

LUNAR REPRODUCTIVE CYCLES OF BENTHIC-BROODING REEF FISHES: REFLECTIONS OF LARVAL BIOLOGY OR ADULT BIOLOGY?¹

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Abstract. Lunar reproductive cycles are common among marine animals. Most hypotheses concerning the adaptive nature of such cycles consider the effects of the tidal regime or moonlight on the dispersal of planktonic eggs or hatchlings away from adult habitats. We determined the reproductive periodicity of 17 paternal-brooding reef fishes at three neotropical sites with different tidal regimes. We used these and published data to assess the explanatory potential of hatchling-dispersal hypotheses, and of other larval-biology and adult-biology hypotheses.

Among the 17 species (15 damselfishes and two blennies), two of which we studied at two sites, we found 14 with lunar and semilunar spawning cycles, one sporadically synchronized spawner, two acyclically variable spawners, and one continuous spawner. In 16 species individual nests experienced frequent alternation of short brood-care and rest periods (brood cycling).

Simple hatchling-biology hypotheses are unable to account readily for the range of variation in the types, precision, and lunar timing of spawning cycles among species within and between depth zones at the same site, or for intra- and interspecific variation in spawning patterns in relation to seasonal and geographic differences in tidal regimes.

The hypothesis that lunar spawning cycles have evolved to maximize the availability of relatively uniform-age larvae that settle during preferred lunar settlement times is supported by some but not all data.

Adult-biology hypotheses can account for the higher frequency of lunar spawning cycles among brooders than nonbrooders, and can accommodate various patterns of reproductive cyclicism and synchronization in brooders. Synchronized activity may be favored in some brooders because colonial spawning provides enhanced defense against egg predators. Further, the cost of brood care may result in reduced egg survivorship, and both brood cycling and the temporal concentration of spawning may reduce egg losses by allowing males to recuperate and increasing benefits to brood-care for them.

Adult-biology constraints may produce variability in spawning patterns. Differences in social systems may determine the ability to form nesting colonies, and to strongly synchronize spawning independently of lunar cues. Changes in short-term food availability may influence the regularity of spawning.

Adult-biology hypotheses represent generally underemphasized alternatives that have at least as much explanatory potential as larval-biology hypotheses. If hatchling biology is of general importance to paternal brooders, there must be considerably more interspecific variability in hatchling ecology than is generally assumed.

Key words: adult biology; coral reef fish; larval biology; lunar reproduction; moonlight; paternal brooding; settlement; spawning cycles; tides.

INTRODUCTION

Patterns of movement, feeding, and reproduction of many intertidal organisms are tightly linked to the tidal regime and hence the lunar cycle (Korringa 1947, Barnwell 1976, Berry 1986, Christy 1986). Many shallow-water tropical reef fishes also have lunar-periodic reproduction (Johannes 1978, Gladstone and Westoby 1988).

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Discussion of the ecological causes of lunar patterns of reproduction of reef fishes has largely followed explanations developed for intertidal invertebrates (e.g., Berry 1986, Christy 1986) in focusing primarily on factors that might influence survival of planktonic eggs or larvae during or shortly after their release from a reef (Johannes 1978, Thresher 1984, Gladstone and Westoby 1988 for reviews). Four specific hypotheses of this type, which we call "hatchling-biology" hypotheses, are as follows. (1) Dispersal of planktonic propagules is timed to assist their movement away

from reef habitats. (a) Buoyant propagules released near the largest high tides are more likely to remain out of reach of reef-based predators and be rapidly flushed away from the reef by strong tidal currents (Johannes 1978, Lobel 1978, Ross 1978, MacDonald 1981, Robertson 1983). Alternatively, (b) moonlight may enhance off-reef movements of photopositive hatchlings by attracting them toward the water's surface (Allen 1972). (2) Synchronized spawning oversaturates predators on planktonic propagules (Keenleyside 1972, Lobel 1978). (3) Spawning cycles of reef fishes match those of reef invertebrates, whose offspring provide food for the larval fishes (Allen 1972). (4) Temporal spacing of cohorts of young larvae reduces food competition among them (Lambert and Ware 1984). The first hypothesis makes predictions concerning both the occurrence and timing of lunar spawning synchronization. Predictions of the remaining hypotheses concern the degree of intra- and interspecific synchronization (hypotheses 2 and 3) or the degree of temporal separation of spawning peaks (hypothesis 4) rather than the specific lunar timing of activity.

The "settlement-linkage" hypothesis (Christy 1978, Kingsford 1980) focuses on the end of the larval life. It proposes that temporal patterns of larval production represent adaptations to maximize settlement of planktonic juveniles. If larvae have relatively fixed development periods, and there are preferred lunar phases for settlement, then there will be selection to time the release of larvae such that most will be competent to settle at the preferred times.

A third category of hypotheses, which were developed largely for fishes, concern factors affecting spawners themselves, the spawning act, and parental activities. Such "adult-biology" hypotheses are of two types. One type invokes lunar cyclic changes in environmental factors that directly influence reproduction. Three hypotheses of this type are that (1) moonlight allows adults to spawn near dawn, when diurnal egg predators are absent (Pressley 1980); (2) moonlight facilitates migration to spawning sites (Colin et al. 1987); and (3) moonlight enhances the ability of adults to guard their eggs (Allen 1972). Three other adult-biology hypotheses propose that synchronization of reproductive activity is beneficial per se. First, synchronization may oversaturate predators on guarded benthic eggs (Foster 1987a, b). Second, synchronized spawning in dense colonies may provide enhanced defense against egg predators due to the collective activities of aggregated males (Loiselle 1977, Dominey 1981, Tyler 1988, Foster 1989). Third, synchronization of spawning may reduce egg mortality that arises due to the cost of paternal care (Dominey and Blumer 1984). Synchronized spawning cycles with regular hiatuses in brooding may select for increased parental investment because they increase clutch sizes during brood periods (Sargent and Gross 1985), and also provide frequent, predictable opportunities for males to recuperate. Eggs deposited during

off-peak parts of a spawning cycle may suffer higher mortality because they are in smaller clutches that are more susceptible to filial cannibalism (Rohwer 1978, Petersen and Marchetti 1989), or because males are in poorer condition due to recent brooding.

Five of the hypotheses we consider here (hatchling dispersal, hatchling-food tracking, moonlight affects spawning or brooding ability, and settlement-linkage) invoke the direct influence of lunar cyclic environmental factors on reproductive success. In the remaining hypotheses the lunar cycle merely provides convenient cues for the synchronization of activity.

In this paper we describe lunar patterns of spawning and larval production by 17 neotropical reef fishes that brood benthic eggs. These include members of the the blennioid genus *Ophioblennius*, and the damselfish (Pomacentridae) genera *Stegastes*, *Abudefduf*, *Chromis*, and *Microspathodon*. These species were studied at three sites in two oceans that experience quite different tidal regimes. All of them produce planktonic larvae from benthic eggs that are laid in a prepared nest and are closely guarded by their male parent until they hatch. We use the data presented here, together with other published information, to assess the general explanatory potential of the hypotheses outlined above. Existing comparative analyses of lunar reproductive patterns of reef fishes have concluded that lunar cycles of activity occur most frequently among species that have benthic eggs, and that the relationship between hatchling biology and the tidal regime is primarily responsible for this pattern (Thresher 1984, Gladstone and Westoby 1988). Consequently we pay particular attention to the hatchling-biology hypotheses.

Previous analyses of the hatchling-biology hypotheses implicitly assume that the requirements and capabilities of hatchlings of different species are essentially the same. Since there is little information to the contrary (see Gladstone and Westoby 1988), we make the same assumption in our analyses of the hatchling-biology hypotheses and of the adult-biology hypotheses that invoke direct environmental influences on reproductive capabilities. For the remaining hypotheses we incorporate known interspecific variation in adult and larval capabilities in the predictions used in each case. We assess the explanatory potential of each hypothesis in terms of the proportion of species that conform to its predictions.

We used the following sets of predictions in our evaluation of each hypothesis:

I. Larval-biology

A. Hatchling-biology

1. *Tidal control of dispersal.*—This hypothesis has two alternative forms that can be applied to geographic variation in spawning cycles. The conventional expression of this hypothesis, which derives from observations on the reproduction of intertidal invertebrates,

proposes that the efficacy of dispersal increases with increasing tidal amplitude. It predicts that lunar hatching cycles should be best developed and best correlated with the tidal regime at large-tide sites. However, it may be that all tides are equally effective at large-tide sites (Robertson 1983), and that tidal variation is most likely to affect dispersal in small-tide situations. This "threshold" hypothesis predicts that relationships between spawning and the lunar cycle should be equally or better developed at small-tide sites than at large-tide sites.

Both forms of the tidal-control hypothesis make three other predictions: (1) Lunar spawning cycles should be best developed and correlated with the tidal regime in species nesting in shallow habitats. (2) The peak(s) of each lunar hatching cycle should occur during the lunar phase in which dispersive tides and diel hatching periods coincide. (3) The timing of lunar hatching peaks and the amount of spawning during each lunar spawning cycle should track seasonal changes in the lunar timing and sizes of appropriate tide series. (4) Spawning cycles of individual species should change in relation to geographic variation in the tidal regime and do so in a consistent manner.

2. *Moonlight control of dispersal.*—Lunar spawning cycles should be unimodal. Hatching should peak during the lunar phase when moonlight is maximal during the nocturnal hatching period.

3. *Oversaturation of hatchling predators.*—There should be low dispersion, unimodal lunar cycles, and pronounced interspecific synchrony of cycles at the same site.

4. *Hatchling-food tracking.*—Different species at the same site should have hatching cycles with similar form and timing.

5. *Hatchling-competition reduction.*—Cohorts of young larvae should be discretely and evenly spaced by low-dispersion, semilunar or shorter period spawning cycles. High-frequency hatching cycles should be synchronous among different local populations of the same species at the same site.

B. *Settlement linkage.*—Lunar spawning cycles should occur in species that have relatively fixed-age settlers and in which there are preferred lunar settlement periods. Lunar spawning cycles may be absent in species that have variable-age settlers or lack preferred settlement periods. A single population should have the same lunar spawning pattern in the same season each year.

II. Adult-biology

A. *Moonlight affects the ability to spawn or brood eggs.*—Cycles should be lunar, unimodal, and synchronous among species at the same and different sites. If moonlight affects spawning activity of dawn-spawners, the cycle should peak between full moon and last quarter. If moonlight affects parental ability, the

spawning cycle should peak several days before full moon.

B. *Oversaturation of egg-predators.*—This hypothesis predicts highly synchronized, infrequent activity by a local population. Synchronization may be lunar cyclic with a peak at any lunar phase, or sporadic. The predator population should be saturable (i.e., incapable of consuming all eggs) when a prey population synchronizes its spawning. The degree of synchrony should be positively correlated with the strength of predation pressure.

C. *Enhanced defense.*—Spawning should be highly synchronized and combined with strong spatial aggregation of nests. Central males in a spawning colony should experience the lowest egg losses from predators. Spawning may be sporadic or cyclic at any frequency and with peaks at any lunar phase.

D. *Cost of care.*—Paternal brooding should be costly, and males should display effects of that cost that reduce egg survivorship. If egg survivorship changes over a spawning cycle it should be lowest at the end of the cycle. Nests should be empty a substantial percentage of the time, with frequent hiatuses in brooding (brood cycling). Population synchronization of brood cycling may be regular or sporadic. In unsynchronized species, individual nests should show brood cycling at similar frequencies to synchronized species. Interspecific variation in the extent of synchronization, and in the frequency and duration of brooding hiatuses, should correlate with variation in the cost of care. Lunar spawning cycles should occur more commonly among paternal brooders than among nonbrooders.

METHODS

Organisms

We obtained data for ten Caribbean pomacentrids: *Abudefduf saxatilis*, *Chromis multilineata*, *Microspatodon chrysurus*, *Stegastes diencaeus*, *S. dorsopunicans*, *S. leucostictus*, *S. partitus*, *S. planifrons* and *S. variabilis*; six Eastern Pacific pomacentrids: *A. trocheli*, *M. dorsalis*, *M. bairdi*, *S. acapulcoensis*, *S. flavilatus*, *S. rectifraenum*, and two blenniids, *Ophioblennius atlanticus* from the Caribbean and *O. steindachneri* from the Eastern Pacific.

Study areas and tidal regimes

Data were collected on the Caribbean species on the reefs of Punta de San Blas, Panama (Robertson 1987: Fig. 1). Data on the Eastern Pacific species were obtained at Isla Taboguilla, Panama Bay, Panama (2 km from Isla Taboga; Porter 1972: Fig. 1), and near Guaymas, Mexico, in the Central Gulf of California (Thomson et al. 1979: Fig. 1). We will refer to these three sites as Caribbean Panama (CP), Pacific Panama (PP), and Pacific Mexico (PM).

United States Department of Commerce Tide Tables (NOAA 1980–1988) show that the three study areas

TABLE 1. Characteristics of the tidal regime at the three study sites.

Site	Tidal amplitude (m)		Type of tides	Constancy of tidal regime
	Mean	Maximum		
Caribbean Panama	<0.3	0.7	diurnal and semidiurnal	Seasonal changes: mix of tide types, diel timing of high tides, relative sizes of spring tides, presence/absence of nocturnal high tides
Pacific Panama	3.9	6.2	semidiurnal	Nonseasonal reversing asymmetry in spring tide amplitudes
Pacific Mexico	1.1	1.4	diurnal and semidiurnal	(Study spanned only June–August)

differ in their tidal amplitudes, tidal periodicities (diurnal and/or semidiurnal), and the seasonal and long-term constancy of the tidal regime (Table 1). Tidal amplitudes are smallest at CP, moderate at PM, and large at PP. Tides are invariably semidiurnal at PP, while CP and PM experience a changing mixture of diurnal and semidiurnal tides. At PP, there is a non-seasonal, reversing asymmetry in spring tide amplitudes: the maximum amplitude of full moon spring tides exceeds that at new moon tides (by up to 1.9 m) for 6–8 mo, then the relationship reverses. At PM, tides were mixed during the study months, and the largest dusk high tides occurred around new and full moons. Seasonal changes in tide patterns at CP are complex. They include changes in (1) the proportion of days in the month in which tides are either diurnal or semidiurnal, and (2) the daily timing of high tides in the same lunar phase (including whether the diurnal high tides occur around midday or midnight) and (3) tidal heights, tidal amplitudes, and differences in amplitudes of semidiurnal tide pairs. The predictability of tidal heights and currents at CP may be reduced by local weather conditions (Glynn 1972, Robertson and Hoffman 1977) and river runoff (D. R. Robertson, *personal observation*).

Observations on spawning and hatching periodicities

Lunar periodicity of spawning.—An individual damselfish or blenny nest is normally used repeatedly over periods of months or years. For each species at CP, a number of nests on a section of reef were individually tagged, visited every 1–2 d, and the number of clutches laid each day was recorded. Eggs of different ages differ in color (e.g., Schmale 1981), which allowed us to record the date each clutch was laid. All eggs of the same color in a nest were defined as one clutch, although more than one female sometimes contributes to a clutch (MacDonald 1973, Marraro and Nursall 1983, our own observations on *A. troschelii*, *C. multilineata*, *S. partitus*, and *S. dorsopunicans*). Data were obtained for each species from at least 15 nests for 3–6 lunar cycles, between June 1981 and July 1988. In addition, daily observations were made on spawning activity in one population of *S. dorsopunicans*, for 3 yr (1984–1987).

A single population of each of *S. leucostictus* and *A. saxatilis* was monitored at 2-d intervals for 1 yr (1987). These data were used to determine if there were seasonal changes in lunar spawning patterns that correlated with seasonal changes in the tidal regime.

At PP three sets of data were obtained. First, from October 1982 to January 1986, a fixed area (≈ 0.15 ha) of subtidal habitat on Taboguilla was visited 3–8 times per month. This area was searched similarly each time, and the numbers of clutches of different ages encountered in nests of each species were recorded. Since the incubation period of eggs of each species was 4–5 d (including the day of laying), each day's observations sampled activity over a 4–5 d interval. To eliminate effects of monthly variation in the amount of spawning, the number of clutches laid on each day was expressed as a proportion of the maximum recorded that month. From these scaled values we derived the average percentage of the lunar month's activity that occurred on each lunar day. Second, during July and August 1985, tagged nests of *M. dorsalis*, *S. flavilatus*, *S. acapulcoensis*, and *O. steindachneri* ($n \geq 19$ nests per species) were visited at 2–3 d intervals over a 50-d period. During each visit, the number and ages of all clutches in each nest were recorded. Third, during October and November of 1987, five sites in the Pearl Islands (≈ 60 km from Taboguilla) were visited at weekly intervals, 3–5 d before and after full and new moons. Spawning and nesting activity by *A. troschelii* was noted at Pearl Island sites described by Foster (1987a, b).

At PM we obtained information at two localities. Data on *S. rectifraenum* and *O. steindachneri* were collected at Punta Santa Inez, 45 km southeast of Santa Rosalia, in July–September 1986. For both species at least 20 nests were monitored at 1–2 d intervals for two lunar cycles. *A. troschelii* was observed daily at Lalo Beach, 12 km northwest of Guaymas, during July 1980, July and August of 1981, and July–September of 1982.

Diel periodicity of spawning and hatching.—Some direct observations were made of spawning. However, no attempt was made to sample nests systematically throughout the 24-h cycle, and we relied largely on an indirect method to establish diel patterns. We collected ≈ 100 eggs from a freshly laid clutch and maintained

them in seawater in glass jars floating in the sea at ambient temperature (28°–30°C). At 2-h intervals for 18 h after laying, the stage of development of the eggs was determined (cf. Shaw 1955), and the water in the jar was changed. Subsequently, samples of 1st-d clutches were removed from nests at different hours of the day and kept in floating jars until \approx 1800, when their stage of development was determined. The time of their spawning was then back-calculated. For each CP species, except *C. multilineata*, we estimated the laying time of at least 25 clutches collected during each of three time periods: before 0730, 0730–1630, and 1630–1800. No new clutches of *C. multilineata* were seen in nests before 1000, and for that species we back-calculated the laying times of 26 clutches collected between 1000 and 1630 and 41 between 1630 and 1800.

At PP no comprehensive observations of spawnings or back-calculation of spawning times were made. Some spawnings were observed and the spawning time of small numbers of clutches were back-calculated for several species.

We never saw any eggs hatch during the day. To establish whether hatching occurred early at night, as noted by Foster (1987a) and MacDonald (1973) for two of our study species, we examined nests containing last-day clutches 0.5 h before sunset and again 0.5–1 h after sunset (using a flashlight).

Statistical analyses of data

We calculated the average distribution of spawning activity over the lunar cycle (mean percent of the lunar month's activity that occurred on each lunar day) for each species at each site. Rayleigh tests were used to test for the occurrence of any nonrandom concentration(s) of activity in those distributions. To estimate the dispersion of activity over the lunar cycle we used the angular variance (Batschelet 1981).

In addition, continuous data series were subject to time-series analyses. Spectral analyses (Platt and Denman 1972) were used to identify statistically significant (99% level) periodicity in reproductive cycles. Auto-correlation analyses were used to define more precisely the periodicity of cycles identified by the spectral analyses. Cross-correlations between the lunar cycle (represented by a sine wave with a 29.5-d period) and reproductive activity were used to determine the lunar phase(s) of peak activity. BMDP (1977) and SYSTAT (1988) computer programs were used for these time series analyses.

Other statistical procedures followed Zar (1974), or Sokal and Rohlf (1981).

RESULTS

I. Diel and lunar patterns of spawning and hatching

A. *Spawning—diel periodicity.*—Our direct observations on spawnings by *Ophioblennius atlanticus* (n

$= 12$), *Stegastes partitus* ($n = 29$), *Microspathodon chrysurus* ($n = 31$) and *S. dorsopunicans* ($n > 100$), plus back-calculated spawning times of at least 75 clutches of each damselfish at CP, indicate that all CP species except *Chromis multilineata* and *Abudefduf saxatilis* spawned almost exclusively around dawn (± 1 h). This agrees with observations by Marraro and Nursall (1983), MacDonald (1973), and Schmale (1981) on *O. atlanticus*, *M. chrysurus*, and *S. partitus*, respectively. Spawning by *C. multilineata* at CP was seen on over 20 different days between 1000–1400. No new clutches were observed in nests before 1000, and back-calculated spawning times all fell between approximately 1000 and 1400. We saw *A. saxatilis* spawn at all daylight hours. Back-calculation from 290 clutches indicates that 65% were laid throughout the period 0400–0800, 10% from 1000 to 1800, and 25% between \approx 2200 and 0400 (see also Cummings 1968, Albrecht 1969).

At PP and PM, no comprehensive attempt was made to identify diel periodicities of spawning. Back-calculation of seven clutches of *S. flavilatus* and nine of *S. acapulcoensis* indicates all were spawned at dawn, although we did see *S. flavilatus* spawn around 1500 on two occasions. Of 17 back-calculated clutches of *M. dorsalis*, 9 were laid around dawn, while 8 may have been laid in the late afternoon the previous day; one spawning was seen at 1600 and three before 0800. We saw colonial spawning by *A. troschelii* at various times between 0830 and 1515 on 18 days at PP and the Pearl Islands. Back-calculated spawning times of 10 clutches indicated they were laid between dawn and several hours afterwards. Based on back-calculation, 27 of 30 clutches of *S. rectifraenum* were laid near dawn, while the remaining three may have been laid the previous afternoon. Spawning by this species was observed at dawn on 21 occasions, and twice between 1400 and 1800. *O. steindachneri* was observed spawning only early in the morning ($n = 40$ spawnings before 0800 at both PP and PM). Thus, most species spawned almost exclusively at dawn, several others showed a dawn peak, but with more variability, and only one (*C. multilineata*) spawned exclusively in broad daylight.

B. Spawning—lunar periodicity

1. The presence and absence of lunar cycles

a. *Lunar species:* Cycles in spawning with a period close to one lunar cycle were evident in 10 species. These included 8 of 10 CP species, 2 of 6 PP species, but none of 3 PM species. In most lunar species, spawning was dispersed over more than half a lunar cycle (Fig. 1, Table 2). Peaks of spawning by the 10 lunar species ranged over most of the lunar cycle (Table 2, Fig. 1).

b. *Semilunar species:* Two of 10 CP species, 2 of 6 PP species and none of 3 PM species were semilunar cyclic. In 3 semilunar species, peaks of spawning occurred during the week preceding the new and full

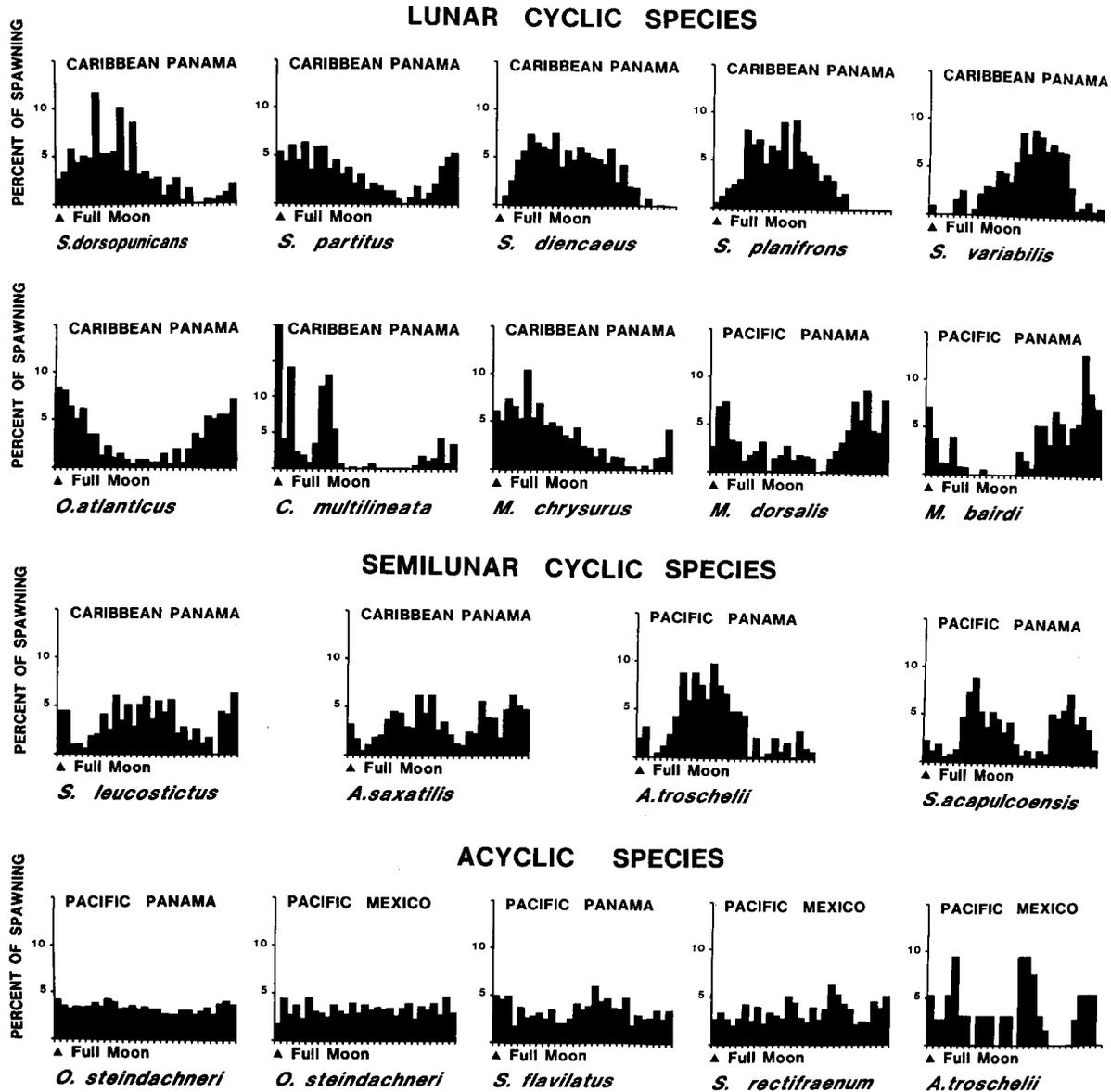


FIG. 1. Average lunar patterns of spawning of the study species. Data are mean percent of the lunar month's activity that occurred on each day.

moons, while in the fourth (*S. leucostictus*) activity peaked almost at the new and full moons (Table 2, Fig. 1).

The semilunar pattern of spawning by *A. troschelii* at PP is not clearly indicated by Fig. 1, mainly because there were consistent differences in the sizes of successive semilunar spawning bouts. During 10 months, *A. troschelii* at PP spawned only around new moon. In six other months there were two spawning bouts, with the amount of activity at new moon exceeding that at full moon. In one month fish spawned only around full moon. Foster (1987a) reports that, in the Pearl Islands, each local population of *A. troschelii* spawned once per lunar cycle, around new moon. We observed five local

populations of *A. troschelii* at Foster's site during the same season as her observations, but sampled the lunar cycle more systematically and completely than she did. We found that, although nine spawning bouts occurred around new moon (± 5 d), three others occurred 3–4 d before full moon. Also, at least three populations spawned at least twice (around the new and full moons) during both sampling months. We conclude that the overall pattern of spawning activity of *A. troschelii* in Panama Bay essentially is asymmetrically semilunar, with the major concentration of activity around new moon.

Although our data show that spawning by *A. saxatilis* at CP is semilunar (Table 2, Fig. 1), Foster (1987a)

TABLE 2. Periodicity of spawning of 17 neotropical fishes, patterns, and test statistics.

Species	Local-ity	Average lunar cycle			Time series analyses			Sample size (months)	
		Median spawning date†	Circular statistics‡		Significant cycling frequencies (d)	Lunar date of activity peak		Avg. lunar cycle	Time series analyses
Z	Disper-sion§	Lunar date†	r¶						
Lunar cyclic									
<i>O. atlanticus</i>	CP	15	12.2***	1.30	2 (0.73), 29 (0.52)	17	0.75	3	3
<i>C. multilineata</i>	CP	19	44.3***	0.66	8 (0.31), 29 (0.35)	20	0.30	6	6
<i>M. chrysurus</i>	CP	21	42.4***	0.72	28 (0.54)	18	0.79	5	5
<i>S. diencaeus</i>	CP	27	33.2***	0.92	30 (0.55)	29	0.61	6	6
<i>S. planifrons</i>	CP	27	29.8***	0.84	29 (0.53)	28	0.76	4	4
<i>S. dorsopunicans</i>	CP	23	23.8***	1.02	3 (0.32), 29 (0.30)	22	0.31	5	5
<i>S. variabilis</i>	CP	3	32.0***	0.87	2 (0.46), 29 (0.35)	7	0.58	4	3
<i>S. partitus</i>	CP	20	11.5***	1.32	2, 30#	20#	...	7	7
<i>M. dorsalis</i>	PP	14	14.6***	1.24	3 (0.40), 23 (0.37)	11	0.54	8	1.7
<i>M. bairdi</i>	PP	12	34.2***	0.83	...††	30	...
Semilunar cyclic									
<i>A. troschelii</i>	PP	13 and 28	25.9***	0.98	21	...
<i>S. acapulcoensis</i>	PP	10 and 25	17.0***	1.18	14 (0.28)	10 and 25	0.49	27	1.7
<i>A. saxatilis</i>	CP	11 and 26	6.0**	1.52	15 (0.19)	11 and 26	0.32	5	5
<i>S. leucostictus</i>	CP	14 and 29	4.7**	1.56	15 (0.34)	12 and 27	0.30	6	6
Acyclic									
<i>O. steindachneri</i>	PP	none	0.23 NS	1.91	none	none	...	30	1.7
<i>O. steindachneri</i>	PM	none	0.30 NS	1.97	2 (0.47)	none	...	2	2
<i>A. troschelii</i>	PM	none	0.61 NS	1.77	none	none	...	5.7	4.5
<i>S. rectifraenum</i>	PM	none	0.19 NS	1.84	8 (0.29)	none	...	2	2
<i>S. flavilatus</i>	PP	none	1.91 NS	1.91	2 (0.26)	none	...	30	1.7

† New moon = day 1.

‡ Z = Rayleigh test: ** $P < .01$, *** $P < .001$, NS $P > .05$.

§ Dispersion = angular variance.

|| Significant cycling frequencies identified by spectral analyses with autocorrelations in parentheses.

¶ From cross correlation with lunar cycle.

From Robertson et al. 1988.

††... = no data.

reports that two populations within 1 km of our study population were acyclic. Our analysis of Foster's data detected a semilunar spawning cycle (Rayleigh test on combined data from two sites: bimodal distribution, $Z = 3.2$, $P < .05$; time series analysis: significant, weak 16-d cycle), with peaks of activity at the same lunar phases as in our study population.

c. *Acyclic species*: In two of six PP species, all three PM species, but none of 10 CP species, we found no indication of lunar or semilunar cycles of spawning. The acyclic species at PM included *A. troschelii*, which was semilunar at PP (Table 2, Fig. 1).

2. *Nonlunar variation in spawning and brooding*.— Besides patterns of synchronization with the lunar cycle, the lunar scheduling of spawning and brooding varied among the study species in five other ways: (a) whether, in species lacking lunar spawning cycles, spawning of the population was sporadically synchronized, intermittently fluctuating, or continuous, (b) whether higher frequency spawning cycles were present, (c) whether, in populations that lacked synchronized brood cycling, individual nests showed unsynchronized brood cycles, (d) the amount of spawning in a nest each month, and

(e) the amount of time males spent brooding each month.

Spawning by *A. troschelii* at PM was not randomly distributed over time. Rather it was highly synchronized, in 2–3 d long bouts of mass activity, separated by periods of total inactivity (Mean Square Successive Difference test for serial randomness [Zar 1974]: 1981 data $C_{54} = 0.42$, $P < .001$; 1982 data $C_{82} = 0.35$, $P < .001$). Spawning males at both PP sites and at the PM site aggregated in colonies with nests 0.5–1 m from one or more neighboring nests. At PM, nesting colonies contained eggs for 6–7 d, then were empty for an average of 5 d (range 1–24 d, $n = 12$) before the next spawning bout. *A. troschelii* at PM was the only species to show sporadic synchronization of spawning.

In *S. rectifraenum* and *S. flavilatus*, spawning occurred all the time in a population at moderate-to-low, fluctuating levels. Individual nests of both species displayed high-frequency brood cycling: In *S. rectifraenum* and *S. flavilatus* 74% of 302 clutches and 95% of 84 clutches, respectively, were laid on one (or two consecutive) days following a period when the nest was empty. Brooding and nonbrooding periods had median

TABLE 3. Rates of clutch deposition and levels of brooding in the 17 study species.

Species	Site	Clutches·nest ⁻¹ ·mo ⁻¹		% time nest was empty	
		\bar{X} and 95% CI	(n)*	Median	Range
Lunar species					
<i>O. atlanticus</i>	CP	4.2 ± 0.7	(25/3)	60	9–84
<i>C. multilineata</i>	CP	1.9 ± 0.3	(20/3)	82	78–90
<i>M. chrysurus</i>	CP	5.5 ± 0.9	(21/3)	49	23–75
<i>S. diencaeus</i>	CP	6.8 ± 0.5	(23/3)	24	12–80
<i>S. planifrons</i>	CP	4.3 ± 1.1	(35/4)	50	23–89
<i>S. dorsopunicans</i>	CP	3.1 ± 0.4	(65/8)	65	27–93
<i>S. variabilis</i>	CP	2.3 ± 0.6	(16/4)	75	24–93
<i>S. partitus</i>	CP	5.8 ± 1.3	(24/4)	43	32–83
<i>M. dorsalis</i>	PP	1.7 ± 0.7	(19/1.7)	82	30–96
<i>M. bairdi</i>	PP	no data			no data
Semilunar species					
<i>A. troschelii</i>	CP	≈ 1.8	(...) [†]	≈ 70	... [†]
<i>S. acapulcoensis</i>	PP	2.1 ± 0.5	(21/1.7)	72	50–90
<i>A. saxatilis</i>	CP	2.0 ± 0.5	(27/3)	77	60–94
<i>S. leucostictus</i>	CP	6.4 ± 1.1	(15/10)	53	1–94
Acyclic species					
<i>O. steindachneri</i>	PM	18.4 ± 1.4	(24/2)	0	0–6
<i>O. steindachneri</i>	PP	14.7 ± 2.1	(19/1.7)	0	0–60
<i>A. troschelii</i>	PM	≈ 2	(...)	≈ 70	...
<i>S. rectifraenum</i>	PM	6.1 ± 0.5	(26/2)	41	24–64
<i>S. flavilatus</i>	PP	2.4 ± 0.5	(20/1.7)	73	49–90

* $n = a/b$; a = number of nests, b = number of months.

[†] Individual nests were not monitored continuously. Estimates of number of clutches per nest per month and time nest is empty are based on (a) average number of clutches observed in a nest, (b) average number of bouts of spawning in the same spawning area by a population each month, and (c) an incubation period of 5 d.

durations of 4 d (range 4–6 d, $n = 72$) and 5 d (range 3–24 d, $n = 58$), respectively, in *S. flavilatus*, and 5 d (range 4–23 d, $n = 137$) and 3 d (range 1–>21 d, $n = 150$), respectively, in *S. rectifraenum*. Such high-frequency brood cycling was evident in only one species with a lunar or semilunar spawning cycle (*C. multilineata*). In *O. steindachneri* at both PP and PM all nests received and contained eggs virtually continuously (Fig. 1, Table 3).

High-frequency, synchronized brood cycles were evident in *C. multilineata* and *S. rectifraenum* (both 8-d period; Table 2). Spawning cycles with even shorter periods (2–3 d) that did not involve hiatuses in brooding activity were detected in four lunar and two semilunar species (Table 2).

There was considerable variation in the frequency of spawning activity in the average nest of each of the different species (Table 3). Extreme conditions range from <2 clutches·nest⁻¹·mo⁻¹ to >18 clutches·nest⁻¹·mo⁻¹. There were no consistent differences in the frequency of clutch deposition among the lunar, semilunar, and acyclic spawners. The average percentage of time that nests were empty ranged from 0 to >80% among the various species. There was considerable interspecific variation among each of the lunar, semilunar, and acyclic groups in both the frequency of clutch deposition and the level of brooding activity, but no consistent differences between these groups (Table 3). The average amount of time the nest was empty in a species was negatively correlated with the average

number of clutches that nests of that species received each month (Pearson $r_{18} = -0.95$, $P < .01$, Table 3), and the most frequently spawning species (*O. steindachneri*) had continuously full nests.

C. *Hatching—diel periodicity.*—Twenty-six clutches of *S. dorsopunicans* observed on four nights disappeared during the 1st h after sunset (three were seen hatching), as did 70 clutches of *S. partitus* observed on six nights, and six clutches of *O. atlanticus* observed on one night. Foster (1987a) observed *A. saxatilis* and *A. troschelii* eggs hatching during the 1st h after sunset, as did MacDonald (1973) for *M. chrysurus*. Since eggs of all 17 species of damselfishes and blennies examined to date hatch just after dusk (Albrecht 1969, Emery 1973, Fricke 1973, MacDonald 1973, Moyer 1975, Moyer and Bell 1976, Ross 1978, Doherty 1983, Ochi 1985, 1986, Foster 1987a, Kohda 1988, Carlson 1990), we assume that eggs of all our study species hatch during that period.

D. *Hatching—lunar periodicity.*—We assume that the lunar periodicity of hatching of each species is equivalent to the lunar periodicity of its spawning lagged by the incubation period. Incubation periods (at 28°–29°C, and including the day on which eggs were laid) varied little among species: 3 d for *C. multilineata*, and 4–5 d for all other study species. Because these incubation times were short and varied so little, hatching cycles only slightly lagged and were only slightly more dispersed than spawning cycles over the lunar cycle (Fig. 2).

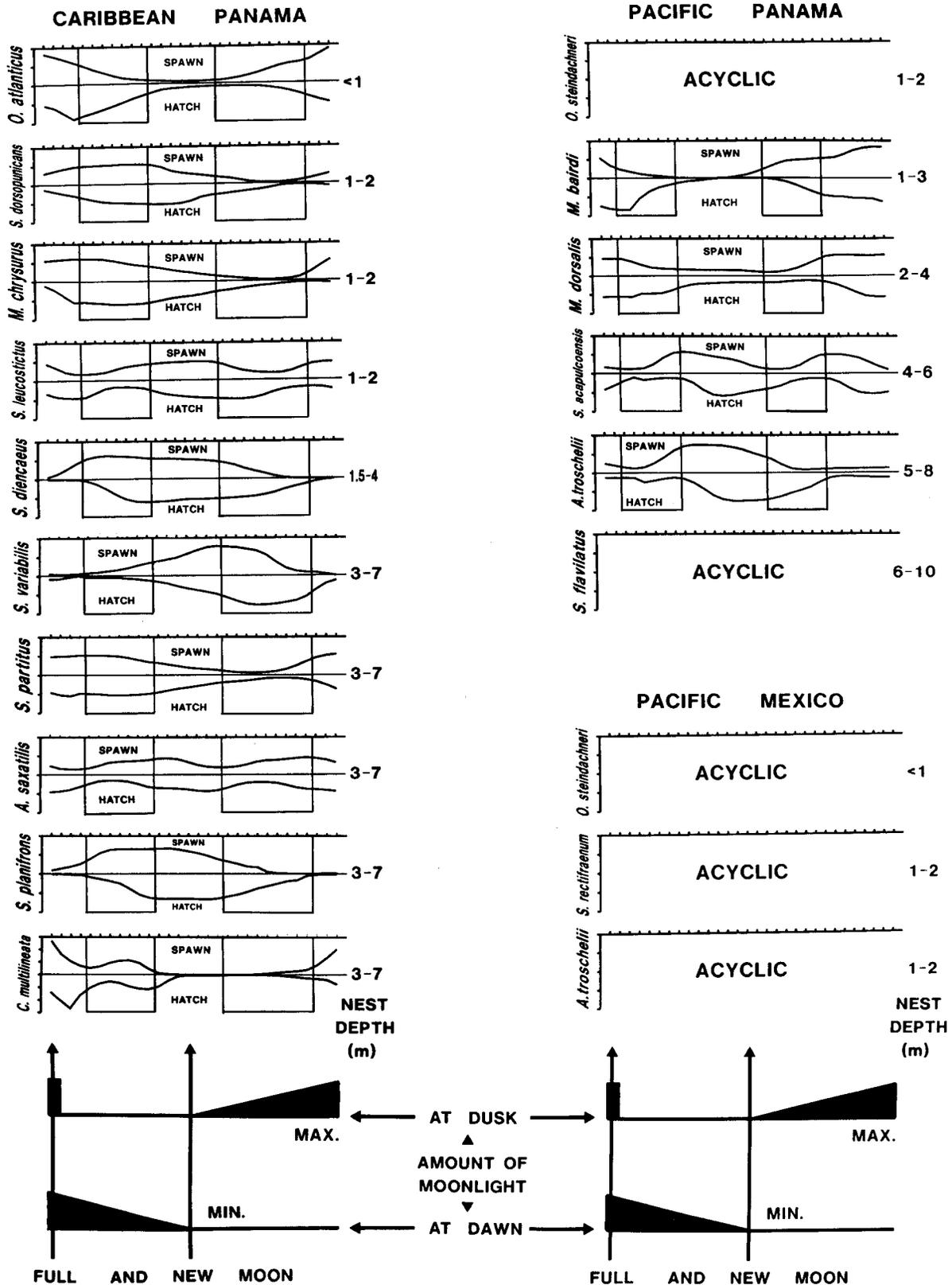


FIG. 2. Lunar spawning and hatching patterns of the study species in relation to the tidal regime, crepuscular moonlight levels, and depth of nesting habitat. Spawning and hatching patterns were derived by smoothing (4253H filter, SYSTAT computer program) the cycles shown in Fig. 1. Boxes enclose periods during which high tides occur at dusk (i.e., from 1 h before to 2 h after sunset).

II. Observations in relation to predictions of the hypotheses

A. Larval-biology hypotheses

1. Hatchling-biology

a. *Tidal control of dispersal; variation among sites in tidal regimes and spawning patterns.*—The tidal amplitude is greatest at PP and least at CP (Table 1). The conventional version of the tidal-control hypothesis predicts that lunar spawning cycles are best developed at the large-tide site and least at the small-tide site, i.e., PP > PM > CP. The threshold version of this hypothesis predicts the opposite trend, i.e., CP > PM > PP. Contrary to either prediction, such cycles were best developed at CP and least at PM (i.e., CP > PP > PM).

(i) *Coincidence of hatching and tidal peaks.*—To maximize hatchling dispersal, lunar hatching peaks should occur when high tides coincide with evening hatching periods. Hatching peaks were centered in those periods in two CP species (*S. variabilis* and *M. chrysurus*) and partly coincided with them in four others (*O. atlanticus*, *S. diencaeus*, *S. partitus*, and *S. dorsopunicans*). In the remaining four CP species, peaks of hatching were centered outside the periods of dusk high tides (Fig. 2). At PP, cyclic peaks of hatching were not centered in periods of dusk high tides in any species, although they partly overlapped those periods in two cases (*M. dorsalis* and *A. troschelii*). Hatching peaks were concentrated outside periods of dusk high tides in the remaining two cyclic species (Fig. 2). At PM, hatching was uniformly distributed throughout the range of variation in tidal conditions at dusk in all three species examined there, since all three lacked lunar spawning cycles.

(ii) *Nesting habitat and tidal tracking.*—At both CP and PP there was no relationship between a species' position on the habitat-depth gradient and the degree of lunar cyclicism of its spawning, the timing of lunar cyclic peaks of activity, or the dispersion of activity over the lunar cycle (Fig. 2). At CP, lunar and semilunar species nested in both shallow and deeper habitats, and hatching peaks of the shallowest group of five species were no better correlated with periods of dusk high tides than were those of five deeper nesting species (Fig. 2). At PP, both the shallowest and deepest species were acyclic, while the species at intermediate depths included both lunar and semilunar types. At PM, all three species at different depths were acyclic (Fig. 2). This lack of consistent patterns of interspecific variation indicates that depth-mediated differences in susceptibility to tidal factors are not responsible for differences in lunar spawning patterns among our study species.

Extreme habitat-related variation in spawning patterns of damselfishes at other localities does follow a pattern predicted by the tidal-control hypothesis. At some sites where damselfishes live in laterally exten-

sive intertidal or lagoonal habitats that are semi-exposed or ponded at low tide, hatchlings released at dusk during certain lunar phases would be unable to disperse (e.g., Doherty 1983). Species in subtidal habitats would not experience such hatchling entrapment. As predicted by the tidal-control hypothesis, semilunar spawning cycles with hatching maxima at lunar phases appropriate for dispersal occur in all species examined in such intertidal habitats, while a great variety of patterns occurs among subtidal species (Table 4).

(iii) *Seasonal variation in lunar spawning cycles and tidal regimes.*—Changes in the lunar timing and sizes of dusk high tides occurred at both CP and PP. In *S. acapulcoensis* (PP), the relative amounts of spawning in the two semilunar bouts changed in relation to the size of dusk high tides. There was a positive correlation between the amount of spawning at new moon (relative to that at full moon) and the amplitude of the largest new moon spring tide (relative to the largest full moon tide): Pearson $r = 0.72$, $P < .01$ ($n = 10$ mo in which new moon tides were greater than full moon tides, and 2 mo with the reverse asymmetry). However, three other PP species showed no such seasonal change in spawning patterns. In *A. troschelii*, asymmetries in sizes of semilunar spawning bouts were not related to tidal asymmetries (Pearson $r = 0.19$, $n = 17$, ns), while *M. dorsalis* and *M. bairdi* spawned only at full moon, regardless of the relative sizes of spring tides at the new and full moons. The fact that *S. acapulcoensis* was the only PP species to show tracking of spring-tide asymmetries is interesting, because its hatching peaks were distinctly out of phase with the lunar periods predicted by the tidal-control hypothesis (Fig. 2).

In *S. leucostictus* (CP) the amount of activity at new moon invariably exceeded that at full moon, and there was, on average, twice as much activity at new moon as at full moon ($n = 16$). In *A. saxatilis* (CP), however, there were no consistent differences in the amounts of activity in the low and full moon spawning bouts (Wilcoxon $T_{17} = 51.5$, ns). Neither of these two semilunar species changed the magnitude of their two semilunar spawning bouts in relation to changes in the magnitudes of the spring tides (*S. leucostictus*, Pearson $r = 0.11$, $n = 18$, ns; *A. saxatilis*, Pearson $r = 0.13$, $n = 17$, ns). Two of three CP species (*S. dorsopunicans* and *A. saxatilis*) exhibited no seasonal changes in either the lunar timing or size of spawning bouts that correlated with seasonal changes in the tidal regime (Table 4). In the third species, *S. leucostictus*, the timing of spawning peaks did track shifts in the lunar timing of dusk high tides, but changes in the amount of spawning each month were negatively related to seasonal changes in the size of dusk high tides (Table 5).

(iv) *Intraspecific geographic variation in spawning patterns and tidal regimes.*—We obtained data on two species at both PP and PM. *A. troschelii* showed different lunar spawning patterns at those sites, while *O. steindachneri* did not. Data exist for six CP species at

TABLE 4. Lunar patterns of reproduction by pomacentrids (P) and blenniids (B) other than those studied here.

Habitat	Species	Locality	Spring tide range (m)	Lunar spawning pattern	Hatching peak(s)	Source
Semi-intertidal reef flats	<i>Pomacentrus flavicauda</i> (P)	Australia	3.0	semilunar	full and new	Doherty 1983
	<i>Glyphidodon biocellatus</i> (P)	Australia	3.0	semilunar	full and new	Thresher and Moyer 1983
	<i>Amphiprion melanopus</i> (P)	Guam	0.7	semilunar	full and new	Ross 1978
Subtidal	<i>Stegastes fasciolatus</i> (P)	Hawaii	0.7	semilunar	full and new*	MacDonald 1981
	<i>Pomacentrus wardi</i> † (P)	Australia	3.0	semilunar	quarters	Doherty 1983
	<i>Chromis dispilus</i> (P)	New Zealand	1.8	semilunar	full and new	Kingsford 1980
	<i>Dascyllus trimaculatus</i> (P)	Red Sea	1.5	acyclic‡	...	Fricke 1973
	<i>Chromis notata</i> (P)	Japan	2.9	variable§	...	Ochi 1986, A. Nakazono, <i>personal communication</i> 1988
	<i>Amphiprion clarkii</i> (P)	Japan	1.6	variable	variable	Ochi 1985
	<i>Pomacentrus nagasakiensis</i> (P)	Japan	1.1	lunar	full	Moyer 1975
	<i>Plectroglyphidodon johnstonianus</i> (P)	Hawaii	0.7	acyclic	...	MacDonald 1981
	<i>Exallias brevis</i> (B)	Hawaii	0.7	acyclic	...	Carlson 1990
	<i>Abudefduf abdominalis</i> (P)	Hawaii	0.7	variable¶	...	Helfrich 1958, Tyler 1988
<i>Abudefduf sordidus</i> (P)	Hawaii	0.7	acyclic	...	Stanton 1985	
<i>Chromis cyanea</i> (P)	Caribbean	0.5	lunar	≈full	DeBoer 1978	

* Approximate, data insufficient for precise resolution.

† Occurs in a range of habitats. Doherty (1983) studied it in a ponded lagoon in which the timing of peak hatching was inappropriate for hatchling dispersal out of the lagoon.

‡ Individual local populations synchronized at nonlunar, variable frequencies.

§ Individual local populations may sometimes have lunar cycles, but different populations may be out of synchrony.

|| Semilunar one year with peaks at full and new moons and acyclic the next.

¶ Semilunar, lunar, acyclic, and cyclic at nonlunar frequencies in different months of the same year and in different years.

other Caribbean sites: *M. chrysurus* at Puerto Rico (MacDonald 1973), *S. partitus* at Florida (Schmale 1981), *S. leucostictus* and *S. planifrons* at Jamaica (M. Itzkowitz, *personal communication* 1989, Williams 1978, respectively), *O. atlanticus* at Barbados (Marraro and Nursall 1983), and *C. multilineata* at Colombia (Albrecht 1969). Although the precision of the data sets varies, each of those species' spawning cycles ap-

pears very similar in form and timing to the cycles of conspecifics at CP. However, the tidal regimes at four of those sites (i.e., all except Colombia) differ from that at CP (National Oceanographic and Atmospheric Administration 1988). The average tidal amplitude at those sites ranges from 1.3 to 3.4 times larger than at CP, and the timing of dusk high tides varies from between 2–3 d before to 3–8 d after those at CP.

TABLE 5. Timing of hatching cycles and levels of spawning activity of three damselfishes in relation to seasonal changes in the lunar timing and size of dusk high tides. Data are medians with ranges in parentheses.

Species	Season* (no. months)	Lunar date(s)† of hatching cycle		No. clutches·nest ⁻¹ ·mo ⁻¹
<i>S. dorsopunicans</i>	Feb–June (15) (Early + small tides)	26 (23–28)		2.8 (1.3–4.3)
	Aug–Dec (15) (Late + large tides)	26 (22–29)		2.0 (1.7–3.0)
<i>S. leucostictus</i>	Feb–June (8)	New moon bout 1.5 (29–5) [<.01‡]	Full moon bout 15.5 (14–17) [<.05‡]	6.5 (3.7–9.4) [<.05‡]
	Aug–Dec (8)	3 (2–6)	18 (17–19)	2.8 (1.8–8.4)
<i>A. saxatilis</i>	Feb–June (5)	29.5 (27.5–5.5) [ns‡]	14.5 (10.5–16.5) [ns‡]	2.0 (1.0–2.4) [ns‡]
	Aug–Dec (11)	28.5 (25.5–3.5)	14.5 (10.5–19.5)	1.8 (1.2–3.3)

* Feb–June: mean height of dusk high tides = 0.11 m (range = 0.0–0.2 m, $n = 60$), median lunar dates of these tides are days 5 and 20. Aug–Dec: mean height of dusk high tides = 0.35 m (range = 0.1–0.5 m, $n = 60$), median lunar dates of these tides are days 7 and 22.

† New moon = day 1.

‡ Mann-Whitney U test.

The best data available are for *S. leucostictus* and *M. chrysurus*. *S. leucostictus* has essentially the same spawning cycle at Jamaica and CP. Jamaica: average (bimodal) distribution; Rayleigh $Z = 3.7$, $P < .05$; average of 1.9 times as much spawning at new moon as at full moon, median lunar dates = days 13 and 26 (M. Itzkowitz, *personal communication* on four lunar cycles of spawning, and see Fig. 1 and Table 2). The tidal regimes are very similar at Jamaica and CP; the lunar timing of dusk high tides is the same and those tides are slightly larger at Jamaica. However, *M. chrysurus* has the same spawning cycle at Puerto Rico and CP, where there are distinct differences in the tidal regimes (see also Pressley 1980). At Puerto Rico, tides have an average amplitude 1.6 times that at CP, and dusk high tides occur 3–8 d after those at CP. Thus, the limited data indicate that geographic variation in lunar spawning patterns of our study species is not consistently correlated with geographic variation in the tidal regime in a manner predicted by the tidal-control hypothesis.

b. *Moonlight control of dispersal*.—This hypothesis predicts unimodal hatching cycles that peak shortly before full moon. Although 10 of the 17 species had unimodal lunar cycles of hatching, in five of those species (*O. atlanticus*, *M. chrysurus*, *S. dorsopunicans*, *S. partitus*, and *C. multilineata*) hatching peaked in the lunar period that lacked early-evening moonlight. In two others (*S. diencaeus* and *S. planifrons*), hatching occurred mainly during the period of low evening moonlight. Hatching peaked during the period predicted by this hypothesis in only two species (*S. variabilis* and *M. dorsalis*, Fig. 2).

c. *Oversaturation of hatchling predators*.—The predicted pattern of low-dispersion lunar cycles with strong interspecific synchrony within a site was not evident. Lunar hatching cycles were lacking at one site, and present in a mixture of types at the other two sites. Even at the site with the greatest development of unimodal cycles (8 of 10 species at CP), activity was well dispersed over the month in most species, and hatching peaks of different species were scattered throughout the lunar cycle with few instances of interspecific synchrony (Figs. 1 and 2).

d. *Hatchling food tracking*.—The predicted pattern of strong interspecific similarity of spawning patterns at a site occurred only at PM where all species were acyclic. At CP and PP there were mixtures of patterns and much interspecific variation in the timing of hatching peaks (Fig. 2).

e. *Hatchling competition reduction*.—This hypothesis predicts strong reproductive cyclicism, a preponderance of (symmetrical) semilunar or higher frequency cycles, and synchrony of hatching peaks among different local populations of conspecifics. These predictions are not strongly supported. Most species do have either semilunar ($n = 4$) or higher frequency (n

$= 9$) spawning cycles. However, activity within a population was poorly synchronized in one semilunar species (*A. saxatilis*, Foster 1987a, 1989), and was unequally distributed between the semilunar bouts in the remaining three. Further, most high-frequency cycles could arise by chance events unrelated to larval-cohort spacing. In *S. partitus*, for example, the female inter-spawning interval is 2 d (Y. Sadovy, *personal communication* 1988). If, by chance, more (or less) than 50% of females spawned on the 1st d of a lunar spawning cycle, that pattern could be entrained and appear as a high-frequency cycle. In five of the nine species the high-frequency cycles had 2-d periods. Such chance events are unlikely to produce the high-frequency cycles with longer periods (e.g., 3–8 d) that occurred in four species (*C. multilineata*, *S. dorsopunicans*, *S. rectifraenum*, and *M. dorsalis*).

Predicted strong synchrony of high-frequency spawning bouts in different local populations of conspecifics did not occur in either of two species for which data are available, *A. troscheli* (Foster 1987a) and *S. dorsopunicans*. In the latter, the high-frequency spawning cycles (3-d period) of two different local populations were synchronized (i.e., significant positive cross-correlation at zero lag) in only 3 of 12 mo. This is no different than what one would expect by chance (one-third of cases). Thus, the data indicate that high-frequency spawning activity conforms to predictions of the hatchling-competition hypothesis in at most four species (*S. acapulcoensis*, *S. rectifraenum*, *M. dorsalis*, and *C. multilineata*).

2. *Settlement-linkage*.—Since there are no data to the contrary we assume that the pattern of settlement at a site is representative for larvae that are produced at the same site. The larvae of damselfishes typically spend weeks in the plankton (Wellington and Victor 1989, and references therein), and it is possible that they could travel between sites at which the adults have different spawning patterns. The apparent lack of intraspecific geographic variation in the spawning cycles of six CP species (see preceding section) indicates that this assumption is reasonable, at least for the Caribbean.

In two damselfishes, *S. partitus* (CP, Robertson et al. 1988) and *Chromis dispilus* (New Zealand, Kingsford 1980), spawning and settlement are lunar cyclic, the settlement cycle mirrors the spawning cycle, and settlers are of relatively fixed age. Spawning of the wrasse *Thalassoma bifasciatum* is acyclic at CP, where its settlement is lunar cyclic and its settlers show considerable variation in age (Victor 1986). These relationships are consistent with the settlement-linkage hypothesis. Further, indirect evidence suggests that both *S. partitus* and *T. bifasciatum* have a preferred settlement period. Both these two species and four other damselfishes with lunar spawning cycles at CP (*S. diencaeus*, *S. dorsopunicans*, *S. planifrons*, and *S. variabilis*) all have uni-

modal lunar settlement cycles with a peak around new moon (Victor 1986, Robertson et al. 1988, D. R. Robertson, *personal observation*).

However, the Japanese damselfish *Amphiprion clarkii* has a unimodal lunar settlement cycle, but its spawning ranges from acyclic to semilunar in the same season of different years (Ochi 1985). This combination of variable spawning and fixed settlement patterns is not predicted by the settlement-linkage hypothesis. The significance of intraspecific geographic variation in the spawning patterns of *A. troschelii* (at PP and PM) cannot be determined, since no data are available on its settlement periodicity or age at settlement at either site. A lack of data also precludes assessment of the significance of intraspecific geographic variation in lunar settlement periodicities (Doherty and Williams 1988) and larval durations (Wellington and Victor 1989). Thus the settlement-linkage hypothesis is supported by several cases that have the most extensive data sets, while variation in spawning in one other case is inconsistent with it.

B. Adult-biology hypotheses

1. *Moonlight affects spawning or brooding ability.*—Both hypotheses predict unimodal lunar cycles, with peaks of spawning between full moon and last quarter, and several days before the full moon, respectively. Even though unimodal lunar cycles occurred in 10 of 17 species, spawning peaks were clearly centered in the period predicted by the brooding ability hypothesis in only 2 of those 10 (*M. dorsalis* and *M. bairdi*, Fig. 2). Spawning peaked during the period predicted by the dawn-spawning hypothesis in only two species (*M. chrysurus* and *S. partitus*). Even among the lunar spawners that did conform to either of these predictions, dispersion of activity over the lunar cycle was such that much spawning occurred outside the predicted periods.

2. *Oversaturation of egg predators.*—This hypothesis predicts a preponderance of low dispersion, unimodal lunar spawning cycles, that predator populations be saturable, and that the degree of synchronization increases with increasing predation pressure.

Pronounced spawning synchrony within a local population occurred in 2 of the 17 study species, *A. troschelii* and *C. multilineata*. Foster (1987a, b) developed this hypothesis to account for differences in the degree of spawning synchrony in *A. troschelii* at PP and *A. saxatilis* at CP, and showed that, as predicted, predation pressure is higher on the more highly synchronized species, *A. troschelii*. However, other data do not strongly support the application of this hypothesis to *A. troschelii*. First, we found that spawning by a local population of *A. troschelii* is substantially more dispersed over the month than Foster (1987a) observed. Second, like Foster (1987a, b), we often saw the pri-

mary egg-predator (*Thalassoma lucasanum*) attack *A. troschelii* nests at the Pearl Islands site, but did not see such predation at PP or PM, where spawning by *A. troschelii* also was strongly synchronized. Third, it seems unlikely that *T. lucasanum* populations in the Pearl Islands could be oversaturated with *Abudefduf* eggs, given (1) the density and size of those populations (>12 000 individuals/ha and 5000 individuals/reef [Warner and Hoffman 1980, Foster 1987a, b and our observations]), (2) the rate at which a school can entirely consume the contents of an *A. troschelii* nest (as few as 100 fish can do so in as little as 4 min; Foster 1987b) and (3) that a colony of 50–175 nests contains eggs for between 8 and 15 d during each spawning bout (Foster 1987a, b and our observations). Thus, even in the case for which it is potentially most relevant, the egg-predator saturation hypothesis is not strongly supported by all data.

3. *Enhanced defense.*—This hypothesis predicts the occurrence of highly synchronized colonial nesting in species that experience strong pressure from egg predators, but no particular lunar pattern of activity. In our study we observed highly synchronized colonial spawning only in *A. troschelii* (at both PP and PM), although it does occur in *A. saxatilis* and *C. multilineata* at other Caribbean sites (Myrberg et al. 1967, Cummings 1968, Albrecht 1969). Foster (1989) found that, as predicted, males in the center of a spawning colony of *A. troschelii* experience lower egg losses than males at the edges of colonies. She also related the weaker development of colonial spawning in *A. saxatilis* to low densities of egg predators and low rates of egg losses at CP. Synchronization of colonial spawning is lunar or semi-lunar cyclic in some cases (Albrecht 1969, Kingsford 1980, present results on *A. troschelii*), and sporadic (*A. troschelii* at PM), or cyclic at varying, nonlunar frequencies in others (Ochi 1986, Tyler 1988).

Synchronized colonial spawning has been observed in 10 species of damselfishes, all of them mobile, schooling planktivores (Abel 1961, Myrberg et al. 1967, Cummings 1968, Albrecht 1969, Fishelson 1970, Swerdloff 1970, Russell 1971, Sale 1971, Thresher 1984, Ochi 1986, Tyler 1988). This spawning pattern has not been recorded among 18 damselfishes in which individual adults of both sexes defend permanent feeding territories (present study and references in Table 5). Thus the occurrence of synchronized colonial spawning may be related to variation in social system structure as well as variation in egg-predation risks.

4. *The cost of care.*—There do appear to be substantial costs to paternal brood care in fishes (Unger 1983, DeMartini 1987). Feeding rates (bites per unit time) of guardian males of four of our study species are substantially reduced during brood-care periods; reductions were 72% in *C. multilineata* (a midwater feeding planktivore), 40% in *M. chrysurus* and *S. dorsopunicans*, and 24% in *S. dienaecus* (all benthic her-

bivores) (D. R. Robertson, *personal observation*). Guardian males of *O. atlanticus* also have reduced feeding rates (Cote and Hunte 1989). Since all the CP and PP species breed year round (D. R. Robertson, *personal observation*) and a nest contains eggs for a substantial percentage of the lunar month (Table 4) males of those species will experience such costs continuously throughout their reproductive lives.

Patterns of reduced egg survivorship predicted by the cost-of-care hypotheses do occur in some of our study species. Filial egg cannibalism of small, young clutches occurs in *S. dorsopunicans*, *M. chrysurus*, and *S. rectifraenum* (Petersen and Marchetti 1989, C. W. Petersen, *unpublished manuscript*). Differences occur in the mortality rates of eggs laid in different parts of the lunar spawning cycle in *O. atlanticus* (Cote and Hunte 1989), and in *M. chrysurus*, but not *S. dorsopunicans* (C. W. Petersen, *unpublished manuscript*). In the former two species, last-laid clutches suffer higher mortality.

The few data available indicate that rates of filial cannibalism and variation in parental-care costs may be positively correlated. The cost of care appears to be very low in the blenny *Exallias brevis*. This fish is highly sedentary, nests in corals on which it feeds, and both sexes spend <1% of their time feeding. As expected, this species also has a very low rate of filial egg cannibalism (<2% of clutches; Carlson 1990). On the other hand, males cannibalize as much as 28%, 21%, and 11% of their own clutches in *S. rectifraenum* (Petersen and Marchetti 1989; C. W. Petersen, *unpublished manuscript*), *S. dorsopunicans*, and *M. chrysurus*, respectively. Males of the latter two experience substantially reduced feeding (by $\approx 40\%$) while brooding.

As predicted, males of 16 of our 17 study species showed brood cycling and spent an average of 24–82% of their time with unoccupied nests each month. Brood cycling was synchronized in 15 of those and synchronized with the lunar cycle in 13 species. In one other species it was lunar cyclic at one site and sporadic at another. In one of the two unsynchronized species, individual nests experienced high-frequency brood cycles. Only one species (*O. steindachneri*) lacked brood cycles and showed continuous parental activity.

The few data available on feeding reduction indicate that the cost of care may be higher for planktivores that range widely when feeding in midwater, than for benthic species that feed and nest inside small permanent territories (see above). Thus we might expect (a) planktivores to spend less time brooding than benthic feeders, and have more highly synchronized spawning, and (b) continuous brooding to be associated with a low cost of care among benthic-feeding species. The most highly synchronized patterns of spawning do occur among the colonially spawning, mobile planktivores (see the preceding section, *Enhanced defense*).

Nests of planktivores we studied did receive fewer clutches each month and spent more time empty each month than did nests of most benthic feeders (Table 3). One continuously brooding, benthic-feeding blenny (Carlson 1990) does appear to experience very low costs of care (see above in this section). We lack data on the cost of care in *O. steindachneri*, a continuously brooding benthic herbivore.

The cost-of-care hypothesis predicts that a lunar spawning cycle should be more common among brooders than nonbrooders. To control for effects of geography, we consider only Caribbean fishes. We are unable to control fully for phylogenetic effects (cf. Felsenstein 1985), since none of the genera and families we compare contain both brooding and nonbrooding species. However, any differences among these families and genera are not due to evolutionary conservatism, since all families of brooders and nonbrooders include both species with and without lunar spawning cycles (Johannes 1978, Thresher 1984, Gladstone and Westoby 1988, this paper: Fig. 1).

While 11 Caribbean benthic-brooders (our 10 CP species, and *Chromis cyanea*; DeBoer 1981) all have lunar spawning cycles, such cycles occur much less frequently among nonbrooders that spawn pelagic eggs (5 of 22 species from eight families, Table 6, $G_{\text{adj}} = 21.01$, $P < .001$). Data assembled by Gladstone and Westoby (1988) support this distinction between pelagic spawners and benthic brooders in a broader range of families and localities. Too few data are available on nonbrooders that produce benthic eggs (see Gladstone and Westoby 1988) to involve them in a quantitative comparison at this time.

DISCUSSION

Hatchling-biology hypotheses

If larvae of different damselfishes and blennies have essentially the same capabilities and requirements for dispersal immediately after hatching, then the hatchling-dispersal hypotheses cannot account for much of the variation in lunar spawning patterns of the damselfishes and blennies. Each prediction of the tidal-control hypothesis is supported in a minority of cases among our study species. We examined eight lunar cyclic species from CP and PP against several predictions from that hypothesis; four failed to conform to any prediction, while four others conformed to some predictions but not others. The tidal control hypotheses appear to be relevant to one extreme situation, since lunar spawning patterns are consistently as predicted in intertidal habitats in which tidally mediated entrapment of hatchlings can occur.

As with the tidal-control hypothesis, the spawning patterns of only a small minority (3 of 17) of our study species conformed to predictions from the moonlight-control hypothesis. At present there is no reason to suspect that any of our study species that conform to

TABLE 6. Lunar patterns of spawning by Caribbean reef fishes that produce pelagic eggs and lack parental care.

Species	Spawning periodicity	Site	Source
Malacanthidae			
<i>Malacanthus plumieri</i>	acyclic, daily	Belize	1
Haemulidae			
<i>Haemulon flavolineatum</i>	weekly	St. Croix	2†
Serranidae			
<i>Hypoplectrus guttavarius</i>	daily (acyclic?)	St. Croix	3
<i>H. nigricans</i>	daily (acyclic?)	Panama	4
<i>Serranus tortugarum</i>	daily (acyclic?)	Panama	4
<i>S. baldwini</i>	daily (acyclic?)	Panama	4
<i>Epinephelus striatus</i>	lunar	Cayman Is.	5
<i>E. guttatus</i>	lunar	Puerto Rico	5
Lutjanidae			
<i>Lutjanus griseus</i>	lunar	Florida	6
<i>L. synagris</i>	lunar	Cuba	7
Pomacanthidae			
<i>Centropyge argii</i>	daily (acyclic?)	Curaçao	15, 16
Scaridae			
<i>Sparisoma rubripinne</i>	daily (acyclic?)	Virgin Is.	8
<i>S. aurofrenatum</i>	acyclic	Puerto Rico	17
<i>Scarus iserti</i>	daily (acyclic)	Panama	9
Labridae			
<i>Thalassoma bifasciatum</i>	daily (acyclic?)	Panama	10, 11
	weak semilunar (?)	Virgin Is.	8
<i>Halichoeres bivittatus</i>	acyclic	Curaçao	12
<i>H. garnoti</i>	acyclic	Curaçao	12
<i>Lachnolaimus maximus</i>	daily (acyclic?)	Puerto Rico	17
<i>Bodianus rufus</i>	daily (acyclic?)	Panama	13
<i>Xyrichtys martinicensis</i>	daily (acyclic?)	Panama	14
Acanthuridae			
<i>Acanthurus bahianus</i>	daily (acyclic?)	Puerto Rico	17
<i>A. coeruleus</i>	lunar	Puerto Rico	17

* Sources: 1. Baird 1988; 2. McFarland et al. 1987; 3. Lobel and Neudecker 1985; 4. E. Fischer, *personal communication* 1988; 5. Colin et al. 1987; 6. Starck 1971; 7. Reschetnikov and Claro 1976; 8. Randall and Randall 1963; 9. K. Clifton, *personal communication* 1987; 10. Warner and Hoffman 1980; 11. R. R. Warner, *personal communication* 1988; 12. Roede 1972; 13. Hoffman 1983; 14. Victor 1987; 15. Bauer and Bauer 1981; 16. Moyer et al. 1983; 17. Colin and Clavijo 1988.

† Spawning pattern was obtained by back-calculation from ages of settling larvae, not by direct observation.

a particular prediction from either hatchling-dispersal hypothesis have characteristics that make them more likely to be influenced by the relevant factor. In order for the hatchling-dispersal hypotheses to be able to explain the variation we observed there would have to be substantial interspecific variation in the ecology of hatchlings. Differences in size-dependent swimming ability of hatchlings seem unlikely to be important. The two *Stegastes* spp. with egg volumes at the extremes of the range among our study species have hatchlings that do not differ greatly in total length (≈ 2.1 mm for *S. partitus* and ≈ 2.6 mm for *S. leucostictus*, D. R. Robertson, *personal observation*). Such size differences seem unlikely to affect dispersal ability on the spatial scale on which tidal effects operate. Gladstone and Westoby (1988) invoked variation in predation risks on hatchlings that results from variation in hatchling toxicity to account for interspecific variation in lunar spawning patterns. It seems doubtful that this explanation could account for the variation among our

study species, particularly differences among congeners. Damselfishes and blennies are not known for any toxicity (Halstead 1978), although some blennies do have poisonous fangs (Losey 1972).

Variation in lunar spawning patterns also is largely inconsistent with the three other hatchling-biology hypotheses. Even among the cyclic species hatching activity is too broadly dispersed over the lunar cycle and insufficiently synchronized in most cases for hatchling-release patterns potentially to have much influence on either (a) saturation of hatchling-predators, (b) reducing food competition between cohorts of young larvae, or (c) to represent tracking of lunar-periodic variation in a common food supply.

We conclude that, if current parsimonious assumptions concerning the ecological similarity of hatchlings are correct, the hatchling-biology hypotheses do not help explain either the presence or absence of lunar spawning cycles in our different study species, or variation in the timing of spawning peaks of cyclic species.

Settlement-linkage hypothesis

Relationships between patterns of variation in age at settlement, and spawning and settlement periodicities in several species support the settlement linkage hypothesis. The combination of a fixed lunar settlement cycle and a variable lunar spawning pattern in one other species is inconsistent with it. Intraspecific geographic variation in spawning or settlement patterns, and in the length of the larval life, can be accommodated by this hypothesis. Stronger tests of the settlement-linkage hypothesis should be possible once data are available on the extent of intraspecific geographic variation in spawning and settlement patterns and larval durations.

Adult-biology hypotheses

Hypotheses that predict peaks of spawning or brooding during specific parts of the lunar cycle because of effects of moonlight on adult capabilities are poorly supported by the data. As with many of the hatchling-biology hypotheses, a few species fit the predicted pattern. However, there is no reason to suspect that those are more strongly affected by the hypothesized factor, and the number of species that fit appears to be no greater than if spawning peaks are randomly distributed over the lunar month.

The egg-predator oversaturation hypothesis appears to have little generality. It is relevant to the few instances of extreme synchronization of activity in a local population, and is not well supported by all of the available data from one highly synchronized species.

Two adult-biology hypotheses that propose intrinsic advantages to population synchronization of spawning are more successful than the hatchling-biology or other adult-biology hypotheses in accommodating the observed variation in spawning patterns. The enhanced-defense hypothesis for synchronized colonial spawning is supported by data on variation in predation rates on nests under different social conditions, and by correlations between interspecific variation in the development of this spawning pattern and in pressure from egg predators.

Predictions of the cost-of-care hypothesis are supported in most cases. Lunar spawning cycles are more common among brooders than nonbrooders. Brooding does carry a cost that may be substantial and may result in increased egg mortality. Lunar synchronized concentration of spawning, which could increase the benefit/cost ratio for broodcare, occurs in 14 of our 17 study species. In 16 species individual males experience frequently recurring nonbrooding periods during which they can, presumably, restore condition that is lost due to the cost of care. In 15 species such brood cycling is synchronized within a population, either sporadically or cyclically at lunar, semilunar, and higher frequencies.

Different patterns of brood cycling and degrees of

spawning synchronization might represent different solutions to the same problem. They may also represent predictable graded responses to variation in the intensity of the problem. Population cycles may arise when brooding activity in individual nests cannot be effectively predicted and controlled by individual females in an unsynchronized population. In at least one case, a lack of brood cycling does appear to be associated with a low cost of care. Data are lacking to show whether a similar situation obtains in the one continuous brooder among our study species.

Lunar cycles of reproduction may represent the most common response to adult-biology problems that can be alleviated by reproductive synchronization, because they are the most effective means available for most species. The lunar cycle provides the strongest, most predictable set of environmental cues available to all individuals of all species. The timing of higher frequency reproductive cycles, on the other hand, must be controlled by social cues or short-term changes in ecological factors, and daily vagaries in the physiology of individuals are more likely to lead to imprecision in high-frequency cycles than in lunar cycles. The ability to synchronize activity independently of lunar cues is likely to be controlled in part by social system structure. The greater variability in the degree of synchronization of spawning with the lunar cycle among schooling species as opposed to solitary territorial species may be due in part to such social constraints.

Some other patterns of variation in spawning also may be due to the action of adult-biology constraints. Synchronized colonial spawning may be restricted to mobile schooling planktivores because they have the social potential for such behavior; this potential is lacking in benthic-feeding species that are solitary and territorial. Weather conditions (Kingsford 1980) or unpredictable temporal variation in food supply may influence the synchronization and regularity of spawning. Considerable intraspecific variation has been observed among planktivorous damselfishes in the extent and temporal patterning of spawning synchronization (this study, Myrberg et al. 1967, Cummings 1968, Albrecht 1969, Ochi 1986, Foster 1987a, Tyler 1988). Similar variability has not been recorded among territorial damselfishes that feed primarily on benthic algae (this study, references in Table 5, and Gladstone and Westoby 1988). This could reflect greater short-term variation in the supply of plankton than in the supply of benthic algae.

The hatchling-biology hypotheses appear less able than adult-biology hypotheses to explain much of the variation in lunar spawning patterns of paternal-brooding reef fishes. Adult-biology factors may be responsible for most spawning patterns. However, the adult-biology hypotheses incorporate known substantial interspecific variation in the ecology and behavior of adult damselfishes and blennies. Since much less is known about the biology of hatchlings and we have

assumed great interspecific similarity in their requirements, the hatchling-biology hypotheses may fail because they are oversimplified. To some extent, greater conformity to the adult-biology hypotheses is to be expected simply because they make less restrictive predictions about the types and timing of lunar spawning cycles than do the hatchling-biology hypotheses. It is clear that we need to know much more about the ecology of all life history stages of these fishes if we are adequately to test and determine the generality of each of the great variety of hypotheses proposed to explain their lunar patterns of reproduction.

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