TEMPORAL COUPLING OF PRODUCTION AND RECRUITMENT OF LARVAE OF A CARIBBEAN REEF FISH[1]

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Abstract. Variation in larval recruitment is thought to have profound effects on the structure of coral reef fish communities, and planktonic processes often are cited as the major factor controlling the temporal and spatial patterns of such recruitment. We looked at the relationship between temporal patterns of larval production and settlement of planktonic larvae of the Caribbean damselfish *Stegastes partitus* at one site and attributed any differences to processes acting in the plankton. In doing so we assumed that the pattern of production we observed was representative of the regime that produced fish that settled in the study area.

We monitored spawning and larval recruitment continuously for 3 yr. Both spawning and settlement followed (unimodal) lunar cycles, and both activities spanned ≈3 wk of the lunar month. Although the form of the average settlement cycle matched that of the average production cycle, monthly settlement episodes were shorter and (slightly) more variably timed than equivalent production episodes. Although monthly variability in the magnitude of settlement was fourfold greater than corresponding variability in the magnitude of larval production, monthly settlement success did not vary in an extreme manner. There was no significant correlation between the magnitude of larval production in a month and of settlement the following month. Daily growth increments in the otoliths of settlers indicated that (1) larvae were ≈5 wk old at settlement, (2) there was low overall variability in age at settlement, (3) there were no differences between the ages of settlers arriving early and late in the monthly settlement period, and (4) age variability among settlers collected on the same day was not different from that among settlers collected on different days.

Hence, the basic lunar periodicity of settlement is determined by the periodicity of production of relatively fixed-age settlers. Planktonic processes enhance the temporal variability of settlement, principally by affecting the magnitude of settlement events, but also by influencing the duration and precise timing of monthly settlement episodes. Planktonic processes also determine that most of a month's successful settlers arrive (and are produced) over a few consecutive days and mix cohorts of larvae that are produced on different days. We conclude that the timing and magnitude of settlement are strongly influenced by both production and planktonic processes, and the latter only partly decouple settlement and production.

Key words: Caribbean; coral reef; damselfish; larvae; lunar cycle; otolith aging; plankton; settlement; spawning.

INTRODUCTION

Most coral reef fishes have a planktonic larval phase (Sale 1981). The return of larvae or juveniles to reefs (settlement) can be highly variable in time and space

(Victor 1983, 1986a, Williams 1983, Sale et al. 1984). Settlement patterns can strongly influence the composition of reef fish communities and the spatial distributions and sizes of populations of individual species (Williams 1980, Sale 1981, Doherty 1983a, Shulman et al. 1983, Victor 1983, 1986a, Sale et al. 1984, Munro and Williams 1985, Sweatman 1985).

TABLE 1. Effects of larval production and planktonic processes on temporal patterning of settlement.

	Expected observations if settlement pattern is primarily influenced by	
	Production activity	Planktonic processes
Variation in magnitudes of production and settlement	Equal variation, with good serial correlation	Different variation, or equal with no serial correlation
Lunar periodicity of production and settlement:		
(a) correlation between mean observed patterns	Good	Poor
(b) correlation between mean oberved pattern and back-calculated pattern	Good	Poor
(c) month variability in observed patterns	Equal	Different
Age of settlers		
(a) overall variability	Low	High
(b) within-day variability	Low (<overall)	High (≈overall)

The temporal patterning of settlement includes daily, monthly, seasonal, and annual variation in both timing and magnitude. Many reef fishes have seasonal cycles of production and recruitment of larvae (Munro et al. 1973, Johannes 1978). Many of those species also have lunar or semi lunar cycles of larval production, and, in some, larval settlement also follows lunar or semi-lunar cycles (Johannes 1978 for review, McFarland et al. 1985, but see Williams 1983, Sale 1985, Victor 1986a).

The patterning of settlement on all these different time scales may be influenced not only by larval production patterns but also by processes that act in the plankton between egg or larval release and settlement, including extrinsic physical or biological processes or some activities of the larvae themselves (Tester and Takata 1953, Helfrich 1958, Randall 1961, McFarland 1982, Victor 1983, Williams 1983, McFarland et al. 1985, Sale 1985). The prevailing view seems to be that planktonic processes are of primary importance in determining settlement patterns (Watson and Leis 1974, Johannes 1978, Doherty 1983b, Shulman 1985). Planktonic processes are thought to be responsible for much of the variation in the timing and magnitude of settlement and to operate on it in an unpredictable and often extreme manner (Luckhurst and Luckhurst 1977, Sale 1981, Victor 1983, Eckert 1984, Doherty et al. 1985, Shulman 1985).

There have been very few studies of how production activity and planktonic processes influence the temporal patterning of settlement (McFarland 1982, Victor 1983, McFarland et al. 1985), and there is no clear picture for any reef fish. Here we present an estimate of the qualitative and quantitative contributions of these two classes of processes to the temporal patterning of larval recruitment of a common Caribbean reef fish, the damselfish *Stegastes partitus*. We consider settlement on the fine temporal scale, i.e., the timing and magnitude of settlement within and between months over the course of the extended season of peak breeding activity. We present two types of quantitative data that

are necessary for such an assessment: information on (1) the magnitude and periodicity of larval production and subsequent settlement, and (2) variation in age among settling fish. Predictions concerning relationships between settlement and production activity and patterns of age variation of settlers that we used to distinguish between the effects of larval production activity and planktonic processes on settlement are listed in Table 1.

METHODS

We collected data on spawning and larval settlement of *Stegastes partitus* at various times between 1981 and 1986 on the shallow reefs of Punta de San Blas on the Caribbean coast of Panama (9°34′ N, 78°58′ W). Reef numbers are from Robertson (1987: Fig. 1).

As with those of other damselfishes (Thresher 1984), successive clutches of eggs of *S. partitus* are laid in a dense monolayer in a nest in the territory of a male. After the female deposits eggs she leaves the male's territory, and the male guards them until they hatch (shortly after sunset 3.5 d after laying [at 28°–30°C]: D.R. Robertson, *personal observation*). Although *S. partitus* spawns and settles throughout the year there is strong seasonal variation in both activities, and both peak during the warmer, wetter part of the year (≈April–November: D. R. Robertson, *personal observation*). Our analysis is primarily restricted to spawning and settlement during this period.

Lunar periodicity of larval production

We distinguished males by their sexual behavior (Schmale 1981) and provided them with nest boxes (hollow terra cotta bricks) to facilitate observation and measurement of clutches. On one reef (Smithsonian-tupo 3) nests were visited every 2 d for six lunar cycles (June–November 1981, December 1981–January 1982; $n = 14$–22 nests per cycle), and the presence of any new clutches in each nest was recorded. Nests on two other reefs (Tiantupo 1W and Porvenir 25, $n = 25$–36 nests per reef) were monitored daily for two lunar cycles,

October–December 1985. New clutches were recorded and measured (maximum + minimum dimension), and the area of each was estimated by treating it as an ellipse. Prehatching mortality was estimated from the proportion of all clutches that was present in the nest for <4 d.

The relation between production of larvae and the lunar cycle was assessed by measuring (1) the proportion of active nests (those that received ≥1 clutch in a lunar month) that received a new clutch each sampling day, and (2) the proportion of the lunar month's production (total area of clutches in all nests) that was laid on each day. We considered the larval production cycle to be equivalent to the spawning cycle, delayed by the incubation period.

Monthly variation in the magnitude of larval production

Variation in a population's larval production depends on both variation in individual output and variation in the number of producers. We used the production activity of individual nests to estimate the former. Knowing the lunar cycle of spawning activity, we monitored production activity of individual nests on two reefs (Smithsoniantupo 3 and Porvenir 25) from April 1983 to May 1986. Each nest on each reef (n = 14–36 nests per reef) was visited five times per lunar month (every 3rd d, beginning at full moon). We recorded the number and the size (area) of each new clutch (i.e., those laid on the sampling day) and the day on which all clutches present were laid. This sampling regime covered the bulk of the spawning cycle (see Results: Spawning and Hatching Periodicity: Lunar Periodicity). From these data we calculated the mean clutch area (square centimetres produced each month by a nest that had an attendant male). Since each nest box provided egg-laying surfaces several times as large as those in most natural nests, production was unaffected by variation in the size of individual nests.

We estimated changes in the size of the producer population by censusing adults (i.e., fish ≥6 cm total length: Schmale 1981) on five small patch reefs. These reefs were censused near the beginning (May) and end (November) of each season of peak breeding from 1983–1985. The data were combined to estimate the percentage difference in the numbers of producers at the start and finish of the breeding season.

Periodicity of settlement

Diel periodicity. — Data were collected from a small isolated patch of corals on reef Aguadargana 1 and from an artificial reef made of 50 terra cotta bricks (each 30 × 30 × 15 cm) set in a sand patch ≈200 m east of reef Point 35. Each reef was visited in the early morning (≈0600) and late afternoon (≈1800) on 6–12 consecutive days around each of four new moons (September–December 1983 for the natural reef, and May, June, August, and November 1984 for the artificial reef). All newly settled reef fishes were collected on each visit.

Lunar periodicity. — Three sets of data were obtained. During the six lunar cycles for which spawning was monitored in 1981–1982 we collected all newly settled *S. partitus* from a small patch reef (Wichubhuala 14, ≈250 m²) every 2nd d. In addition, from January 1984 to December 1985 (24 lunar cycles), we collected all new *S. partitus* settlers from a second small patch reef (Aguadargana 2, 63 m²) daily. To reduce possible effects of interactions between residents and arriving settlers (Shulman et al. 1983, Sweatman 1985), all resident damselfishes were removed at the start of this period and damselfish settlers of all species were collected daily. Similar daily collections of settlers were made from a third small reef (28 m², immediately south of West Barrier 19S) from October to December 1985 and throughout 1986 (i.e., 15 lunar cycles). Only months that yielded ≥15 individuals were used in the analyses of between-month variability in the timing of settlement, and only months that yielded ≥25 fish were used to estimate the mean distribution of settlement over the lunar cycle.

Monthly variability in the magnitude of settlement

We assessed variation in the numbers of settlers arriving in each lunar month during the peak breeding season using data from (1) the daily collections of settlers from reef Aguadargana 2 during 1984–1985, and (2) monthly counts (January 1983–December 1986) of the numbers of settlers made during the 5 d preceding full moon in 12 permanent plots on six undisturbed reefs. These reefs were spread as much as 3 km apart.

Age determination of settlers

Otolith growth increments (Panella 1971, Victor 1982, Brothers et al. 1983, McFarland 1985) were used to estimate the length of larval life of *S. partitus* settlers. Settlers from the daily collections (1984–1985) were preserved in 95% ethanol. Growth increments in the sagittae of those fish were defined as for other species (Victor 1982, 1983, 1986b, Brothers 1984, Campana and Neilson 1985) and counted with the use of a compound polarizing microscope at 400× magnification. At least three repeated counts were made of the increments in the clearer of each fish's two sagittae until a consistent number (i.e., ±1) was obtained.

Estimation of the age of fishes from otolith increments requires verification of the periodicity of formation. This usually is daily (Victor 1982, Campana and Neilson 1985). Stress can affect increment formation (Panella 1980). This effect can be exploited to determine the normal pattern of formation by inducing a recognizable growth anomaly and determining the subsequent rate of increment addition in the field (Victor 1982). A group of 12 juvenile *S. partitus* was kept in a dark insulated container for 4 d and then was placed on an isolated patch reef that lacked other conspecifics. After 25 d we collected all fish from that reef, as well as another set of similarly sized control fish.

All 8 experimental fish, but none of 12 control fish, had a growth anomaly 24–25 (median 25) increments in from the otolith edge. We assume that increments also were formed daily prior to settlement.

Data analyses

Data on the temporal patterns of spawning and settlement were subjected to several types of time-series analyses. We used spectral analysis to estimate the relative contributions to variance by cycles of different frequency, i.e., the "power spectrum" of the frequencies. In a power spectrum, peaks are statistically significant if they exceed the lowest trough in the spectrum by more than one confidence interval, and the dominant cycling frequency corresponds to the peak with the greatest spectral power (Jenkins and Watts 1968, Platt and Denman 1975). Here we used a 99% CI because our time series were relatively short. In addition, autocorrelograms were used to establish with greater precision any statistically significant periodicities identified by the power spectra. Cross-correlograms, which reveal lagged relationships between different time series by computing correlation coefficients between the two series with varying time lags, were used to examine relationships between patterns of activity and the lunar cycle (as represented by a 29.5-d sine wave) and among different activities. The "Polsta" computer package (Green 1983) was used for these time-series analyses. Other statistical procedures follow Batschelet (1981) and Sokal and Rohlf (1981).

Assumptions

In examining patterns in the timing and magnitude of larval production and settlement within a 15-km² complex of reefs and attributing differences in those patterns to the action of processes in the plankton, we are making some assumptions. We are assuming that either the system we examined was a closed one (larvae that settled in that area were produced there) or that the system is not closed, but, at all sites of origin of fish that settle there, relative outputs of larvae are synchronized with the pattern we recorded at San Blas Point.

The assumption that larvae that settle on San Blas Point reefs were produced in synchrony with the lunar cycle of production we observed is supported by two pieces of evidence. First, as we show below, the back-calculated lunar cycle of production of settlers that we collected did not differ, statistically, from the lunar cycle of spawning we observed. Second, at the only other site for which data are available (Florida), the lunar cycle of spawning by S. partitus appears to be essentially the same as the cycle we recorded (see Schmale 1981).

The assumption that the magnitude of between-month variation in production we observed is representative probably is conservative. The two S. partitus populations in which we monitored spawning were on reefs that were relatively sheltered from adverse sea
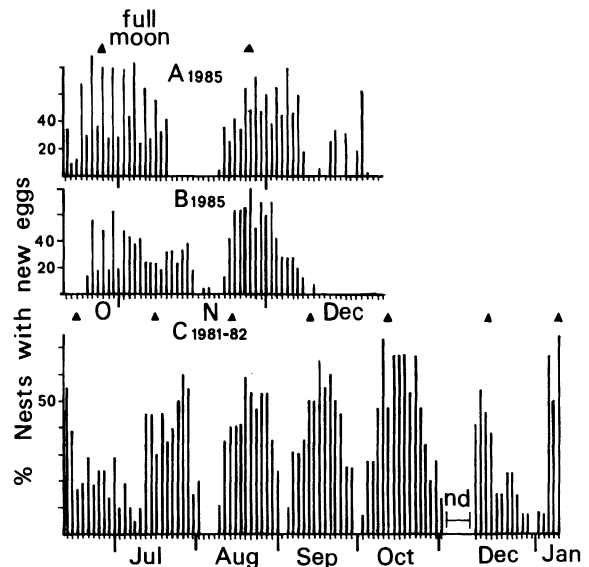

FIG. 1. Spawning activity of Stegastes partitus (percent of nests that contained new eggs on each observation day). ND = no data. (A and B) Concurrent, daily observations on two populations (Reefs Tiantupo 1W and Porvenir 25). (C) Observations at 2-d intervals on a third population (Reef Smithsoniantupo 3).

conditions. One was in as sheltered a situation as any available. Other, unmonitored populations of S. partitus were in more exposed localities. Monthly variation in spawning activity was more variable and more reduced during the season of adverse weather in the more exposed of the two monitored populations (D. R. Robertson, personal observation). Thus overall variability may be somewhat higher than what we recorded.

RESULTS

Spawning and hatching periodicity

Lunar periodicity. — Spawning activity was episodic, and the percentage of nests that received new eggs each day indicates that spawning tracks the lunar cycle (Fig. 1). If clutch size, egg-laying activity, and clutch mortality varied independently, then the lunar periodicity of larval production might not accurately be described by data on the presence or absence of egg laying on each day of the lunar cycle. Our data show, however, that the average distribution of spawning by Stegastes partitus during the lunar cycle, as measured solely by the presence of new clutches, did not differ significantly from the distribution based on the size of those clutches (Fig. 2D and E; Kuiper's $K = 660$, NS). Secondly, the average pattern of premature clutch disappearance did not differ from that of laying activity over the lunar cycle (Fig. 2D and F; Kuiper's $K = 960$, NS). Consequently we measured the periodicity of spawning by S. partitus using only data on the presence or absence of new clutches on each day.
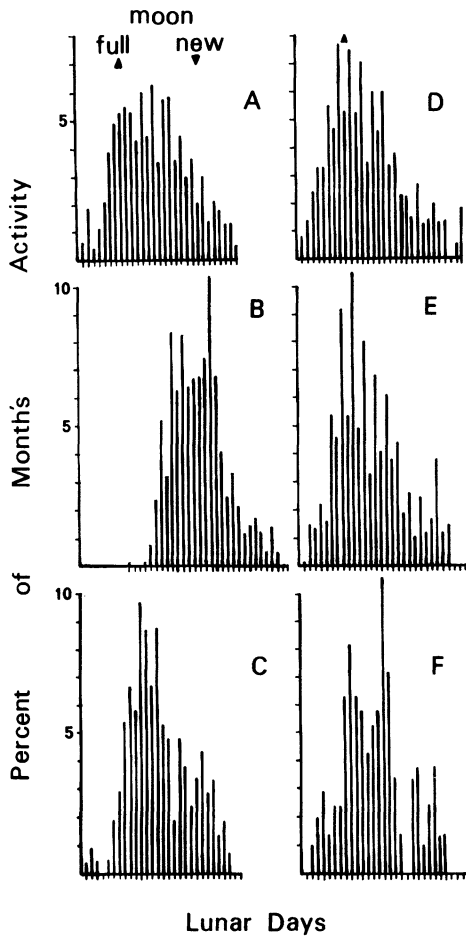
FIG. 2. Spawning activity of *Stegastes partitus* (percent of the lunar month's activity that occurred on each lunar day). (A) Average cycle of spawning activity (derived from data in Fig. 1). (B) Average cycle of settlement (derived from all months [$n = 13$] in which >25 settlers were collected, 1981–1986). (C) Back-calculated cycle of hatching activity (derived from otolith ages and settlement dates of 206 fish collected during 1984–1985). (D) Average cycle of production activity as described by the presence/absence of new clutches. (E) Average cycle of production activity as described by the presence and size of new clutches. (F) Average cycle of premature clutch losses. Data for D, E, and F are from the two reefs in Fig. 1A and B.

Spectral analysis of the 1981–1982 spawning data shows that there was one statistically significant cycle of activity of about one lunar period in length (Fig. 3A). An autocorrelogram of the same data shows a cycling period of 30 d, and a cross-correlogram of those data with the lunar cycle shows a peak 5 d after full moon (Fig. 3C and E, Table 2). Similar analysis of the 1985 data gives very similar results, indicating that there was little variability in the spawning cycle (Table 2). In 1985, peak activity occurred ≈3 d after full moon (Table 2). The difference in the timing of peak activity in 1981–1982 vs. 1985 indicated in these analyses may have been due to differences in the intervals between

observations that we used in these 2 yr (i.e., 2 d vs. 1 d). Overall, spawning extended over an interval of ≈3 wk of the lunar cycle and peaked ≈3 d after full moon (Fig. 2). In all but one case the spawning cycle was unimodal (Fig. 1). In this case, unusual, stormy weather 3–5 d before the new moon of December 1985 may have temporarily inhibited spawning and produced a bimodal cycle in one population (Fig. 1A) and an abbreviated cycle in another (Fig. 1B).

We compared data from two concurrent months' observations on two reefs (Fig. 1A and B), plus one other randomly chosen month's data on spawning seasonality on two other reefs. The patterns were statistically different: Kuiper's $K = 8760, 9451$, and 6899; all $P < .01$. Thus, since monthly variability in the spawning cycle follows independent patterns on different reefs, each month's combined production from all reefs on San Blas Point probably approximates the average cycle (Fig. 2A).

Monthly variation in the magnitude of production.— Production from individual nests varied by a factor of 2–3 (average 2.5) from month to month (Table 3). The population censuses show that the number of potential producers changed little over the course of a breeding season. The percentage change in the total number of fish (range = 200–250 individuals) on the monitored patch reefs from the beginning to the end of each of the three seasons varied from 7.3 to 9.4%. Consequently, change in population size across the breeding season probably has very little influence on the degree of variation in production during the course of the breeding season.

Settlement periodicity

Diel periodicity.—On the natural reef, *S. partitus* settlers were collected more commonly at dusk than at dawn (Table 4). The reverse pattern was much more strongly evident from collections from the artificial reef; almost all specimens of *S. partitus,* and other species, were collected at dawn (Table 5). We attribute this difference in results to differences in the availability of shelter on these two reefs; small holes in the substrate in which fish could hide unobserved during the dawn collection period were present only on the natural reef. We conclude that settlement by *S. partitus,* and other species, occurs primarily at night (and/or crepuscularly).

Lunar periodicity.—Settlement activity was strongly periodic (Fig. 4A–C). A spectral analysis of the 1981–1982 data shows one statistically significant cycle of activity (Fig. 3B), the inferred period of which approximates that of the lunar cycle (28 d from the autocorrelogram; Fig. 3D). Separate spectral analyses of 1984, 1985, and 1986 data show similar peaks of activity, although the inferred periodicities from the autocorrelograms were 25, 26, and 31 d respectively (Table 2). Settlement was essentially restricted to a 3-wk period (Fig. 2B). Cross-correlograms show that settle-
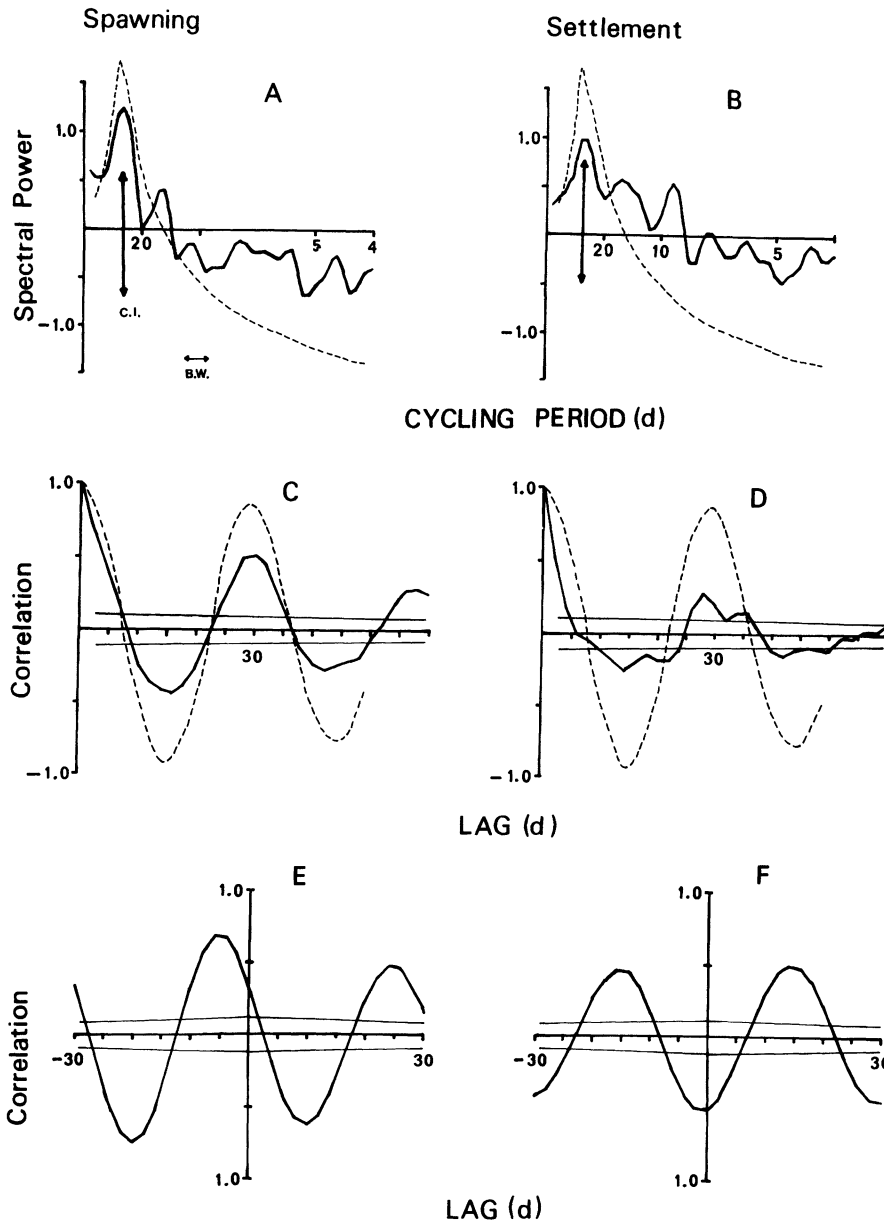
Fig. 3. Analyses of the lunar periodicity of spawning and settlement by *Stegastes partitus* during 1981–1982. (A and B) Power spectra, c.i. = 99% confidence interval (1.28) for spectral estimates; B.W. = band width (0.0417) of the spectral window used in the computation. Solid line = power spectrum of observations; dashed line = power spectrum of sine wave model of the lunar cycle (period 29.5 d). (C and D) Autocorrelograms. Horizontal lines indicate 99% confidence interval of correlations resulting from a random binomial process. (E and F) Cross-correlograms for activity vs. the lunar cycle. Horizontal lines indicate 99% confidence intervals. Interval between zero and the nearest positive peak indicates the lag of peak activity after the full moon.

ment peaked shortly before new moon (Fig. 3F, Table 2; median = 1 d before new moon; Fig. 2B).

The average distribution of settlement during the lunar period did not significantly differ from the average distribution of spawning over that period (Fig. 2A and B; median dates aligned, Kuiper's $K = 2130$, NS). However, the periodicities of settlement and spawning did differ in two ways. First, the bulk of each month's settlement occurred in a relatively short pe-

riod: $\geq 75\%$ of a month's settlement occurred during a 5–13 d period (median = 8 d, $n = 13$ mo [1981–1986] in which ≥ 25 settlers were collected), whereas the same percentage of a population's spawning took a significantly longer period of 10–16 d (Fig. 1; median = 14 d, $n = 8$, Mann-Whitney $U = 99.5$, $P < .001$). (These differences probably do not reflect sampling error caused by our having monitored settlement on single, very small patch reefs. Since patterns of set-

TABLE 2. Lunar periodicity of spawning and settlement implied by power spectra and correlograms.

Activity	Data set	Cycling period*	Time of peak activity†	No. of months
Spawning§	1981–1982	30 d	Full moon + 5 d	6
	1985 A	27 d	Full moon + 3 d	2
	1985 B	29 d	Full moon + 3 d	2
Settlement‡	1981–1982	28 d	New moon + 1 d	6
	1984	25 d	New moon − 1 d	3
	1985	26 d	New moon − 5 d	4
	1986	31 d	New moon − 1.5 d	6

* Power spectra of each data set show a significant peak of activity (at the 99% level) of about one lunar period in each case. The cycling period is derived from the autocorrelograms of the same data.
† Indicated by cross-correlograms of activity vs. the lunar cycle.
§ A = reef Tiantupo 1W; B = Porvenir 25.
‡ 1981–1982: Reef Wichubhuala 14 (see Fig. 4C); 1984 and 1985: Reef Aguardargana 2; 1986: Reef West Barrier 19S.

tlement over the course of a single lunar cycle were very similar on pairs of reefs 3 km apart [Fig. 5], it is unlikely that a short settlement pulse occurring on one reef represented a subsample of a temporally more extensive pulse that affected different reefs at slightly different times.) Second, there was greater variability in the timing of settlement than of spawning. The autocorrelograms indicate a greater difference between the inferred cycling period of settlement and the lunar cycle period than is the case for spawning (Table 2). The cross-correlograms indicate greater variation in the timing of peak settlement than is the case for peak spawning (Table 2). However, both of those differences were relatively small.

Monthly variation in the magnitude of settlement.—Both the daily collections and monthly counts of the numbers of settlers arriving during wet seasons show that monthly settlement varied as much as 30-fold between months (average of ≈12-fold for the 3 yr; Table 3). The coefficient of variation of the magnitude of settlement exceeded that for spawning by a factor of 2–3 (Table 5).

There was no statistically significant serial correlation in the magnitude of spawning each month and settlement activity in the month during the 3 yr studied

($r = 0.16$, NS; following Box and Jenkins [1970], spawning and settlement data were passed through a first-differences filter to remove seasonal trends). We estimated the effect of this serial decoupling of these two activities on the variation in the magnitude of settlement as follows. First the magnitude of each month's activity was scaled relative to the minimum (=1) recorded in the year. Then we compared the difference between the scaled values of production in each month and settlement in the following month. Over the 3 yr this difference ranged from 0–15-fold, with a mean of 3.8. Although monthly variation in settlement success was greater than that in spawning success, settlement occurred in all months of the year and did not vary in an extreme manner: 31.3% of months contributed ≥ the mean monthly level of settlement over the course of 4 yr (1983–1986), and 41.9% of wet season months contributed ≥ the mean monthly level occurring in the wet season.

Age of settlers

Settlers ranged in standard length from 10.4 to 15.0 mm, although variation in their size was low ($\bar{X} = 13.0$ mm, CV = 6.2%). Counts of otolith growth increments indicate that the age of settlers ranged from 31 to 45

TABLE 3. Monthly variability in spawning and settlement of *Stegastes partitus*.

		Spawning			Settlement	
		Area of eggs laid·nest⁻¹·month⁻¹ at two reefs (cm²)			No. settlers collected per month at Augadargana 2	Total no. settlers counted per month at 12 sites
Year		Smithsoniantupo 3	Porvenir 25	Total for both reefs		
1983	$\bar{X}$	181	102		no data	22.4
	range	122–273	56–153			3–60
	CV (%)	31.9	42.3	33.1		83.1
1984	$\bar{X}$	151	127		10.1	52.7
	range	117–226	83–191		2–17	14–96
	CV (%)	24.2	32.5	21.4	60.0	51.2
1985	$\bar{X}$	112	124		13.7	53.8
	range	62–158	75–196		0–31	10–148
	CV (%)	30.7	35.5	30.3	98	82.9
Average	CV (%)	28.9	36.9	28.2	79.0	72.4

TABLE 4. Collections of *Stegastes partitus* settlers from an isolated natural reef around new moons in 1983.

Month	Number collected at		Number of days
	Dawn	Dusk	
September	19	53	13
October	1	2	7
November	1	5	7
December	2	2	7
Total	23 ***	62	34

*** χ^2 $P < .001$; H_0: equal numbers at the two times of day.

d. Overall age variation was low (cv = 6.9%), and 85% of the settlers were 34–40 d old ($\bar{X}$ = 36.5, SE = 0.18, n = 206). Thus, almost all fish settled around the second new moon after they hatched. The limited data indicate that the variance in age among settlers collected on the same reef on the same day did not differ from the overall variance in age (six variance ratio tests for days that provided 6–9 individuals, all $P > .05$). Furthermore, there were no statistically significant differences in the mean age or size of settlers (or the variance in their ages or sizes) collected during each of the three lunar quarters in which settlement occurred (Table 6).

Back-calculated periodicity of larval production

We compared the average distribution of (observed) hatching over the lunar cycle with the distribution of hatching of all settlers collected during 1984–1985 (back-calculated using their otolith ages and dates of collection). No difference was evident (Fig. 2A and C; Kuiper's K = 1600, NS).

Using the back-calculated hatching dates of settlers that arrived in 7 mo (1984–1986, n = 13–36 settlers per month), we compared the time span over which ≥75% of a month's settlers were produced with the duration of ≥75% of a month's spawning activity. These hatching periods were consistently shorter (median = 8 d) than equivalent spawning periods (median = 14 d, $U_{7,8}$ = 48, $P < .05$). Thus, fish that settle during the relatively short monthly settlement episodes are produced during an episode of similar duration.

DISCUSSION

Our data show that there is distinct lunar periodicity in both of the major transitional events in the larval life of *Stegastes partitus*, i.e., the release of larvae from a reef, and their return to reefs about 5 wk later. Both the diel and lunar periodicities of settlement by larval reef fishes may be related to risks of predation by fishes on arriving settlers, with such risks being reduced at night (Johannes 1978, Williams 1983), particularly during relatively moonless nights (McFarland et al. 1985, Victor 1986a). Our data are consistent with that hypothesis: they indicate that settlement by *S. partitus*, and other species, is maximal during the night (or crepuscularly), and they also show that settlement by *S. partitus* occurs principally on relatively moonless nights.

Our data on production and settlement and the age variation of settlers show how the temporal patterning of settlement is determined by both production activity and planktonic processes. The unimodal lunar cycle of

TABLE 5. Newly settled fishes collected around new moons in 1984, from an isolated artificial reef.

Family	Species	Number collected at		Number sampling occasions fish were collected at			
				Dawn		Dusk	
		Dawn	Dusk	Days	Months	Days	Months
Pomacentridae	*Stegastes partitus*	13 *	2	9	4	2	2
	S. dorsopunicans	3	2	2	2	2	2
Acanthuridae	*Acanthurus coeruleus*	3	0	3	2	0	
	A. bahianus	11 *	0	9	4	0	
	A. chirurgus	7 *	0	6	2	0	
Pomacanthidae	*Pomacanthus paru*	12 *	0	9	3	0	
Lutjanidae	*Ocyurus chrysurus*	1	0	1	1	0	
	Lutjanus spp.	21 *	0	12	3	0	
Haemulidae	*Haemulon* spp.	3	0	1	1	0	
Apogonidae	*Astrapogon punctatus*	19 *	0	11	4	0	
	A. quadrisquamatus	5	0	4	2	0	
	A. maculatus	14 *	2	9	3	2	2
	A. townsendi	1	0	1	1	0	
	A. aurolineatus	2	0	2	1	0	
	Phaetoptyx sp.	72 *	8	23	4	7	4
Holocentridae	*Myripristis jacobus*	1	0	1	1	0	
	Adioryx coruscus	1	0	1	1	0	
Sciaenidae	*Equetus* sp.	1	0	1	1	0	
Total		190	14	37	4	10	4
Number days sampled each month (Sep, Oct, Nov, Dec)				6, 12, 9, 10 (Total 37)			

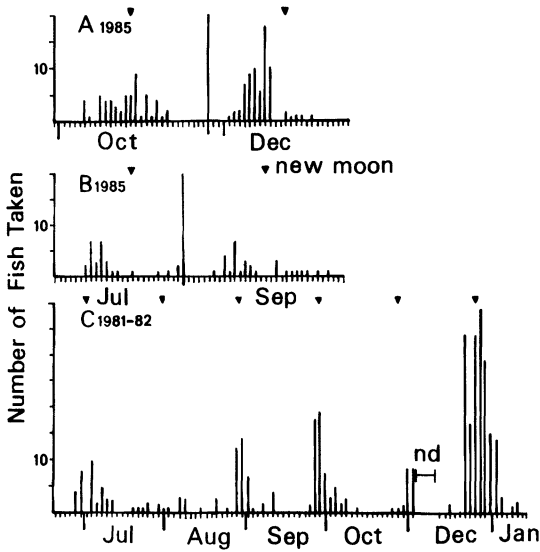* χ^2 $P < .01$; H_0: equal numbers at the two times of day.

FIG. 4. Settlement activity of *Stegastes partitus*. (A and B) Numbers of settling larvae collected each day of the lunar cycle (A and B are from reefs West Barrier 19S and Agua-dargana 2). (C) Number of settlers collected at 2-d intervals from reef Wichubhuala 14.

settlement and its concentration around new moon appear to be determined by the lunar periodicity in production of relatively fixed-age settlers. Planktonic processes have four types of effects. First, they enhance variation in the magnitude of settlement from month to month beyond that caused by variation in the magnitude of production. By decoupling serial monthly variation in the magnitude of settlement from such variation in spawning, planktonic processes increase variation in the magnitude of settlement by an average factor of four. However, such decoupling does not produce extreme variation in monthly settlement success. Second, planktonic processes increase variability in the timing of monthly settlement pulses beyond that caused by variation in production, although that increase in variability is relatively small. Third, such processes restrict most of a month's settlement to a relatively short episode in comparison with the spawning episode. This effect is due to some nonrandom process selectively eliminating most larvae other than those produced over a few consecutive days rather than some process(es) concentrating a random sample of all larvae. Variation in the precise timing of monthly settlement pulses indicates some variation in the timing of the action of these planktonic processes. Fourth, the limited data on variability in ages of settlers that arrive on the same day indicate that each month's select group of successful hatchlings becomes mixed in the plankton and thus that planktonic processes determine precisely when individual larvae settle. Our data do not indicate when between hatching and settlement the planktonic processes that affect settlement operate or whether they are biological or physical. The role of planktonic pro-

cesses in determining the settlement pattern of *S. partitus,* while substantial, could easily have been greater. Because spawning occurs over a large proportion of the lunar month, the timing of settlement could have been relatively independent of the production pattern if major settlement events regularly comprised hatchlings drawn from off-peak parts of the production cycle. Such decoupling would be more likely to occur if there were more variability in the age at settlement rather than the relatively fixed age we observed in *S. partitus.*

What is known about how production and planktonic processes affect settlement patterns in other reef fishes? McFarland et al. (1985) have demonstrated that a Caribbean grunt (Haemulidae) has a semilunar cycle of settlement, and that the magnitude of its settlement events varies considerably. The variability in age at settlement of that species ($CV = 13.4\%$) is relatively larger (but absolutely much smaller) than in *S. partitus.* Although McFarland et al. (1985) did not observe spawning, they did find differences between settlement periodicity and the back-calculated spawning periodicity, the former being more strongly semilunar than the latter. They suggested that planktonic processes are the principal determinant of settlement periodicity in that grunt. Victor (1983, 1984, 1986a) found that, in a Caribbean wrasse, (1) settlement is episodic, with variably timed peaks occurring around the new moon, (2) overall settler age variability is higher (both absolutely and relatively [$CV = 12.6\%$]) than in *S. partitus,* and (3) settlers arriving on the same day comprise a full mixture of daily hatching cohorts. Since unpublished data of other workers indicated acyclic spawning by that wrasse, Victor (1983, 1986a) concluded that planktonic processes were primarily responsible for settlement periodicity. Helfrich (1958), Randall (1961), and Ochi (1985) examined spawning and larval settlement of three Pacific fishes and reached similar conclusions. Both Sale (1985) and Williams (1983) maintain that planktonic processes are primarily responsible for the timing of settlement because neither author found lunar periodicity in settlement by a range of species, and they asserted that most reef fishes have lunar-periodic spawning (there is evidence for the latter: Doherty 1983b).

Data on settlement in the studies cited above ranged from counts of presumed new settlers at daily (Williams 1983, McFarland et al. 1985, Ochi 1985, Victor 1986a) or slightly longer intervals (Helfrich 1958), to collections of settlers at weekly intervals (Randall 1961, Sale 1985). Potential problems associated with these methods include accurate recognition of new settlers, effects of early mortality, (particularly if such is high and/or density dependent), and, especially, interactions between arriving settlers and existing residents (Shulman et al. 1983, Sweatman 1985). Only two studies found no evidence of lunar periodicity to settlement (Williams 1983, Sale 1985), and they were both conducted at the same site, the enclosed lagoon of One-
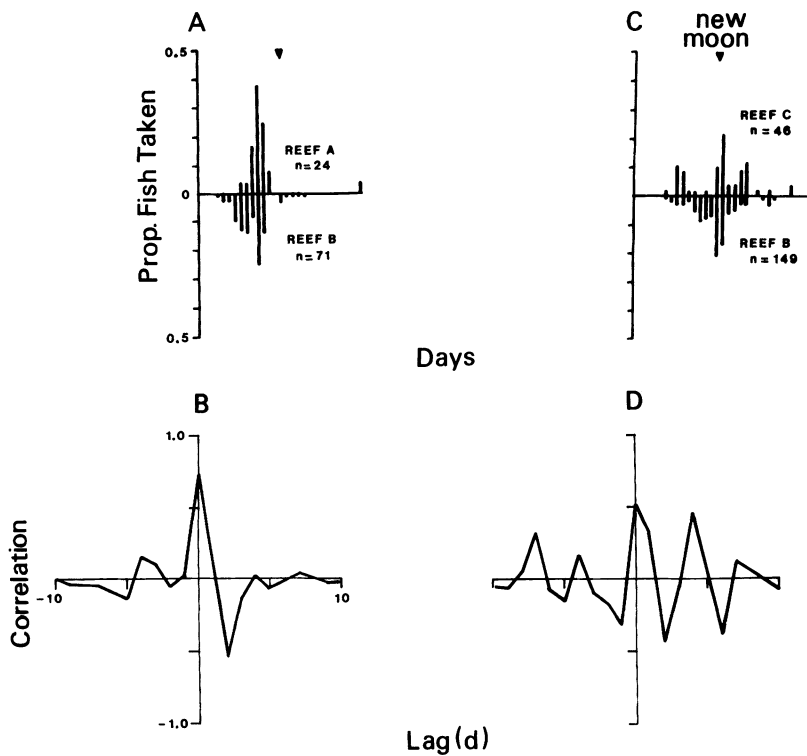
FIG. 5. Correlation in the concurrent daily pattern of settlement by *Stegastes partitus* on pairs of reefs. (A and C) Daily settlement pattern on pairs of reefs. Reef A = Aguadargana 2; B = West Barrier 19S; C = Aguadargana W. (B and D) Cross-correlations between concurrent patterns (data were passed through a first-difference filter to remove the lunar trend: Box and Jenkins 1970). At zero lag, (B) $r = 0.74$, $P > 99.99\%$; (D) $r = 0.52$, $P = 99.5\%$.

Tree Reef (Australia). As Sweatman (1985) has pointed out, settlement levels at One-Tree Lagoon are low, possibly because geomorphological features of the site restrict access to settlers: water exchange between the sea and lagoon occurs only around high tide and is very limited during neap tides. These restrictions could regularly disrupt lunar settlement cycles. Such disruption would compound the difficulty of detecting such cycles statistically because so few fish arrive. The question of whether fish settlement at One-Tree Reef is lunar periodic requires further examination.

Given these shortcomings we cannot say how representative *S. partitus* is in terms of the influences of production activity and planktonic processes on the temporal patterning of settlement of reef fish larvae in general. However, the potential for the production pattern to influence the settlement pattern strongly should be greater for species that have demersal eggs (such as *S. partitus*) than for those that have planktonic eggs, because active larvae have a greater potential for control of their destinies than do passive planktonic eggs. The degree of temporal linkage between spawning and settlement patterns will also be influenced by the degree to which age-at-settlement varies, both absolutely and relatively.

If settlement is most likely to be successful around a particular portion(s) of the lunar cycle (e.g., new moon) then the success of a strategy of producing moderately long-lived larvae that have a relatively fixed age-at-settlement is going to depend on monthly settlement

TABLE 6. Standard lengths of, and numbers of increments in the otoliths of, *Stegastes partitus* settlers collected during different lunar phases. Data are means and 95% CI.

	Moon phase			
	Last quarter ± 3 d	New moon ± 3 d	First quarter ± 3 d	F*
Standard length	13.0 ± 0.15	12.9 ± 0.14	13.0 ± 0.34	NS
n	97	121	39	
No. increments	36.5 ± 0.52	36.5 ± 0.57	36.6 ± 0.85	NS
n	89	80	34	

* One-way ANOVA. Bartlett's test for homogeneity of variances: length $\chi^2 = 6.71$, NS; increments $\chi^2 = 1.77$, NS.

success being moderately predictable rather than highly variable and strongly influenced by stochastic processes. Our data indicate that such is the case for *S. partitus*. First, there is a good degree of coherence between the lunar periodicities of larval production and settlement. Second, although (nonseasonal) monthly variation in settlement success was decoupled from monthly variation in the level of production, monthly variation in settlement success was not extreme. Since few doubt that the temporal patterning of settlement does influence the structure of coral reef fish communities, our study indicates that patterns of larval production on a variety of temporal scales need to be taken into account. Their influence needs to be assessed and the factors that produce them determined. Planktonic processes by themselves, although certainly important, are not necessarily overwhelming or capricious in their influence.

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