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Ecology, Vol. 75, No. 8. (Dec., 1994), pp. 2185-2203.

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PLASTICITY, CONSTRAINT, AND OPTIMALITY IN REPRODUCTIVE TIMING¹

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Abstract. Synchronous release of gametes or larvae by marine animals may be controlled by as many as four environmental cycles thereby enabling an array of reproductive timing patterns. Cohesive scenarios that account for the diversity of reproductive patterns are rare and tests of their adaptive significance have been even rarer. By exploiting plasticity in the timing of larval release, we isolated proximate factors regulating reproductive synchrony and provided evidence that predation ultimately may best explain the diversity of hatching patterns by brachyuran crabs. Tides entrain reproductive rhythms by many crabs, and therefore spatial and temporal variation in tides produces intraspecific variation in reproductive patterns. This was demonstrated by determining the timing of larval release of the same or sibling species of intertidal crabs in Pacific semidiurnal and Caribbean mixed semidiurnal tidal regimes on the two coasts of the Republic of Panama. The time of larval release varied during the year in the Caribbean, where entraining physical cycles exhibited complicated changes in phase, but not along the Pacific coast, where the phase relationships among physical cycles varied little year-round. Crabs timed larval release relative to the light–dark, tidal phase, and tidal amplitude cycles, but not the lunar cycle, suggesting that three rhythms determined when larvae were released. For each species we ranked these rhythms by the degree to which larval release kept phase with their entraining physical cycles. The species-specific hierarchies of rhythms we observed match those expected if the time of larval release minimizes predation on females, embryos, and newly hatched larvae. Such hierarchies enable crabs to track phase shifts of cycles in variable tidal environments and may enhance reproductive success across tidal regimes. However, larval release may be timed better in some tidal regimes than others due to differences in the phasing of environmental cycles. In some tidal regimes, larval release cannot be synchronized with all three physical cycles during the year, and hierarchies of rhythms may determine the timing and duration of breeding.

Key words: hatching rhythms; larval release; plasticity; predation; tides.

INTRODUCTION

Phenotypic plasticity is common among plants and animals and may be exploited to investigate the evolution of life history traits (Bradshaw 1965, Stearns 1989, Lessels 1991). Variation in traits may be correlated with environmental variables, thereby suggesting causes for their evolution (Endler 1986). However, environmental variables often covary leading to many possibilities. The number of possible explanations for the adaptive value of traits may be reduced by studying the trait when or where correlations between environmental variables are decoupled. Close correlations between the expression of plastic traits, their relative performance, and environmental variables will suggest the most likely cause of selection for the trait. For example, this approach has been used to identify causes of cycломorphosis in *Daphnia* (Dodson 1989) and variation in oviposition site by butterflies (Rauscher 1978). Phe-

notypic plasticity also may be used to identify proximate and ultimate causes of reproductive synchrony by marine animals.

Many marine animals may synchronize the release of gametes or larvae with respect to the light–dark, tidal, tidal amplitude, or lunar cycles. The tidal cycle refers to the semidaily or daily cycle of high and low tides, whereas the tidal amplitude cycle is the biweekly (i.e., every 2 wk) cycle of daily differences between the height of high and low tides that is usually synonymous with the spring–neap cycle. A famous example of synchronous reproduction is the California grunion, *Leuristhes tenuis*, that invades beaches on new and full moons to spawn eggs at the high tide line (Clark 1925). Larvae hatch 2 wk later on nocturnal maximum amplitude high tides. Other intertidal spawning fishes, coral reef fishes, and crabs also spawn eggs or hatch larvae on nocturnal maximum amplitude high tides near new and full moons (Johannes 1978, Forward 1987). Despite the prevalence of this timing pattern, proximate and ultimate causes for it are not entirely clear. It generally remains uncertain whether biweekly hatching patterns are cued by fluctuations in moonlight or tidal amplitude, because lunar and tidal amplitude cycles

¹ Manuscript received 5 May 1993; revised 11 March 1994; accepted 5 April 1994.

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are correlated throughout most of the world (Barnwell 1976). Furthermore, predation often is hypothesized to be the ultimate cause of reproductive synchrony by marine animals (Johannes 1978, Frank and Leggett 1982, Morgan 1987), but supporting evidence is limited.

Plasticity in the timing of spawning and larval release can be used to help resolve these questions. Four tidal regimes exist worldwide and each exhibits different phase relationships between tidal, tidal amplitude, light-dark, and lunar cycles (Barnwell 1976). Consequently the timing of reproduction, which is cued by these environmental cycles, also must differ across tidal environments. Furthermore, temporal changes in reproductive timing also are expected in some tidal regimes but not others. They are not expected in semidiurnal tidal regimes (two high tides and low tides per day) because the phasing of the four physical cycles that entrain reproductive rhythms and, hence, the timing of reproductive events, exhibits regular periods year-round. In contrast, in diurnal (one high and low tide per day) and mixed semidiurnal (usually two, but sometimes one, high and low tides per day) and mixed diurnal (usually one, but sometimes two high and low tides per day) tidal regimes, the tidal and tidal amplitude cycles shift during the year relative to the light-dark and lunar cycles and should induce temporal variation in the timing of reproduction. However, plasticity in the timing of reproduction and its effects on reproductive performance are poorly known, because most studies of reproductive timing have been conducted in semidiurnal tidal environments that prevail worldwide.

We studied plasticity in reproductive timing to identify proximate and ultimate causes of the timing of larval release by intertidal brachyuran crabs. The timing of larval release by the same or sibling species of crabs that live in semidiurnal and mixed semidiurnal tidal environments was determined to document plasticity in this trait, the mechanisms that give rise to it, and the probable effects of variation in reproductive timing on reproductive success. We chose to study intertidal crabs because reproductive patterns of this group and their underlying mechanisms are relatively well known.

Female crabs attach fertilized eggs to their abdominal appendages where they are held until they hatch. Females of intertidal species typically incubate their eggs in burrows or crevices and emerge only to release larvae (Christy 1978, 1982, Saigusa 1982, Salmon 1987). The timing of larval release is controlled by endogenous clocks with free-running periods that approximate the periods of environmental cycles to which they are entrained. Circadian (solar day) rhythms, entrained by the light-dark cycle, and circatidal (lunar day) rhythms, entrained by cues associated with tidal phase, have been demonstrated for several species (see DeCoursey 1983, Forward 1987 for reviews). There

also is some evidence of circasemilunar (biweekly) rhythms that may be entrained either by moonlight (Saigusa 1988) or by cues associated with the tidal amplitude cycle; however, entrainment of hatching by the tidal amplitude cycle has not yet been demonstrated for crabs. Thus, crabs have circadian, circatidal, and circasemilunar oscillators that enable timing of larval release by as many as four environmental cycles.

With few exceptions (Christy 1978; S. G. Morgan, *unpublished manuscript*) the timing of larval release by intertidal crabs has been studied on coasts with semidiurnal tides and has been found to vary little. In this tidal environment, most species release larvae at night near the time of high tide on the days of the lunar month with the largest amplitude nocturnal tides, which usually occur just after the full and new moons (DeCoursey 1983, Forward 1987). As a consequence, newly hatched larvae may be swept rapidly by ebb currents at night away from shallow waters where planktivorous fishes abound (Christy and Stancyk 1982, Morgan 1987, 1990). Recent interspecific comparative (Morgan and Christy 1994) and experimental studies (S. G. Morgan and J. H. Christy, *unpublished manuscript*) show that predation on newly hatched larvae by diurnal planktivorous fishes partly explains the timing of larval release by intertidal crabs. Predation on embryos and females also may ultimately determine the timing of larval release because females remain near burrows and other refuges to release larvae (Morgan and Christy 1994).

Because the timing of larval release appears to be critical for reproductive success, plasticity is expected on coasts where the phase relationships among environmental cycles that entrain hatching change throughout the year. A hierarchical arrangement of endogenous rhythms is one way crabs might track these complex changes. The degree of synchrony of larval release relative to each entraining environmental cycle would indicate the relative importance or rank of each cycle and its associated rhythm in timing this event. For example, if the largest amplitude tides during the lunar month occurred during the day and crabs released larvae at dusk during ebb tide, then the circadian rhythm would be more important than the circatidal or circasemilunar rhythms to the timing of larval release. Hence, plasticity in the timing of larval release may result from the interaction of genetically proscribed rankings of environmental cues with endogenous timers. The main advantage in this timing system is the flexibility it allows in timing larval release across tidal environments. Without such a mechanism, each population must adapt genetically to local tides (Neumann 1986).

Rankings of rhythms likely result from the effects of selective pressures on life history traits; species that share pertinent life history traits and experience similar selective pressures may have similar rankings of rhythms. If planktivorous fishes determine the timing

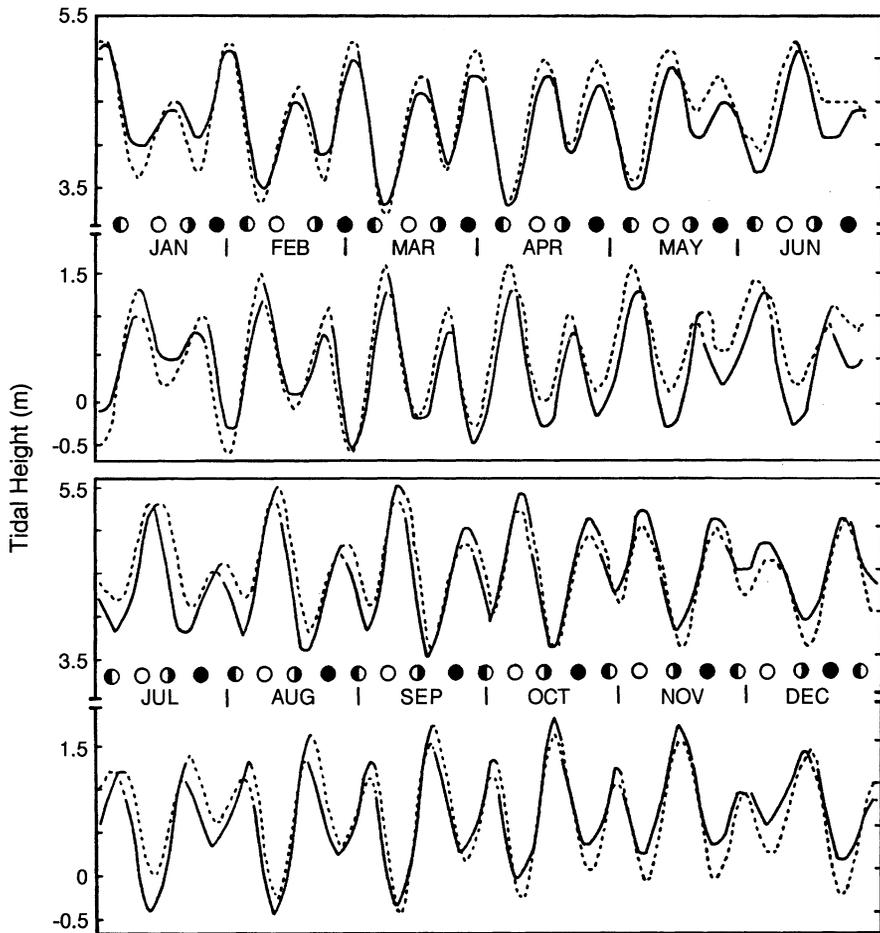


FIG. 1. Daily nocturnal (—) and diurnal (---) predicted high (upper lines) and low (lower lines) tides relative to lunar phase (○ and ● = full and new moons, respectively; ◐, ◑ = quarter moons) at Balboa, which is located on the Pacific coast of Panama, during 1987.

of larval release, then species that hatch conspicuous larvae may hatch only at night, whereas species with inconspicuous larvae may sometimes hatch during the daytime (Morgan and Christy 1994). Therefore, the circadian rhythm may exert greater control over the timing of larval release by species that hatch conspicuous larvae than for those that hatch inconspicuous larvae. If ovigerous females release larvae from refuges to avoid predatory fishes, then all intertidal crabs should release larvae on high tides following inundation. Furthermore, species that live high on the shore should release larvae only on maximum amplitude high tides, but those living low on the shore may or may not release larvae at this time depending on the vulnerability of larvae to fishes (Morgan and Christy 1994). Releasing larvae on maximum amplitude tides may rapidly transport larvae from shorelines as well as enable females to release larvae near refuges. Therefore, larvae that are released low in the intertidal zone and are not especially vulnerable to fishes may hatch on high tides of any amplitude.

Two conditions must be satisfied to demonstrate hierarchical arrangements of rhythms regulating larval release: (1) phase relationships among entraining environmental cycles must vary and (2) larval release must be observed for several cycles until organisms clearly are tracking some cycles over others. We have satisfied both conditions by examining larval release repeatedly in a semidiurnal tidal regime on the Pacific coast of Panama, and in a mixed semidiurnal tidal regime along the Caribbean coast. On the Pacific coast, simple, large amplitude tides with a maximum amplitude of 6.2 m inundate and expose the intertidal zone twice each day. The phase relationship between the tides and the light-dark cycle varies with a predictable semilunar period throughout the year (Fig. 1). For example, large amplitude tides peak at dusk just after full and new moons year-round. The only change in the tidal pattern is from a nonseasonal reversing asymmetry in maximum tidal amplitude relative to the lunar phase (Fig. 1). In the mixed semidiurnal tidal environment on the Caribbean coast, tidal patterns are

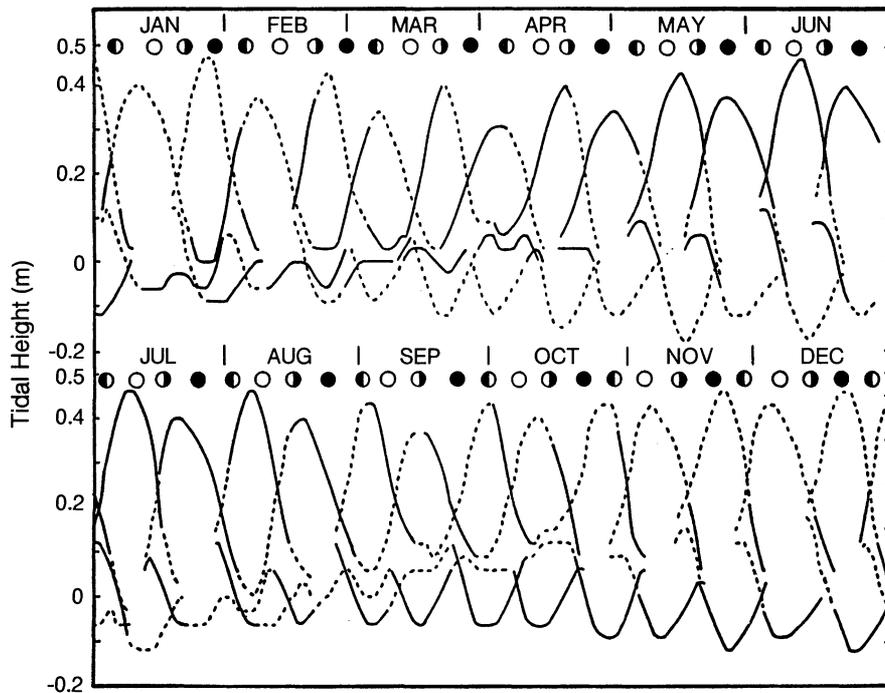


FIG. 2. Daily nocturnal (—) and diurnal (---) predicted high (upper lines) and low (lower lines) tides relative to lunar phase (○ and ● = full and new moons, respectively; ◐, ◑ = quarter moons) at Colon, which is located on the Caribbean coast of Panama, during 1987.

complex (Fig. 2). During some months, maximum amplitude tides coincide with new and full moons, during other months they are in phase with quarter moons. When semidiurnal tides prevail, either daytime or nighttime tides may be higher depending on the declination of the moon relative to the equator. During periods with diurnal tides, high tides may occur only during the day or the night.

We selected study animals based on several criteria: (1) crabs had to live on both coasts of Panama, (2) species had to be closely related, and (3) either the vertical zonation of adults on the shoreline or the potential vulnerabilities of newly hatched larvae had to differ. Species pairs should be closely related to ensure that similar proximate and ultimate factors shape the timing of larval release and to demonstrate spatial plasticity in hatching rhythms. Zonation of adults and larval vulnerabilities should differ among species pairs to determine whether or not various hierarchies of rhythms result from differing vulnerabilities to predators. *Pachygrapsus transversus* (Grapsidae) occurs on both coasts.

Cataleptodius taboganus (Xanthidae) and *Uca galapagensis* (Ocypodidae) live on the Pacific coast and were paired with their Caribbean relatives *Cataleptodius floridanus* and *Uca rapax*. These species pairs are believed to be close relatives based on morphological traits of adults (Rathbun 1918, 1930, Crane 1975) and because the Panama land bridge last isolated populations of these species $\approx 3.1\text{--}3.5 \times 10^6$ yr ago (Keigwin 1982). *Pachygrapsus* releases inconspicuous larvae from the midintertidal zone; *Cataleptodius* releases conspicuous larvae from the lower shore; and *Uca* releases conspicuous larvae from the high intertidal zone.

If predation influences the timing of larval release, then we predict the following. First, the tidal amplitude cycle rather than the lunar cycle likely synchronizes biweekly hatching patterns for all three pairs of species, because tides sweep larvae from shorelines or because intertidal crabs may release larvae near refuges following inundation. Second, tidal amplitude rhythms should

TABLE 1. Relative importance of environmental cycles entraining hatching rhythms of intertidal crabs from Panama as predicted if predation regulates the timing of larval release. Low numbers indicate cycles that may be more important.

<i>Pachygrapsus</i>	<i>Cataleptodius</i>	<i>Uca</i>
1. Tidal amplitude	1. Light-dark	1. Light-dark
2. Tidal	2. Tidal	1. Tidal amplitude
3. Light-dark	2. Tidal amplitude	2. Tidal
4. Lunar	3. Lunar	3. Lunar

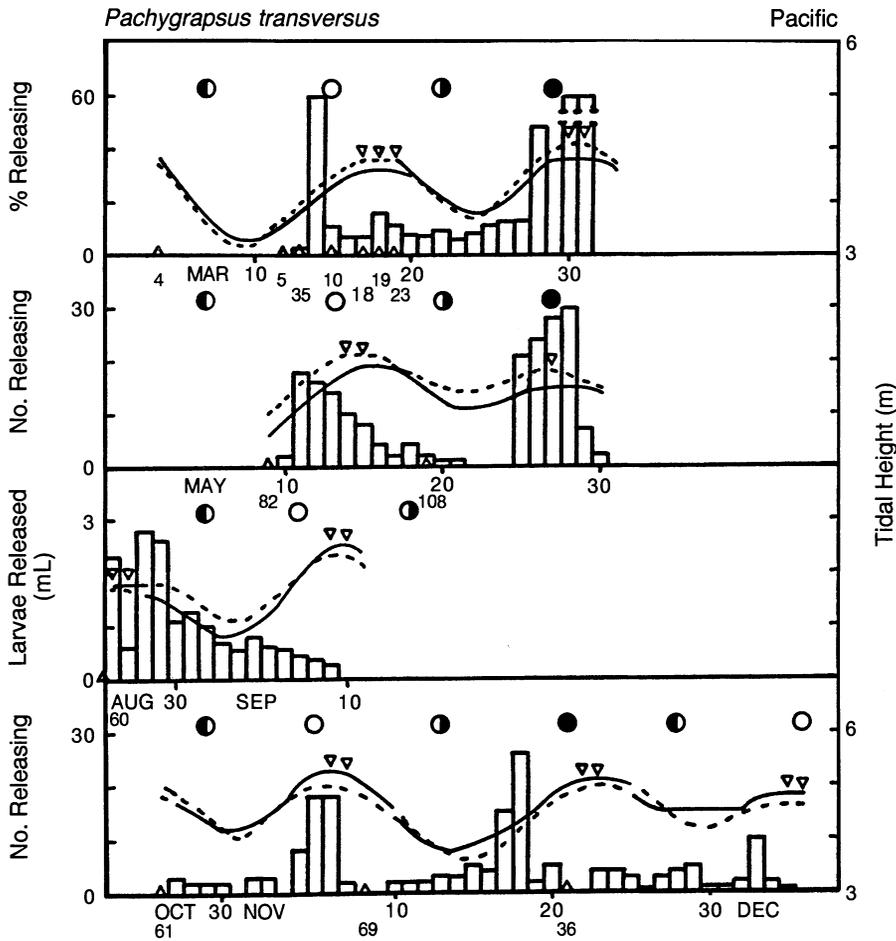


FIG. 3. Larval release by *Pachygrapsus transversus* on the Pacific coast relative to lunar and tidal amplitude cycles during 1987. The number of females releasing larvae, percentage of females releasing larvae, or volume of larvae hatched were measured depending upon the time of year. Daily nocturnal and diurnal high tides are indicated by — and ---, respectively. ▽ represent maximum amplitude tides. The date and number of females collected are indicated by Δ and associated numbers.

exert more influence on the timing of larval release for species that live in the middle and upper intertidal zone than for those that live low on the shoreline. Crabs that live higher on the shore could only release larvae from their refuges on maximum amplitude tides (*Uca*, *Pachygrapsus*), whereas those species living low on the shore would be inundated daily by high tides (*Cataleptodius*). Third, all three pairs of species should synchronize larval release with high tides so that larvae may be released near refuges and transported from shorelines. Fourth, circadian rhythms should exert less influence on the timing of larval release for species that hatch comparatively inconspicuous larvae (*Pachygrapsus*) than for those species with larvae that are highly visible to planktivorous fishes (*Uca*, *Cataleptodius*). Fifth, species that hatch conspicuous larvae along the Caribbean coast of Panama (*Uca*, *Cataleptodius*) may not reproduce during months lacking nocturnal high tides (December and January), whereas spe-

cies that hatch inconspicuous larvae may do so (*Pachygrapsus*).

If predation ultimately regulates the timing of larval release, then the relative importance of environmental cycles entraining hatching rhythms are as predicted in Table 1. Tidal amplitude and tidal cycles may be most important in regulating the timing of larval release by *Pachygrapsus* because only maximum amplitude high tides inundate refuges of most crabs. The tidal amplitude cycle may exert greater influence than the tidal cycle because most crabs only will be immersed on days when maximum amplitude tides occur. Larvae of this crab may hatch during the daytime and nighttime because they are less visible to fishes than are larvae of the other two species; hence, the light-dark cycle may be less important than tidal amplitude and tidal cycles. Conspicuous larvae of *Cataleptodius* may hatch only at night when burrows are inundated so that light-dark and tidal cycles both may be important.

TABLE 2. Timing of larval release (± 1 SD) relative to lunar, tidal amplitude, tidal, and light-dark cycles of three pairs of closely related species of crabs from the Pacific and Caribbean coasts of the Republic of Panama. Timing of larval release was determined several times throughout reproductive seasons. These data were combined prior to analysis for hatching relative to light-dark and tidal cycles but were not combined for hatching relative to tidal amplitude and lunar cycles. The range of larval release times by Caribbean species relative to light-dark and tidal cycles is reported parenthetically to emphasize the variability in timing due to seasonal shifts in phasing of environmental cycles. All values of Rayleigh's r

Cycle	Pacific Ocean				Caribbean
	Timing	SD	r	n	Timing
		<i>Pachygrapsus transversus</i>			<i>Pachygrapsus transversus</i>
Lunar	2 d < O < 5 d	2.3–3.4 d	0.6213–0.7457	114–194	6 d < O < 1 d
Tidal amplitude	2 d < MAT < 2 d	2.3–3.4 d	0.6213–0.8582	51–166	2 d < MAT \leq 1 d
Tidal	HT	38 min	0.8848	134	HT (90 min < HT < 60 min)
Light-dark	0600 and 1800	69 min	0.8350	134	1900 (1530–2200)
		<i>Cataleptodius taboganus</i>			<i>Cataleptodius floridanus</i>
Lunar	O < 4 d	1 d	0.9116	172	4 d < O < 2 d
Tidal amplitude	MAT \leq 1 d	1.7 d	0.7839	172	MAT \leq 2 d
Tidal	HT < 30 min	48 min	0.8414	30	HT < 90 min (4 h < HT < 3 h)
Light-dark	1830 h	33 min	0.9898	30	1900 (1830–1930)
		<i>Uca galapagensis</i>			<i>Uca rapax</i>
Lunar	O < 1 d	1.1 d	0.9738	234	2 d < O < 2 d
Tidal amplitude	MAT	0.6 d	0.9903	234	MAT
Tidal	HT < 30 min	13 min	0.9318	137	HT < 3 h (HT < 2.5, 3 h)
Light-dark	0400	15 min	0.9979	137	2200 (1900 and 2300)

Releasing larvae on maximum amplitude tides will enhance transport of these vulnerable larvae from shorelines, but *Cataleptodius* may not be as tightly constrained to release larvae at this time as are the other two species, which may release larvae from refuges only during these tides. *Uca* larvae are more conspicuous and adults live higher in the intertidal zone than *Pachygrapsus* so that light-dark, tidal amplitude, and tidal cycles all may be important in regulating larval release. However, the tidal cycle may be less important than the tidal amplitude cycle because refuges only will be immersed on maximum amplitude tides.

MATERIALS AND METHODS

Field sites and collections

Pacific field sites were located in the rocky intertidal zone on the east side of Naos Island, an intertidal mud flat with a rock bank near Rodman Naval Station, and the upper reaches of tidal creeks in a mangrove forest at Diablo Heights. All sites are within ≈ 2.5 km of the Pacific entrance of the Panama Canal. Caribbean sites were reef flats and mangroves near Fort Sherman to the west, and Galeta Naval Station to the east of the Caribbean entrance to the Panama Canal.

Ovigerous *P. transversus* were collected at night with the aid of a flashlight at Naos Island and Fort Sherman. Gravid *C. taboganus* were collected at Naos Island by turning over stones during daytime low tides and *C.*

floridanus were collected from beneath coral rubble while snorkeling near Fort Sherman. Ovigerous *Uca* were dug from burrows during daytime low tides at Diablo and Galeta. A few *U. vocator* were accidentally collected initially with *U. rapax*. However, peaks of larval release were unimodal, suggesting that larvae of these two species hatch at the same time.

The timing of larval release by *C. taboganus* was determined during December 1983 and January, February, May, and October 1984 and has been reported in full (Christy 1986). Here we have analyzed these data using new methods that permit direct comparison to the other species. Larval release by *C. floridanus* and *P. transversus* was determined 4 times during 1987. Hatching by *Uca* was monitored only twice in the Caribbean and 3 times in the Pacific in 1987 because neither species reproduced year-round.

Larval release relative to lunar and tidal amplitude cycles

Ovigerous females were kept individually in the compartments ($4.5 \times 4 \times 4$ cm) of plastic trays with seawater until their embryos hatched. Trays with Pacific crabs were floated in flow-through seawater tables under a translucent roof in an outdoor pavilion at Naos Island. Trays with Caribbean crabs were shaded with fabric and floated in a rack in a lagoon near the Galeta site. Thus, females incubated their embryos at ambient

were highly significant except for larval release by *Cataleptodius floridanus* relative to lunar and tidal amplitude cycles in April. ○ = new and full moons, ◐ = quarter moons, MAT = maximum amplitude tides, HT = high slack tide, dawn = 0600 and dusk = 1830.

Caribbean		
SD	<i>r</i>	<i>n</i>
<i>Pachygrapsus transversus</i>		
2.1–4.1 d	0.2267–0.6820	72–201
1.5–2.5 d	0.5456–0.7903	54–110
72 min	0.8206	240
(56–78 min)	(0.7926–0.8859)	(60)
167 min	0.7672	240
(61–142 min)	(0.8254–0.9657)	(60)
<i>Cataleptodius floridanus</i>		
1.6–2.7 d	0.5167–0.8041	43–117
0.6–2.7 d	0.4908–0.9626	39–95
127 min	0.7078	188
(32–115 min)	(0.7536–0.9778)	(41–60)
42 min	0.9836	188
(9–46 min)	(0.9798–0.9991)	(41–60)
<i>Uca rapax</i>		
1.4–1.7 d	0.7789–0.8460	33–52
1.4–1.5 d	0.8005–0.8253	33–52
37 min	0.9492	128
(26–39 min)	(0.9438–0.9754)	(43–85)
120 min	0.8670	128
(51, 67 min)	(0.9581, 0.9747)	(43–85)

seawater and light conditions. Each day the number of females that released larvae was counted. As shown by previous studies (Christy 1982, 1986, Christy and Stancyk 1982), these methods allow accurate estimates of daily variation in the number of crabs that release larvae in the field.

We used these daily counts to measure the magnitude of larval release when we collected many ovigerous females on a single day. Ovigerous females were held until all crabs released larvae and then more ovigerous females were collected from the field \approx 7–10 d later. We usually collected 50–100 crabs each time. When ovigerous females were difficult to find, we collected them over several days and calculated the daily percentages of females that released larvae. Finally, when ovigerous females were very rare, we measured the volume (in millilitres) of larvae that were hatched each day using the method described below. Data were analyzed separately when different measures of larval release were recorded.

Larval release relative to tidal and light–dark cycles

The timing of larval release relative to the tidal and light–dark cycles was determined in the field at the Rodman and Naos sites for Pacific populations of *P. transversus* and *C. taboganus*, respectively, and at Fort Sherman for all Caribbean crabs. Approximately 40–60 ovigerous *P. transversus* and *C. floridanus* were

placed with flat rocks inside a fiberglass-coated wooden box (92 × 20 × 16 cm inner dimensions) that was anchored in the intertidal zone. The box had a removable clear plexiglass top. The top and walls of the box had holes that were screened with 153- μ m mesh Nitex cloth. The two species were separated by a vertical partition that divided the box. Two pump hoses were attached to the ends of the box. The other ends of the hoses were coupled alternately to a manual diaphragm pump (4 L per stroke) that was located above the water line. The pump discharged into a 10-cm diameter plankton net (153- μ m mesh). Larvae released by females in the box were collected by pumping (50–60 strokes) enough seawater through the screened openings to replace at least 3.5 times the volume of seawater in the box and hose. Collections were made every 30 min beginning when the hoses were covered and ending when they were exposed by tides. Larvae were preserved in 5% buffered formaldehyde solution and the amount of larvae released during each 30-min interval was measured volumetrically in graduated test tubes. The timing of larval release by Pacific *P. transversus* and *C. taboganus* was determined by the same method, except each species was monitored at different times. The timing of larval release by *U. rapax* also was determined the same way, except a larger (100 × 50 × 40 cm), bottomless box that was buried 24 cm in the sediment was used. Ovigerous females occupied 20 cm deep burrows that were made with a coring device.

This method could not be used to determine the timing of larval release by *U. galapagensis*, which lives in the upper reaches of tidal creeks and is immersed by very little water even on the highest tides. Instead, ovigerous females were placed in compartmented trays that were placed in a rack and anchored to the creek bed. Screened holes in the bottom of each compartment allowed water to flow in and out of the trays. At 30-min intervals the trays were raised briefly to the surface (<70 cm) and the number of crabs that released larvae was counted. During the day, crabs were kept in seawater tables at Naos Island to prevent crabs from overheating because a preliminary study revealed that this species released larvae only at night.

Data analysis

Rayleigh's test (Batschelet 1981) was used to detect peaks in timing of larval release relative to the four environmental cycles. This test is appropriate for analysis of biological rhythms when periods of cycles are predetermined. The test compared the magnitude of the *r* statistic, a measure of the temporal concentration of release times (range: 0 to 1), to that expected if crabs released larvae uniformly during a given physical cycle. If the *r* statistic was significantly large, then the mean angle and angular deviation of the distribution identified the peak time and dispersion of larval release

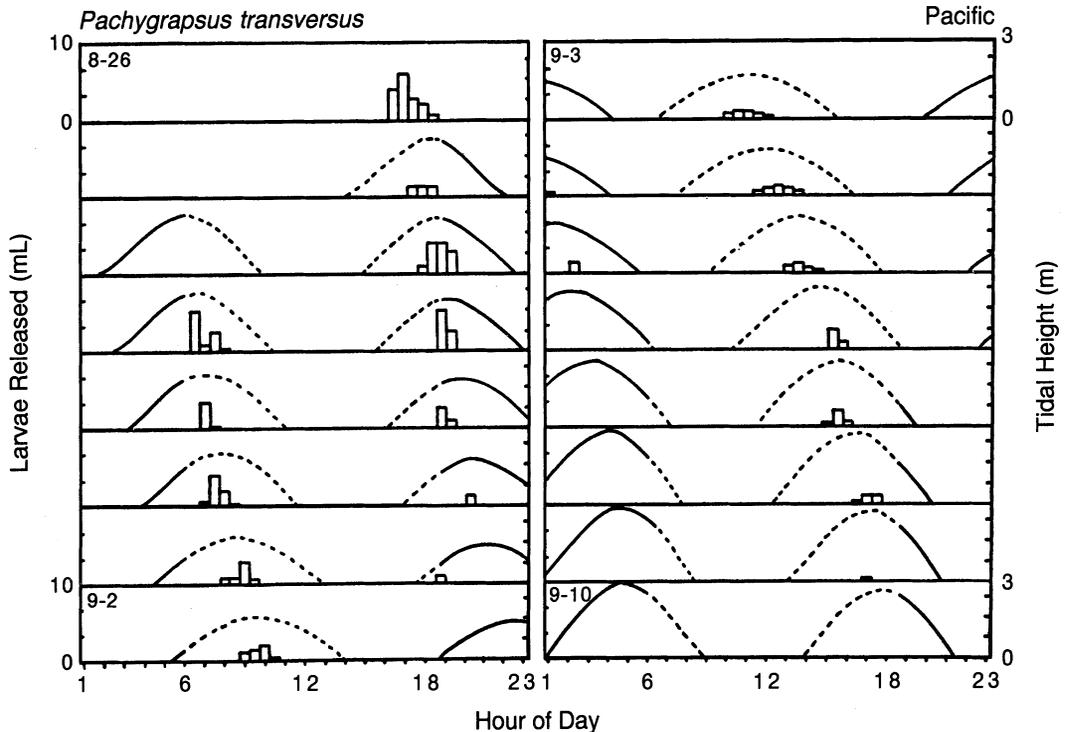


FIG. 4. Volume of larvae released by *Pachygrapsus transversus* on the Pacific coast relative to light-dark and tidal cycles from 26 August to 10 September 1987. Morning and afternoon tides were equal on 26 August; morning tides increased until they were 40 cm higher than afternoon tides by 1 September and then decreased until the two tides were similar by 9 September. Nocturnal and diurnal portions of high tides are indicated by — and ---, respectively. Tides were not measured on 26 August and the morning of 27 August.

(reported as ± 1 SD in Table 2). Bimodal distributions were combined so that they were unimodal before analysis. Data collected at different times during the year on the time of larval release relative to a given environmental cycle were combined except when different measures of release were used or when the timing of release relative to tidal amplitude cycles on the Pacific coast was analyzed. On the Pacific coast, the durations of the ascending phase (lowest to highest) and the descending phase (highest to lowest) of the 15-d tidal amplitude cycle alternated between 6 and 9 d, and 9 and 6 d. Hence, data were grouped into these two categories before analysis.

Sample sizes varied considerably depending on whether or not all data could be combined. Data on larval release relative to tidal and light-dark cycles always could be combined but data on larval release relative to tidal amplitude and lunar cycles usually could not be combined. Consequently, hierarchies of rhythms could not be determined simply by comparing r values because larger sample sizes tended to result in larger r values. Instead, statistics were used to identify the timing of larval release and standard deviation relative to each environmental cycle. High r values indicated that all four environmental cycles examined were potentially important for species along the Pacific coast, where phasing of these cycles was regular. Hi-

erarchies of rhythms were inferred by determining the magnitude of departures in the timing of larval release by Caribbean crabs during the year from patterns shown by crabs in the Pacific ocean. Rhythms that varied most from one sampling period to the next were assigned a lower ranking than those that varied less during the year.

RESULTS

Seasonal reproduction

Although we followed reproduction for only 1 yr, our data suggest that *Cataleptodius* and *Uca* may breed seasonally and that *Pachygrapsus* probably does not. Ovigerous *P. transversus* were common in populations on both coasts year-round. On the Pacific coast, ovigerous *C. taboganus* were very rare from May through August. On the Caribbean coast, only 3.8% of *C. floridanus* that were collected in April had eggs, but 35–41% of them were ovigerous in collections that were taken from August to December when we ended this study. Ovigerous *U. galapagensis* were abundant in July, when we first collected them, through December. At our study sites, this species stops breeding and surface activity is greatly reduced shortly after the onset of the dry season in January when the sediment in its habitat turns to cracked mud. We collected ovigerous

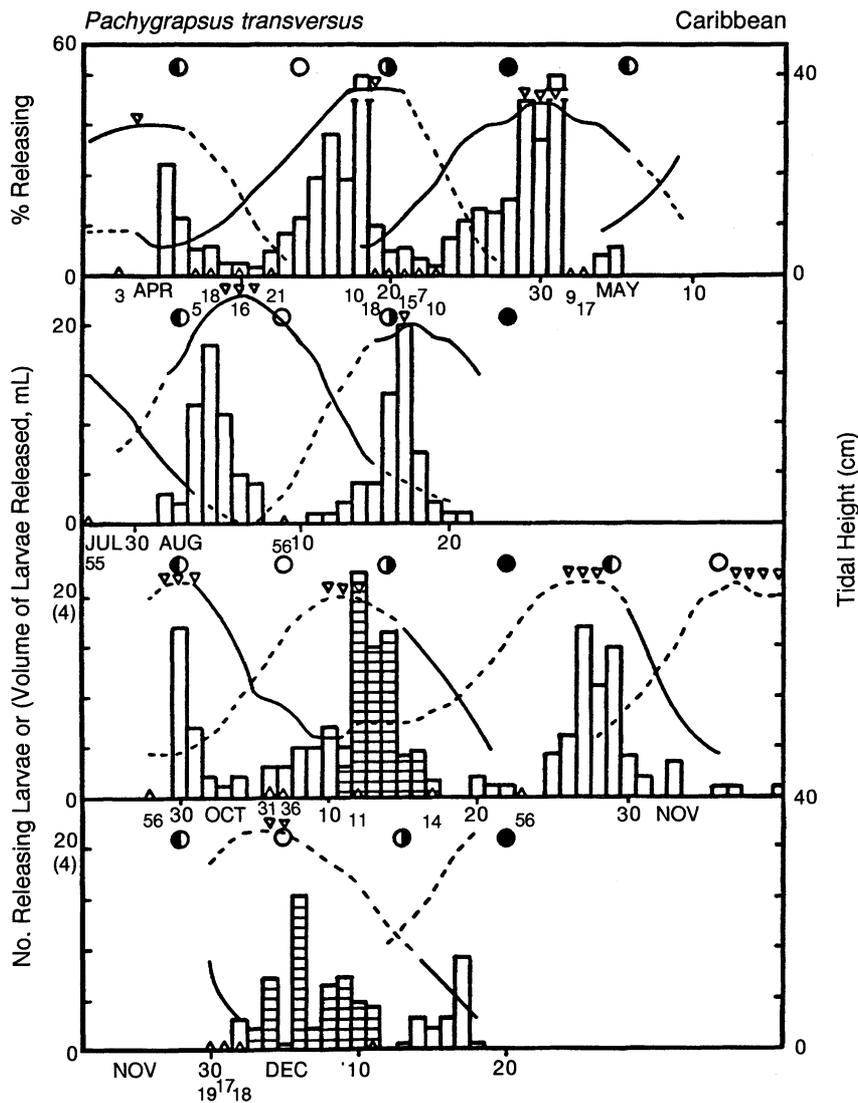


FIG. 5. Larval release by *Pachygrapsus transversus* in the Caribbean relative to lunar and tidal amplitude cycles during 1987. The number of females releasing larvae, percentage of females releasing larvae, or volume of larvae hatched (hatched bars) were measured depending upon the time of year. Scale numbers in parentheses are for volume of larvae released. Daily nocturnal and diurnal high tides are indicated by — and ---, respectively. ▽ represent maximum amplitude tides. The date and number of females collected are indicated by Δ and associated numbers.

U. rapax in August and early October but were unable to find any thereafter.

Pachygrapsus

Timing of larval release.—On the Pacific coast, *P. transversus* released larvae 0–2 d before the full and new moons (except during late August and early September) and within 2 d of spring tides throughout the year (Fig. 3, Table 2). Larvae were released on the higher of the two semidiurnal high tides that occurred during the daytime (Fig. 4, Table 2). Crabs first released larvae on late afternoon tides. As high tides moved through dusk and dawn, this species released larvae on both tides and then switched to higher morning tides.

Larvae continued to be released on the higher daytime tide until, presumably, the cycle repeated.

On the Caribbean coast, *P. transversus* released larvae from 1 to 6 d before quarter moons, but always within 2 d of maximum amplitude tides (Fig. 5, Table 2). Hence, hatching was entrained by the tidal amplitude rather than the lunar cycle. The timing of larval release relative to the light–dark and tidal cycles was more variable in the Caribbean than the Pacific populations of this species (Figs. 4 and 6, Table 2). Release was monitored on 13 d with one high tide and 17 d with two high tides. As on the Pacific coast, crabs released larvae during both daytime and nighttime. However, in contrast to the Pacific pattern, Caribbean *P.*

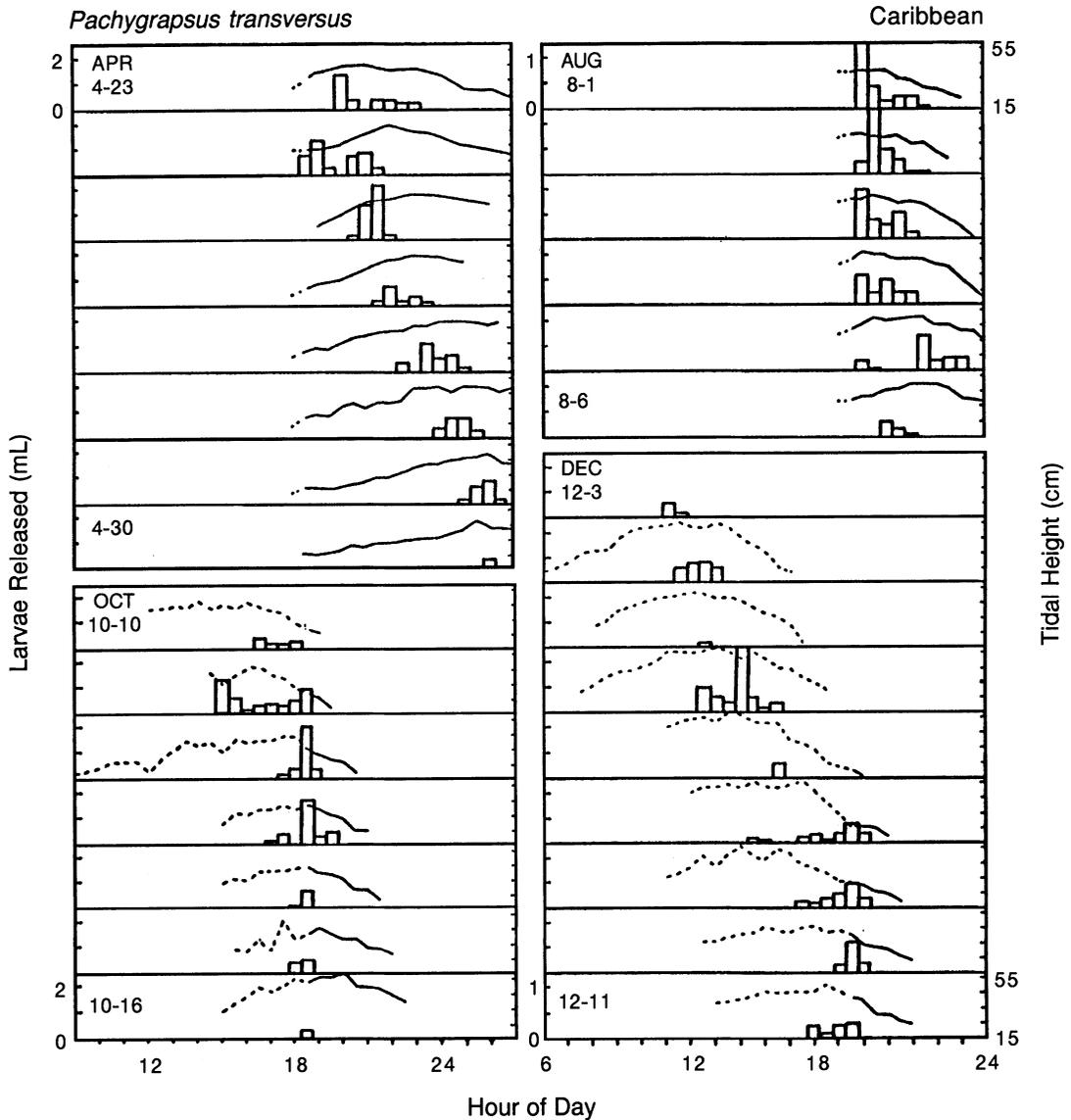


FIG. 6. Volume of larvae released by *Pachygrapsus transversus* in the Caribbean relative to light-dark and tidal cycles in April, August, October, and December 1987. Nocturnal and diurnal portions of high tides are indicated by — and ---, respectively. Tides were not measured on 3 December.

transversus always released larvae only once per day (Fig. 6). On 15 of the 17 d with two high tides, crabs released larvae on the higher tide. During April and August, high tides progressed from just after dusk through the evening. Crabs initially released larvae at dusk during late flood tides. As high tides occurred later in the evening, crabs switched to release larvae during slack high tides. A strong influence of the light-dark cycle also was evident during October and December, when high tides progressed from about midday to late afternoon. Crabs first hatched near slack high tides. As high tides occurred later in the day, crabs shifted rapidly to release larvae at dusk during ebbing tides.

Hierarchies.—*Pachygrapsus transversus* always released larvae within 2 d of maximum amplitude tides regardless of lunar phase and whether these tides peaked in the late afternoon (Pacific) or from the early afternoon through midnight (Caribbean). On the Pacific coast, larval release was more closely timed to tidal than light-dark cycles; crabs released larvae on the higher tide that always occurred during the day. The light-dark cycle was more influential in regulating larval release by Caribbean populations; when maximum amplitude tides peaked in the late afternoon, crabs released larvae just after dusk on late ebb tides. Nevertheless, the tidal cycle still exerted more influence than the light-dark cycle because Caribbean crabs al-

ways released larvae during high tides, never during low tides, but often released larvae during the daytime. Thus, the relative importance, in descending order, of the remaining three physical cycles for the timing of larval release by *P. transversus* appeared to be: tidal amplitude, tidal height, and light-dark cycles. The lunar cycle apparently does not regulate the timing of larval release.

Cataleptodius

Timing of larval release.—On the Pacific coast, *C. taboganus* released larvae highly synchronously ≈ 1 d after maximum amplitude tides and 3 d before quarter moons (Fig. 7, Table 2). Most larvae were released 30 min after high tide and within 1 h of last light (Fig. 8, Table 2).

On the Caribbean coast, *C. floridanus* released larvae asynchronously relative to tidal amplitude and lunar cycles in April when few crabs spawned (Fig. 9). Later in the year when reproduction increased, this species released larvae from 4 d before to 2 d after quarter moons and 0–2 d after maximum amplitude tides (Fig. 9, Table 2). The timing of release relative to the tidal cycle ranged from 4 h before (April) to 3 h after (December) high slack tide but always occurred within 1 h of last light (Fig. 10, Table 2).

Hierarchies.—*Cataleptodius floridanus* released larvae near last light during high tides. However, the light-dark cycle may exert greater influence than the tidal cycle because larvae were released by Caribbean crabs within 1 h of last light but varied from 4 h before to 3 h after high slack tides. Both species of *Cataleptodius* usually released larvae 1 or 2 d after maximum amplitude tides when their habitat was immersed at dusk. These conditions occurred at various times relative to the lunar phase between coasts, suggesting that larval release was not entrained by moonlight. To release larvae biweekly, *C. floridanus* could not always release larvae on early ebb tides as did *C. taboganus*. Instead, *C. floridanus* had to release larvae during early flood or late ebb tides depending on the month. In December, peak larval release was delayed by 5 or 6 d following maximum amplitude tides when tides began to inundate crabs at dusk (Fig. 10). Therefore, the tidal cycle is more important than the tidal amplitude cycle in regulating larval release by this species. Hence, in descending relative importance, the light-dark, tidal, and tidal amplitude cycles appeared to determine when *Cataleptodius* released larvae.

Uca

Timing of larval release.—Hatching by Pacific *U. galapagensis* was highly synchronous. Females released larvae monthly, just after full moons on the largest amplitude tides and on the higher of the two semidiurnal tides (Fig. 11, Table 2). Only these tides were high enough to flood the upper tidal creeks where this species lives. Larvae were released early in the

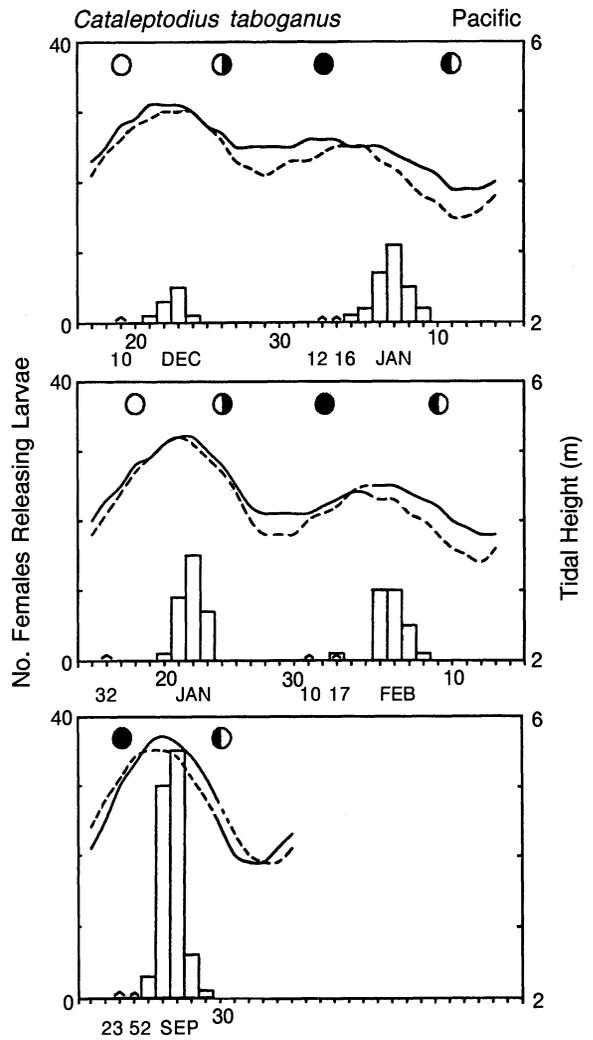


FIG. 7. Number of *Cataleptodius taboganus* releasing larvae on the Pacific coast relative to lunar and tidal amplitude cycles during 1983 and 1984. Daily nocturnal and diurnal high tides are indicated by — and ---, respectively. ∇ represent maximum amplitude tides. The date and number of females collected are indicated by Δ and associated numbers.

morning within 30 min after slack high tide (Fig. 12, Table 2).

On the Caribbean coast, *U. rapax* released larvae over several days on both biweekly maximum amplitude tides that inundated their habitat (Fig. 13, Table 2). However, ovigerous females were much more numerous in the population preceding tides of greatest amplitude. The lunar cycle had little effect on the timing of release because larvae were released from 2 d before (August) to 2 d after (December) quarter moons. This species always released larvae at night, but during mid-ebb tides (Fig. 14) rather than just after slack high tide as did *U. galapagensis* on the Pacific coast.

Hierarchies.—Larval release was timed precisely rel-

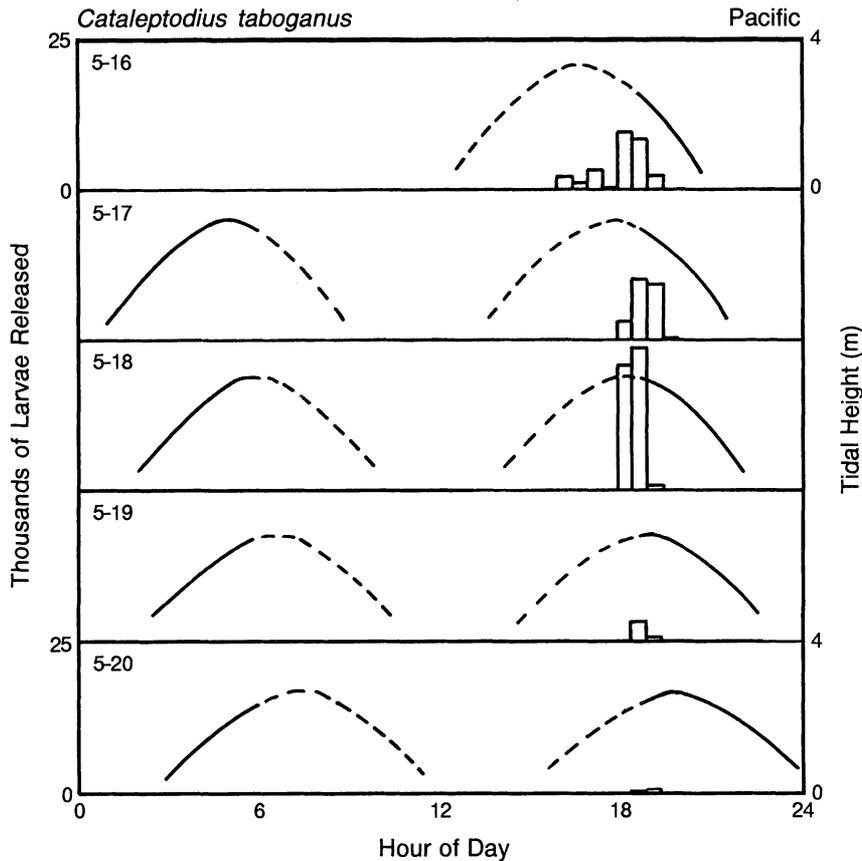


FIG. 8. Number of larvae released by *Cataleptodius taboganus* on the Pacific coast relative to light-dark and tidal cycles in May 1984. Nocturnal and diurnal portions of high tides are indicated by — and ---, respectively.

ative to the tidal amplitude cycle on both coasts, but not relative to the lunar cycle on the Caribbean coast where these two cycles are decoupled. Both species released larvae during darkness early in the morning. Larval release occurred just after high tide on the Pacific coast but during ebb tide on the Caribbean coast. The close timing of larval release relative to tidal amplitude and light-dark cycles on both coasts suggests that these cycles had a greater influence on the time of release than did the tidal cycle. Hence, we suggest that the tidal amplitude and light-dark cycles were more important than the tidal cycle to the timing of larval release by *Uca*.

DISCUSSION

Plasticity

Crabs in this study timed larval release relative to the tidal amplitude, tidal, and light-dark cycles. On the Pacific coast of the Republic of Panama, phase relationships among these cycles vary little over the year. Consequently, we observed little intraspecific variation in the timing of larval release.

On the Caribbean coast, phasing of the tidal amplitude, tidal, and light-dark cycles showed complex in-

tra-annual variation as did the timing of larval release. During April and August, *P. transversus* released larvae at night near the time of high tide; during October and December most crabs released larvae during the afternoon or at dusk on ebbing tides (Fig. 6). In different months, *C. floridanus* released larvae at different times relative to the tidal amplitude and tidal cycles but almost always just after dusk.

Plasticity in the timing of larval release by intertidal crabs evidently results from differences in the degree to which the three hatching rhythms are coupled to their corresponding physical cycles. We know that the light-dark and tidal cycles entrained circadian and circatidal rhythms, because larval release was advanced or delayed relative to slack high tide depending on the time of day. In addition, crabs displayed a third bi-weekly or circasemilunar rhythm that was cued by the tidal amplitude cycle rather than the lunar cycle. This rhythm was particularly evident in *U. rapax* and Caribbean *P. transversus* that released most larvae on maximum amplitude tides independent of the phase relationships between these tides and the light-dark and tidal cycles. Further, both species of *Uca* apparently tracked monthly inequalities in tidal amplitude, because all *U. galapagensis* and most *U. rapax* larvae

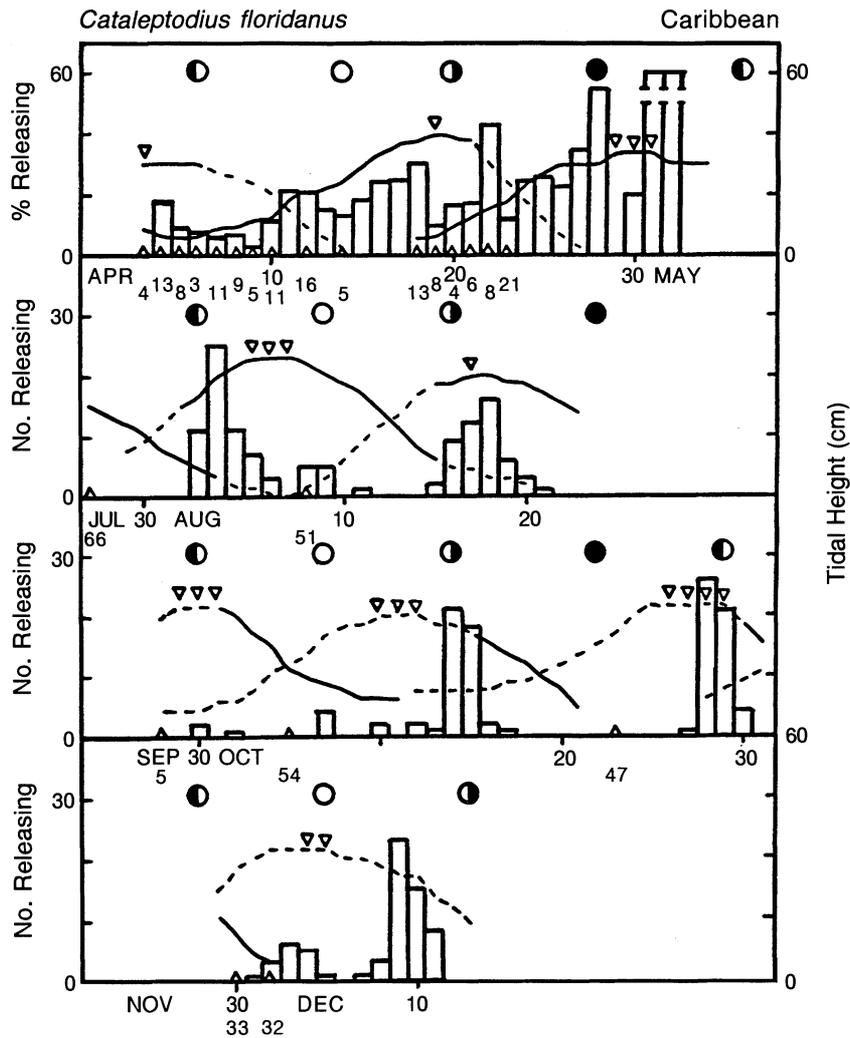


FIG. 9. Number or percentage of *Cataleptodius floridanus* releasing larvae in the Caribbean relative to lunar and tidal amplitude cycles during 1983 and 1984. Daily nocturnal and diurnal high tides are indicated by — and ---, respectively. ∇ represent maximum amplitude tides. The date and number of females collected are indicated by Δ and associated numbers.

were released on the larger of the two biweekly sets of maximum amplitude tides each month. Reproductive cycles of other intertidal crabs (Christy 1978; S. G. Morgan, unpublished manuscripts) and fishes (Greely 1984, Hsiao and Meier 1986) also clearly track the tidal amplitude rather than the lunar cycle. However, the lunar, not the tidal amplitude cycle apparently entrains semilunar and lunar rhythms of larval release by some semiterrestrial crabs (Gifford 1962, Wolcott and Wolcott 1982, Saigusa 1988). Therefore, the cues that entrain the circasemilunar rhythm vary according to where species live, and it is possible that multiple cues may time larval release in species that range widely in the intertidal and supratidal zones.

Species-specific hierarchies of rhythms

We have shown that three rhythms jointly determine the timing of larval release and that they do not each

exert equal influence. These rhythms were arranged hierarchically on the basis of the relative degree to which they were entrained by their respective physical cycles as revealed by the magnitudes of advances or delays in the timing of larval release relative to each cycle.

Hierarchies of rhythms obtained for *P. transversus* differed on the two coasts. Crabs in both populations always released larvae on maximum amplitude tides making this the most important physical cycle. On the Pacific coast, larvae were released only on slack high tides but mostly during the daytime. In contrast, daytime larval release by Caribbean crabs sometimes was avoided by advancing or delaying hatching relative to high slack tide. Specifically, larval release by Caribbean crabs shifted from slack high tides to late ebb tides as high tides approached dusk (Fig. 6). During the equivalent tidal progression on the Pacific coast, crabs con-

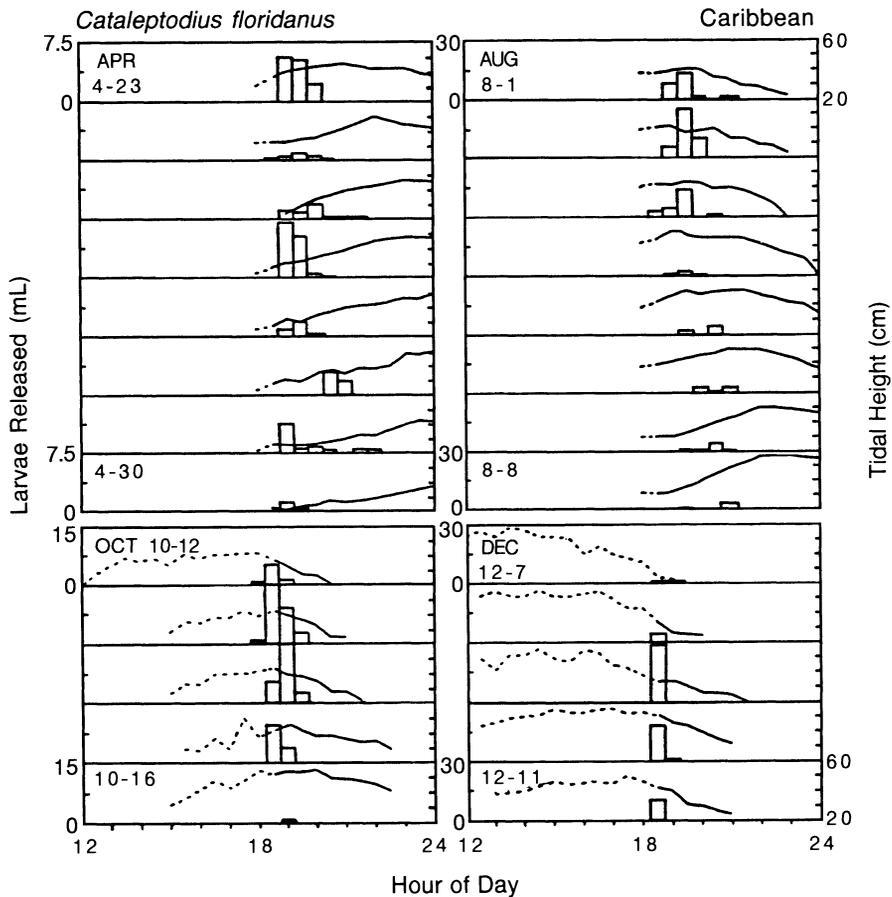


FIG. 10. Volume of larvae released by *Cataleptodius floridanus* in the Caribbean relative to light-dark and tidal cycles in April, August, October, and December 1987. Nocturnal and diurnal portions of high tides are indicated by — and ---, respectively.

tinued to release larvae near high slack tides just before dark. Although larval release in both populations of this species is more closely timed to tidal than light-dark cycles, the variation may be explained by differences in light intensity near the benthos on the two coasts. At slack high tide, crabs on the Pacific coast are covered by 4–6 m of turbid water compared to a maximum of ≈ 0.5 m of clear water on the Caribbean coast. Hence, the level of illumination during late afternoon Pacific high tides may be insufficient to initiate phase shifts to dusk. This alternative could be tested experimentally.

Hierarchies of rhythms of *U. rapax* and *P. transversus* on the Caribbean coast were similar but the phasing of the rhythms was different. Like most fiddler crabs (DeCoursey 1983, Salmon et al. 1986, Forward 1987), *U. rapax* released larvae on nocturnal maximum amplitude ebbing tides and never during the daytime as did *P. transversus*. Less variation in the timing of larval release was observed for *U. rapax* because this species stopped breeding during months with only daytime maximum amplitude tides.

Unlike the other species, the light-dark cycle clearly determined when *C. floridanus* released larvae. This species released larvae at dusk regardless of the phasing of the other cycles. Except during March and April when crabs resumed reproduction, *C. floridanus* released larvae near maximum amplitude tides but larval release sometimes shifted to very early flood tides or very late ebb tides to do so. Asynchrony in biweekly rhythms of larval release is evident in other crabs following reproductive quiescence (Dollard 1980, Christy 1982), but it remains unexplained. Thus, synchrony of larval release by *C. floridanus* relative to environmental cycles suggests a hierarchy of rhythms that regulates the timing of larval release. The same hierarchy also may regulate the timing of larval release by its sibling species on the Pacific coast, where the relative importance of environmental cycles cannot be disentangled because cycles remain in phase during the year.

Adaptive significance of hierarchies

Results of this study suggest that predation on ovigerous females, embryos, and larvae largely may regu-

late the timing of larval release. All crabs examined released larvae on high tides thereby enabling them to remain near refuges and minimize predation on females and embryos. Crabs that live in the middle and upper intertidal zones, such as *Uca* and *Pachygrapsus*, necessarily released larvae on maximum amplitude tides because only these tides reached their habitats. *Uca galapagensis* released larvae just after high tide, on the higher semidiurnal tide and the greatest amplitude tides of the lunar month, because they were inundated only at this time. Crabs that live low in the intertidal zone are immersed by all high tides and may release larvae throughout the tidal amplitude cycle (Morgan and Christy 1994). However, many crabs do not as illustrated by *Cataleptodius*. These species may release larvae during periods of maximum amplitude tides because larvae are transported most rapidly from shorelines where planktivorous fishes abound (Weinstein 1979, Morgan 1990, Sogard and Able 1991, Ayvazian et al. 1992, Sasekumar et al. 1992, Baltz et al. 1993).

By releasing larvae at night, crabs also reduce the risk of predation on larvae by diurnally foraging planktivorous fishes. Only species with larvae that are relatively inconspicuous to fishes release larvae during both the day and night (S. G. Morgan and J. H. Christy, unpublished manuscript). The color and amount of larval pigment largely determine their vulnerability to planktivorous fishes. In feeding trials, larvae of *C. ta-*

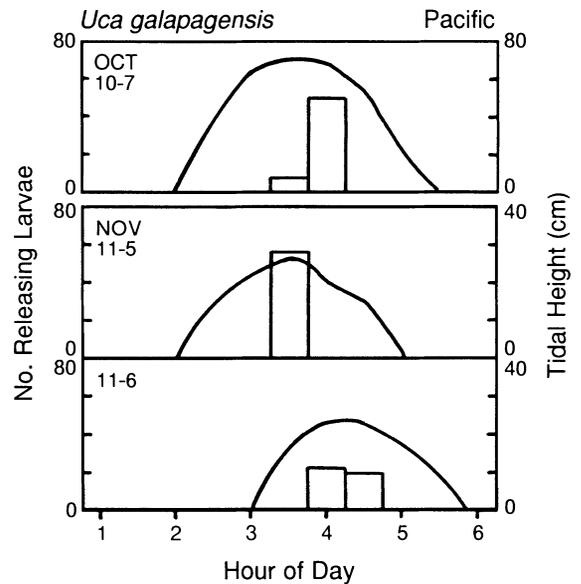


FIG. 12. Number of *Uca galapagensis* releasing larvae on the Pacific coast relative to light-dark and tidal cycles in October and November 1987. Nocturnal high tides are indicated by —.

boganus were rendered highly vulnerable to fish by their red yolk and chromatophores, whereas larvae of *P. transversus* were eaten significantly less often due to their less conspicuous color (S. G. Morgan and J. H. Christy, unpublished manuscript). Although we have not determined the vulnerability of *U. galapagensis* or *U. rapax* to planktivorous fishes, their brown color should make them highly visible. Thus, *Cataleptodius* and *Uca* larvae are released only at night when they are least likely to be detected by fishes, and *P. transversus* larvae sometimes hatch during the daytime because they are less vulnerable to predation.

Species-specific hierarchies of hatching rhythms match those predicted in Table 1 thereby suggesting that predation on ovigerous females, embryos, and larvae ultimately may regulate the timing of larval release. *Uca* released larvae on maximum amplitude tides because only then could females release larvae safely near refuges high in the intertidal zone. Consequently, *Uca* larvae are transported rapidly away from their predators. Their larvae probably are relatively visible to fishes, which favors nocturnal release even when such timing leads to release on ebbing tides. *Cataleptodius* larvae are very conspicuous and preferred by planktivorous fish. Predation produces strong selection for nocturnal larval release during high tides. Release near maximum amplitude high slack tides is less important than for *Uca* and *Pachygrapsus* because *Cataleptodius* lives low in the intertidal zone and is immersed for long periods during each tide. *Pachygrapsus transversus* lives higher in the intertidal zone than *Cataleptodius* and therefore larval release coincides more closely to

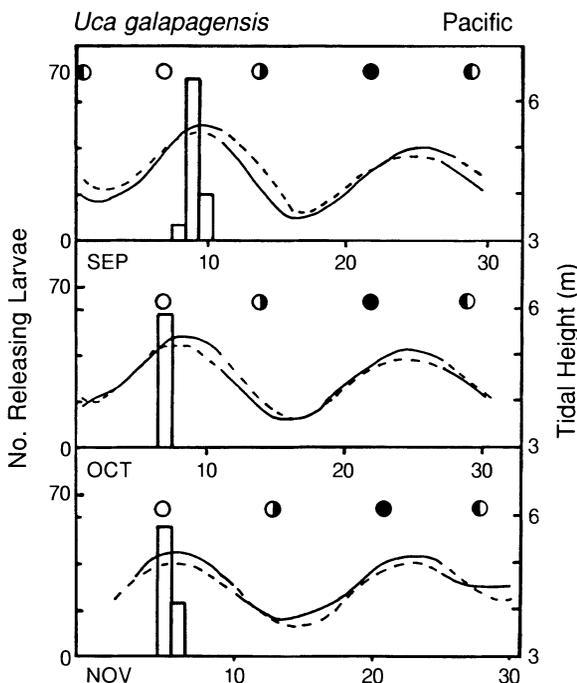


FIG. 11. Number of *Uca galapagensis* releasing larvae on the Pacific coast relative to lunar and predicted tidal amplitude cycles during 1987. Daily nocturnal and diurnal high tides are indicated by — and ---, respectively.

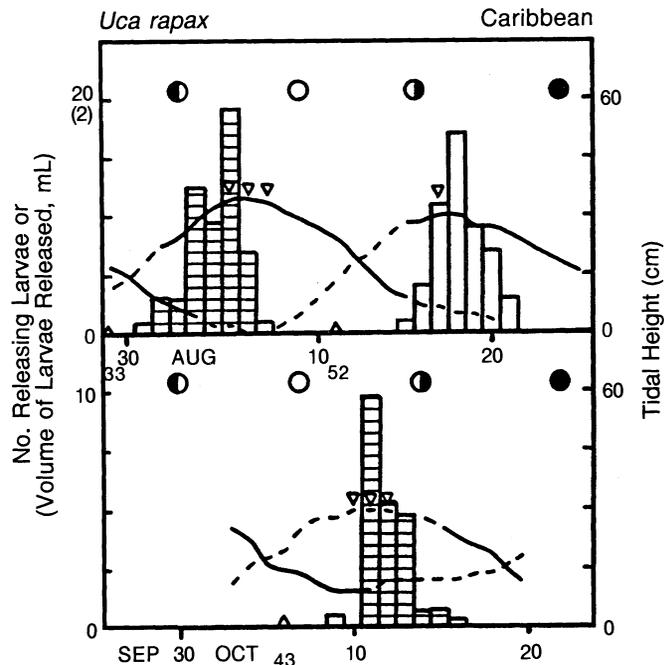


FIG. 13. Number of *Uca rapax* releasing larvae or volume of larvae released (hatched bars) in the Caribbean relative to lunar and tidal amplitude cycles in August and October 1987. Scale numbers in parentheses are for volume of larvae released. Daily nocturnal and diurnal high tides are indicated by — and ---, respectively. ▽ represent maximum amplitude tides. The date and number of females collected are indicated by △ and associated numbers.

maximum amplitude high tides. However, its larvae are less visible to fishes and release occurs during daytime and nighttime.

Optimality and constraint in the timing of larval release

In semidiurnal tidal environments, such as that on the Pacific coast of Panama, the phasing of physical cycles persistently enables crabs to release larvae when females, embryos, and larvae may best escape predation. Most crabs release larvae when large amplitude high tides peak at dusk biweekly (Forward 1987). Species that do not follow this pattern (Christy 1986, Morgan and Christy 1994) have larvae that are relatively protected from predation by diurnal planktivorous fishes (S. G. Morgan and J. H. Christy, *unpublished manuscript*). Thus, in semidiurnal tidal environments, the timing of larval release may be optimal because reproductive success is maximized year-round regardless of species zonation and larval vulnerability to predation.

In contrast, in mixed semidiurnal tidal environments, such as that on the Caribbean coast of Panama, variation in the phasing of the light-dark, tidal, and tidal amplitude cycles may expose larvae to predation more than in semidiurnal tidal regimes. For example, during July and August, crabs released larvae when nocturnal maximum amplitude high tides occurred near dusk (Figs. 2, 6, 10, 14). From November through

January, nocturnal high tides of any amplitude were rare. Crabs, such as *P. transversus*, may release larvae near high slack tides (Fig. 6) resulting in rapid transport of larvae away from abundant planktivores in shallow water. However, larvae will all be exposed to potentially heavy predation during daytime larval release. The rapid shift in the time of release by *P. transversus* to dusk as tides progressed in the afternoon (Fig. 6) indicates these costs are significant. Other species, such as *C. floridanus*, may delay larval release to dusk when tides are ebbing (Fig. 10), thereby reducing predation on larvae. However, flooding tidal currents may return larvae to shallow waters until the subsequent afternoon, resulting in substantial losses to planktivorous fishes. Although hierarchies of rhythms should reduce losses to predators, both patterns may decrease reproductive success from that realized earlier in the year. The timing of larval release may be suboptimal during months when nocturnal maximum amplitude high tides do not occur and when nocturnal high tides of lesser amplitude are rare. Along the Caribbean coast of Panama, reproductive success should be (1) best from mid-May through mid-July, (2) higher from April through September than from October through March, and (3) worst in December and January.

Especially adverse phasing of environmental cycles during December and January may have limited reproductive seasons of two of the three species from the Caribbean. Reproduction by *C. floridanus* and *U. ra-*

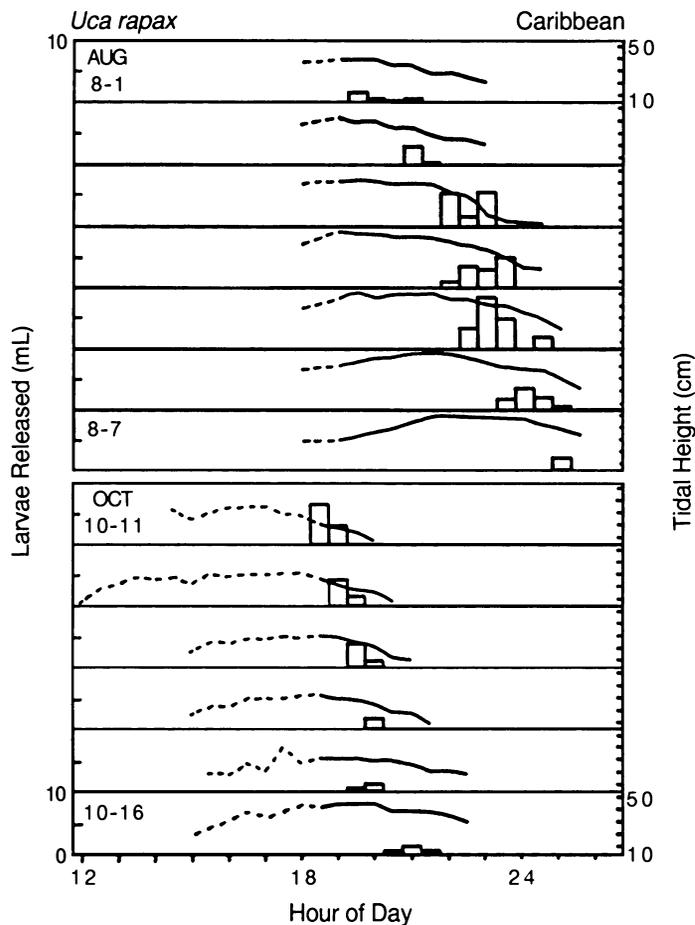


FIG. 14. Volume of larvae released by *Uca rapax* in the Caribbean relative to light-dark and tidal cycles in August and October 1987. Nocturnal and diurnal portions of high tides are indicated by — and ---, respectively.

pax may have ceased in December because even low amplitude nocturnal high tides were rare during these months. The breeding season of *U. rapax* was briefest because females released larvae only on maximum amplitude nocturnal tides that occurred during ≈ 7 mo of the year (Fig. 2). *Cataleptodius floridanus* lives low in the intertidal zone and need not release larvae only on maximum amplitude tides. This species had a longer breeding season perhaps because nocturnal tides peaked well before dawn for 9 mo of the year. However, breeding ceased from January through March when low tides occurred at dusk. Limited reproduction began in April when evening high tides returned. *Pachygrapsus transversus* was the only Caribbean crab that apparently bred year-round. Larvae of this species are relatively well protected from predation by planktivorous fishes and could be released even during adverse conditions.

Where mixed semidiurnal tides prevail, crabs that live high in the intertidal zone or have vulnerable larvae generally may be constrained to breed during months with nocturnal maximum amplitude high tides. Crabs that live lower in the intertidal zone and have

protected larvae may continue to breed year-round despite suffering reduced reproductive success during months when these tides rarely occur.

CONCLUSIONS

The timing of larval release by intertidal crabs is plastic. The timing of this event is jointly controlled by circadian, circatidal, and circasemilunar rhythms that are entrained, respectively, by light-dark, tidal, and tidal amplitude cycles. It is likely that this timing system evolved because predation on females, embryos, and larvae not only varies between phases of each cycle but also differs among cycles depending upon species-specific life history traits. Species that live high on the shore may release larvae synchronously on maximum amplitude high tides because their refuges are inundated then, whereas species that live low on the shore may have greater flexibility in the timing of larval release relative to the tides. Larval survival generally may be greatest on maximum amplitude tides, early ebb tides, and shortly after dusk, because conspicuous larvae have the most time to diffuse from siblings and

disperse from shorelines and are transported from shorelines most rapidly before dawn when planktivorous fishes resume feeding. Larvae that are released by some species during daytime low amplitude tides are inconspicuous and largely may escape foraging fishes even though transport from shorelines is slow. Rankings of rhythms differ for species that release conspicuous and inconspicuous larvae, and these hierarchies generally restrict release of conspicuous larvae to periods when predation is low.

Hierarchies of rhythms allow crabs to track phase shifts of cycles in variable tidal environments, thereby reducing predation during larval release and, on average, enhancing reproductive success across tidal regimes. However, larval release cannot be timed optimally across all tidal environments because variation in the phasing of environmental cycles ensures that larvae will be released at different times. Survival of newly hatched larvae may be highest in semidiurnal tidal regimes where favorable phasing of physical cycles occurs throughout the year. In other tidal regimes, larval release cannot be synchronized with all three physical cycles during the year, and hierarchies of rhythms may ensure that some species cease reproducing.

The flexible timing system of intertidal crabs seems well suited to the life histories of these animals. Although adults move little, their larvae disperse widely and may often settle in tidal environments that are very different from those experienced by the source population. Hence, fixed timing systems that require adaptation to specific local tidal conditions would fail in competition with flexible systems that allow crabs to time release appropriately across a range of tidal environments.

We have identified proximate and ultimate factors that may regulate the timing of larval release by intertidal crabs worldwide. With knowledge of local tides, species distributions, and larval colors and morphologies, the timing of larval release by unstudied species can be predicted following the arguments we have presented in this paper. Failure of these predictions should lead to studies that improve understanding of the mechanisms and adaptive significance of the timing of larval release by intertidal crabs.

ACKNOWLEDGMENTS

Jessica Bordua assisted in the field, and valuable comments on several drafts of the manuscript have been provided by Skyli McAfee. We thank Lieutenant Colonel Corson Hilton and Major Robert Bernard for granting access to Fort Sherman and for facilitating research conducted there. Financial support for this research was provided by a postdoctoral fellowship from the Smithsonian Institution.

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