We cannot be sure, but out of the 1,478 recently settled French grunts we have aged, not one exceeded 20 d from fertilization. Such a developmental process would be crucial in their survival; if they do not drift over suitable substrates on which to settle after 2 wk, they would perish offshore.

Our observations of a strong semilunar periodicity in French grunt recruitment, coupled with what seems to be a relatively fixed or invariant larval duration, could be the result of a number of different combinations of spawning and survivorship. Because we can only determine fertilization dates for individuals that have successfully recruited, we cannot be certain whether the apparent periodicity in spawning is an accurate representation of the temporal pattern of grunt reproduction. At the other extreme, it may be the result of relatively continuous spawning activity, the products of which survive differentially with respect to semilunar environmental variables.

Surprisingly, for such common fishes, little is known about spawning in haemulids. They produce pelagic eggs and larvae (Breder and Rosen 1966; Saksena and Richards 1975). Recently, paired spawning has been described for *Hapalogenys mucronatus* in aquaria (Suzuki et al. 1983). On six

specific attempts to validate spawning in French grunts in the sea at St. Croix, two of us (McFarland and Shulman) failed to observe reproductive activity during dusk, but we did observe what appeared to be sporadic spawning by small groups of tomtate grunts, *Haemulon aurolineatum*, within large schools of these fish. These limited data suggest that grunts, like many reef fishes, cast pelagic eggs into the water column at dusk. We emphasize, however, that there are no data about their daily spawning habits.

Two hypotheses offer explanations for the dominant semilunar periodicity of fertilization and settlement.

Hypothesis 1. Assumption: Spawning follows a semilunar rhythm with breeding peaks closely coupled to the quarter moons (and/or intermediate monthly tides). If reproductive activities in French grunts follow a semilunar cycle, and pelagic life is programmed for 15 d, then settlement should occur most often during the quarter moons and intermediate monthly tides, which it does (see Table 3, Fig. 6). This hypothesis, however, does not account for the weekly peaks in settlement and fertilization (Table 3; Figs. 2, 3, 5), which contradict the assumption of the hypothesis.

Hypothesis 2. Assumption: Spawning is relatively constant from day to day, and larval existence restricted to about 15 d. Consistent daily reproductive effort could produce a continuous pool of grunts in the plankton. As a result, only those larvae that are favored by "correct" currents that disperse them inshore around 15 d will settle, and/or successful recruitment may also depend on favorable currents dispersing the eggs at the time of reproduction. At St. Croix we suspect that current conditions are most favorable to settlement during the quarter moons and intermediate tides. The weekly peaks that are associated with full and new moons (Table 3) could represent recruitment in less favorable currents than occur around the quarter moons. These currents, nevertheless, must allow some larvae through the "filter screens" that all recruits must pass through to join a reef community (Smith 1978). The semilunar rhythm of fertilization and settlement observed in settling grunts would, under this hypothesis, be explained by semilunar rhythms in currents favorable to settlement.

The time of day when settlement occurs and, especially, the amount of darkness at night may also relate to successful settlement. Although data are scarce, some reef fishes settle from the plankton at night (e.g., acanthurids – Randall 1961; McFarland, unpubl. data). We do not have similar direct observations for French grunts, but we suspect settlement is nocturnal because the number of PL-1's remained fairly constant on most census sites throughout each day. Nocturnal settlement behaviors would temporarily remove recruits from the attack of reef piscivores, especially if accomplished during the dark of the moon. During full moons, recruits presumably would be subject to higher rates of predation by planktivores than during other phases of the moon (Hobson et al. 1981). The number of grunts settling during full moons should be low, which it is (Fig. 4). In contrast, if length of darkness is a dominant factor to successful settlement, then the highest influx of recruits should coincide with the new moons, and intermediate numbers with quarter moons, which they do not (Fig. 4). The recruitment dynamics, nevertheless, indicate higher influxes of PL-1's when some degree of darkness occurs during each night (Fig. 4). We hypothesize that recruitment is dependent primarily on favorable currents, with predation possibly acting as a secondary selective force.

Reversals in surface currents and oppositely flowing currents in the upper 30 m, which could affect the dispersal of larvae, are known to occur at St. Croix and at Puerto Rico (Gladfelter et al. 1978; Lee et al. 1978; Molinari et al. 1980). Their local patterns, however, remain unknown. Eddy formation to the west of the island of Barbados, produced by Karmen trails as the generally west-setting current passes the island, has also been postulated to retain the pelagic stages of inshore species (Emery 1972). It is reasonably well established that seasonal shifts in local current gyres in the vicinity of Hawaii favor the settlement of various species of reef fishes (Sale 1970, 1980; Johannes 1978). In addition, spawning is often synchronized to disperse eggs and larvae away from reefs and into offshore currents (Johannes 1978; Lobel 1978). But specific currents do not always trigger spawning, as Colin (1982) reported for several reef fishes at Puerto Rico. In these instances, rhythmic spawning often can be related to the lunar cycle, but significantly, some species spawn every day. Depending on the time of spawning, dispersal routes for fish eggs and larvae can vary over short-time periods because of reversals in currents.

The daily behaviors and distributions of grunts at sea are unknown. Do larval grunts passively drift with currents? Or do they seek different depths at different times of the day? Active behaviors that would utilize differences in currents have been invoked to explain the retention of pelagic larval fishes and invertebrates close to the island of Oahu (Leis 1982). Similar activities by larval French grunts

could explain their absence in collections taken offshore (Richards 1981).

We have provided substantial evidence that French grunts recently recruited from the plankton are fertilized about 15 d earlier, and that these processes most closely correlate with the quarter moons and intermediate tidal excursions. Is this a general pattern that occurs throughout the Caribbean and western Atlantic where French grunts are most abundant? Or is the lunar-tidal correlation the result of local conditions? We have no answer at present, because it requires repeating the investigation in other localities. Different current regimes and local hydrographic conditions in other regions might elicit different recruitment patterns. The much weaker weekly fertilization and settlement patterns, for example, that are associated with full and new moons (Table 3) might dominate recruitment in other locales.

There is a seeming order in the rain of young French grunts from the plankton. Over the period of this study young grunts following a semilunar timetable appeared on over half of the census sites 70% of the time (range 59 to 94%). Although we could not discern any special characteristics of these sites that attracted grunts, the sites were never preoccupied by other species. Settlement certainly did not appear to be a random phenomenon. The recurrent order in the occupation of space by settling French grunts, however, may reflect only their high abundance in the reef communities at St. Croix (Gladfelter and Gladflelter 1978). Large populations produce large numbers of offspring and this alone might swamp available sites. In this regard we stress that the census settlement sites are not main reefs, but isolates adjacent to them. Indeed, large coral domes in the census area which sustained large populations of older juvenile French grunts never sustained populations of PL-1's. Without manipulative studies of grunts on the settlement sites, however, it is impossible to ascertain to what extent recruitment is influenced by a resident population (Shulman et al. 1983). We can conclude only that the recruitment of French grunts from the plankton has high temporal and spatial predictability at St. Croix.

Fishes in the family Haemulidae represent a dominant component of the tropical reef fish community and constitute a major part of the trap fishery in western Atlantic and Caribbean waters (Dammann 1980; McFarland 1980). The findings presented in this study provide insights that are critical to the management of any fishery for grunts. For example, the relatively short larval existence in French grunts, which also occurs in white and tomtate

grunts (Brothers and McFarland 1981), implies that dispersal does not occur over very long distances. Whether local populations of grunts are self-sustaining or dependent on interisland transport is unknown. Answers will require precise knowledge of spawning habits of each species of grunt, careful analysis of local and general current regimes, and, if possible, the behavior of the larvae. If local populations are self-sustaining, then overly lenient limits on the harvest of adult grunts could seriously limit recruitment. In contrast, if recruitment shows large spring and fall peaks in other species of grunts, as it does in French grunts, and the seasonality in recruitment is geographically widespread (e.g. Munro et al. 1973), then closure of a grunt fishery for a few months during periods of peak recruitment would probably assure maintenance of the local populations.

ACKNOWLEDGMENTS

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