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ADAPTIVE SIGNIFICANCE OF THE TIMING OF LARVAL RELEASE BY CRABS

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Abstract.—The adaptive significance of synchronous larval release by marine animals has been elusive. The hatching times of 10 species of intertidal crabs were determined and compared to those expected if crabs release larvae when predation on females, embryos, and newly hatched larvae is least. The safest time to release larvae occurs during the largest-amplitude nocturnal high tides of the lunar month. Crabs throughout the intertidal zone can release larvae near their refuges, and larvae will be transported rapidly at night from shorelines where diurnal planktivores abound. High and middle intertidal species released larvae at this time, which suggests that predation on all three life stages ultimately may synchronize reproduction. Unlike these species, low intertidal crabs are inundated every day, and therefore females could release larvae near refuges daily. Although one low intertidal species did release larvae every day and often during the daytime, two other species released larvae during the safe period. The timing of larval release by low intertidal crabs varies with the vulnerability of their larvae to planktivorous fishes. The hatching times of 46 species worldwide support our contention that predation, primarily on newly hatched larvae, and not other sources of mortality, selects for synchronous hatching by crabs.

Reproductive synchrony is widespread among plants, birds, mammals, amphibians, insects, fishes, and marine invertebrates because offspring mortality varies predictably during environmental cycles (Janzen 1971; Johannes 1978; Gochfeld 1980; Tauber and Tauber 1981; Findley and Cooke 1982; Rathcke and Lacey 1985; Taylor and Karban 1986; Giese and Kanatani 1987; Ims 1990). Seasonal reproduction places offspring in favorable temperature, light, rainfall, or food conditions, which thereby enhances their chance of survival (Rathcke and Lacey 1985; Giese and Kanatani 1987); however, the adaptive significance of short-term, intraseasonal reproductive cycles often is obscure. Predation is perhaps the most commonly cited cause of short-term periodicities in reproduction, because early life stages of many species may be especially vulnerable to predators. Reproductive synchrony may facilitate avoidance of predators (Morgan 1990), confusion of predators (Hamilton 1971), swamping of predators (Darling 1938), and collective defense of offspring (Kruuk 1964). A single antipredatory mechanism is unlikely to explain reproductive synchrony among diverse taxa that reproduce at different

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times, nor can predation solely account for the many differences in reproductive timing among organisms (see, e.g., Olson 1983; Petersen et al. 1992).

Among marine animals alone, species may time reproduction by one or more of four environmental cycles and at different phases of each cycle, including lunar, tidal amplitude (biweekly cycle of differences between the height of high and low tides that is usually synonymous with the spring-neap cycle), tidal (semidaily or daily cycle of high and low tides), or light-dark cycles (see Palmer 1974; Johannes 1978; DeCoursey 1983; Giese and Kanatani 1987; Morgan 1995). Marine animals typically have evolved endogenous timing mechanisms that presumably minimize fatal errors in reproduction by enabling animals to anticipate and reliably time spawning of gametes and hatching of larvae. Consequently, elaborate timing mechanisms produce arrays of reproductive patterns in mollusks and polychaetes (Korringa 1947), echinoderms (Pearse 1975; Lessios 1991), ascidians (Olson 1983), marine insects (Neumann 1986), sponges (Amano 1988), corals (Babcock et al. 1986), and fishes (Johannes 1978; Robertson et al. 1990). Many specific hypotheses have been proposed to explain the adaptive significance of these reproductive patterns, but few cohesive scenarios have been developed to account for the diversity of patterns that occurs among even closely related species.

However, a common scenario for the adaptive significance of reproductive synchrony has been proposed for coral reef fishes and intertidal crabs despite considerable differences in life histories. Researchers (Johannes 1978; Christy 1982*b*; Morgan 1990) have proposed that reproduction by intertidal and shallow water fishes and crabs is timed to minimize predation. Many of these animals release gametes or larvae on nocturnal maximum-amplitude high tides when adults, embryos, or larvae are least likely to be seen by predatory fishes and are most likely to be transported away from reefs and nearshore coastal areas that generally harbor more predators than offshore waters. This may explain similar reproductive synchronies among these animals, but differences in life histories must be considered to fully understand the range of timing patterns shown by each group. First, it must be understood why many species of shallow water and intertidal fishes and crabs do not spawn or hatch at this time. Second, it is not clear whether reproductive synchrony among these diverse animals enhances survival of adults, embryos, or larvae, and the answer may differ for each group. Therefore, the search for common explanations of the adaptive value of reproductive synchrony among diverse taxa may best begin by more thoroughly understanding the effect of various selective pressures on the reproductive timing of each group. Here, we develop a paradigm for the adaptive significance of the timing of larval release by crabs.

Previous studies have suggested that vulnerability of adults, embryos, or larvae to visual predators largely may determine when intertidal crabs release larvae relative to the four environmental cycles. Female crabs incubate eggs beneath abdominal appendages until larvae hatch. Ovigerous females of intertidal species typically incubate eggs in burrows or crevices before emerging to release larvae (see, e.g., Christy 1982*a*; Saigusa 1982; Salmon 1987). At this time, the risk of predation on females, embryos, and larvae increases. Females of many species release larvae at night when visual predators are less likely to prey on them or

their offspring (DeCoursey 1979; Christy 1982*b*). Variation in moonlight appears to be unimportant because intertidal crabs release larvae biweekly near new, full, or quarter moons (Forward 1987; Morgan 1995). Furthermore, biweekly peaks in larval release appear to be cued by environmental factors that are associated with the tidal, not the lunar, cycle (Morgan and Christy 1994).

All intertidal crabs that have been examined release larvae near the time of high tide, and some species release larvae biweekly near maximum-amplitude high tides (DeCoursey 1983; Forward 1987). Predation may be less for females (DeCoursey 1979) or their broods (S. G. Morgan and S. T. McAfee, unpublished manuscript) when crabs release larvae from entrances of inundated refuges than when they walk to the water's edge. Furthermore, by hatching on high tides, larvae of all species may avoid planktivorous fishes because ensuing ebb tides transport larvae from shorelines, where planktivorous fishes abound (Christy 1982*b*; Morgan 1987*a*, 1990). Many fishes enter productive nearshore habitats to forage, reproduce, and develop during summer months, when crabs reproduce (Weinstein 1979; Boesch and Turner 1984; Thayer et al. 1987; Morgan 1990; Sogard and Able 1991; Ayvazian et al. 1992; Rountree and Able 1992; Sasekumar et al. 1992; Baltz et al. 1993). Even if the biomass of fishes is greater offshore, the risk of predation may be greater inshore owing to the prevalence of young fishes in highly productive coastal areas. Young fishes are exclusively zooplanktivorous regardless of their dietary preferences as adults, and even zooplanktivores may switch as adults to larger prey than crab larvae (Mulkana 1966; Thayer et al. 1974; Hunter 1980; Morgan 1990). Larvae that hatch on maximum-amplitude high tides would be transported offshore fastest. Thus, visual predators may be avoided most effectively if larvae are released on nocturnal maximum-amplitude high tides, a timing pattern that is common among intertidal crabs (Christy and Stancyk 1982; Salmon et al. 1986; Forward 1987). Larvae of species that hatch at other times may not be particularly vulnerable to visual predators because of their morphologies and colors (Christy 1986; Morgan 1990; S. G. Morgan and J. H. Christy, unpublished manuscript).

Preferences of fishes for newly hatched crab larvae may be determined by interspecific differences in the length and number of protective spines, body size, and the amount and color of yolk and chromatophores (Christy 1982*b*, 1986; Morgan 1987*b*, 1989, 1990; S. G. Morgan and J. H. Christy, unpublished manuscript). Long-spined, large-bodied larvae are difficult for small-mouthed planktivorous fishes to swallow, and cryptic colors decrease the visibility of larvae to fishes. Many crab larvae rely on these morphological defenses rather than evasive or escape behaviors (Morgan 1987*b*, 1989, 1990). Little information exists on the relationship between predation and attributes of adult crabs or embryos. However, the vulnerability of crabs to predators may vary with body size, coloration, and evasive behaviors, and the susceptibility of embryos may depend on the color and size of the brood.

The timing of larval release ultimately may depend on whether adults, embryos, or larvae are most vulnerable to predators. If females or embryos are most at risk, then crabs should remain near refuges to release larvae. The safest time for intertidal crabs to release larvae would be at night. Species that live high in the

TABLE 1

PREDICTED TIMING OF LARVAL RELEASE BY INTERTIDAL CRABS RELATIVE TO LIGHT-DARK, TIDAL AMPLITUDE, AND TIDAL CYCLES IF PREDATION ON OVIGEROUS FEMALES OR THEIR EMBRYOS IS THE PRIMARY SELECTIVE FORCE

Vertical Zone of Females	Light-Dark Cycle	Tidal Amplitude Cycle	Tidal Cycle	Synchrony
High	Night	Monthly maximum	High	Strong
Middle	Night	Biweekly maxima	High	Moderate
Low	Night	Asynchronous	High	Weak

NOTE.—The lunar cycle has been omitted because it is not used by intertidal crabs to time larval release. However, predictions would match those for the tidal amplitude cycle because the two environmental cycles are coupled along the Pacific coast of Panama. Predicted synchrony of larval release by species that inhabit different areas of the intertidal zone also is shown.

TABLE 2

PREDICTED TIMES OF PEAK HATCHING BY VULNERABLE AND WELL-DEFENDED LARVAE OF INTERTIDAL CRABS IF PLANKTIVOROUS FISHES ARE THE PRIMARY SELECTIVE AGENT THAT REGULATES THE TIMING OF LARVAL RELEASE

	Light Cycle	Tidal Amplitude Cycle	Tidal Cycle
Vulnerable	Night	Maximum-amplitude tides	High
Well defended	Night and day	Asynchronous	High and low

NOTE.—Vertical zonation should not influence the timing of larval release (see text). Vulnerable larvae should be transported from shorelines most rapidly during maximum-amplitude tides, and well-defended larvae may not be swept offshore as quickly if they are released irrespective of tides.

intertidal zone should release larvae near maximum-amplitude high tides because only then will they be immersed. Species that occur lower in the intertidal zone will be immersed more often during the lunar month and for longer periods during each tide, and hatching patterns should be less synchronous (see table 1). These predictions assume that crabs and embryos are equally susceptible to visual predators, and may be complicated by interspecific differences in vulnerabilities.

If planktivory is the ultimate factor that determines the timing of larval release, then two predictions follow (table 2). First, species with larvae that are most vulnerable to predation should hatch near nocturnal maximum-amplitude high tides, and those with inconspicuous well-defended larvae should hatch less synchronously with respect to these environmental cycles. Second, crabs should release larvae at this time regardless of their position in the intertidal zone. Even species with vulnerable larvae from the lower intertidal zone should release larvae on maximum-amplitude high tides, when the risk of planktivory is least, even though they can safely release larvae from refuges on lower-amplitude tides.

If predation on adults, embryos, and larvae together influence the timing of larval release, then peak hatching should occur at the times predicted in table 3. All intertidal crabs should release larvae when their burrows are inundated. Because high intertidal species will be inundated only by the higher of the semi-

TABLE 3

PREDICTED TIMES OF PEAK RELEASE OF VULNERABLE AND WELL-DEFENDED LARVAE BY SPECIES OF CRABS THAT LIVE IN DIFFERENT AREAS OF THE INTERTIDAL ZONE IF PREDATION ON ADULTS (OF EMBRYOS) AND LARVAE BOTH REGULATE THE TIMING OF LARVAL RELEASE

VERTICAL ZONE OF FEMALES	TIMING OF LARVAL RELEASE					
	LIGHT-DARK CYCLE		TIDAL AMPLITUDE CYCLE		TIDAL CYCLE	
	Vulnerable	Defended	Vulnerable	Defended	Vulnerable	Defended
High	Night	Night and day	Monthly	Monthly	High	High
Middle	Night	Night and day	Biweekly	Biweekly	High	High
Low	Night	Night and day	Biweekly	Asynchrony	High	High

NOTE.—Timing is shown relative to light-dark, tidal amplitude, and tidal cycles. High intertidal crabs are predicted to release larvae on the highest amplitude tides of the month, middle intertidal species should release larvae biweekly during both sets of maximum-amplitude high tides, and low intertidal crabs may release larvae on high tides every day (asynchronously with respect to the tidal amplitude cycle).

monthly spring tides, they should release larvae once a month. Middle intertidal species should release larvae biweekly because they will be inundated by both spring tides, but perhaps not by neap tides. Because all high tides inundate low intertidal species, those with well-defended larvae should hatch daily and species with vulnerable larvae should release them biweekly to facilitate transport from shorelines. Species with vulnerable larvae may hatch at night when many planktivorous fishes do not feed, and those with better-defended larvae may hatch during the day and night.

This study was undertaken to determine whether predation by visual predators primarily explains both similarities and differences among hatching patterns of crabs. We also examined whether predation on offspring or adults primarily shapes the timing of larval release by crabs. We exploited the high diversity of crabs in the extensive intertidal zone (6.2-m tidal range) on the Pacific coast of the Republic of Panama to test the predictions that were outlined in tables 1–3. We determined the timing of larval release by 10 species of crabs from the low, middle, or high intertidal zone. The preference of a planktivorous fish for five of these species was tested and reported elsewhere (S. G. Morgan and J. H. Christy, unpublished manuscript). We use the results of both studies to test predictions of the impact of visual predators on the timing of larval release by these 10 species as well as by 46 species of crabs worldwide. Finally, we show that other proposed selective agents do not adequately explain hatching rhythms of crabs.

MATERIAL AND METHODS

Study Animals and Field Sites

We determined hatching patterns of four species of crabs from the low intertidal zone: three xanthids (*Cataleptodius taboganus*, *Xanthodius sternbergii*, and *Eurypanopeus planus*) and one porcellanid (*Petrolisthes armatus*). Three species

from different families represented the middle intertidal zone: one xanthid (*Eurypanopeus depressus*), one ocypodid (*Uca beebei*), and one grapsid (*Pachygrapsus transversus*). *Pachygrapsus transversus* ranged throughout the rocky intertidal zone but was categorized as occurring in the midintertidal zone based on its median distribution. Three species belonging to two families inhabited the uppermost reaches of the intertidal zone: two ocypodids (*Uca galapagensis* and *Uca oerstedii*) and one grapsid (*Sesarma rhizophorae*). In addition, a few individuals of several other species of brachyuran crabs from the upper intertidal zone showed similar hatching patterns and were combined into one group. These were the grapsid (*Goniopsis pulchra*), the xanthid, (*Panopeus purpureus*), and the ocypodid (*Uca argillicola*).

Crabs were collected and the timing of larval release of crabs relative to the day-night and tidal cycles was determined at three field sites near the Pacific entrance to the Panama Canal. Hatching by *C. taboganus*, *X. sternberghii*, *E. planus*, *P. armatus*, and *P. transversus* was studied on the east side of Naos Island where these species live under boulders and stones in the intertidal zone. *Uca beebei* and *E. depressus* were studied at a site near Rodman Naval Station in Diablo Heights where a muddy sand flat is bounded landward by mangroves and a bank of boulders. Hatching by all six species of high intertidal crabs was determined near mangroves at the heads of two tidal creeks.

Determination of the Timing of Larval Release

The timing of larval release by *Cataleptodius taboganus*, *Xanthodius sternberghii*, *Eurypanopeus planus*, and *Petrolisthes armatus* was determined in 1983 and 1984 and has been reported elsewhere (Christy 1986). Larval release by *Uca galapagensis* and *Pachygrapsus transversus* was studied in 1987 and also has been reported (Morgan and Christy 1994). Here we present the results of these studies in summary form. Hatching patterns of *Eurypanopeus transversus*, *Uca beebei*, *Uca oerstedii*, *Sesarma rhizophorae*, and the combination of *Uca argillicola*, *Panopeus purpureus*, and *Goniopsis pulchra* were studied in 1987 and are reported fully here. The timing of larval release remains constant within and among years in these Pacific coastal sites (Christy 1986; Morgan and Christy 1994).

Elsewhere we have described in full the three techniques we used to determine when crabs release larvae (Morgan and Christy 1994). At the Naos Laboratories, we held ovigerous females individually in compartmented plastic trays at ambient seawater and light conditions, and we checked them daily for larval release. The date of larval release is determined once eggs are spawned. This method yields accurate estimates of hatching patterns relative to lunar and tidal amplitude cycles as long as crabs are maintained at ambient conditions (Christy 1982*b*, 1986; Morgan and Christy 1994).

We determined hatching patterns relative to light-dark and tidal cycles in the field where tides reinforce rhythms (Salmon et al. 1986). Ovigerous *P. transversus*, *C. taboganus*, *E. planus*, *E. transversus*, *X. sternberghii*, and *P. armatus* and smooth, flat rocks were placed inside a rectangular wooden box (92 cm × 20 cm × 16 cm, inner dimensions) that was sheathed with fiberglass and covered with a removable Plexiglas top. The walls and top of the box were perforated with holes that were screened with 153- μ m mesh Nitex cloth. A vertical partition

divided the box into two equal compartments so that hatching by two species could be monitored at the same time. The box was anchored in the intertidal zone amid natural populations of the species. A 60-ft pump hose connected a manual diaphragm pump to either end of the box. The pump discharged through a hose into a 10-cm diameter plankton net (153- μ m mesh) that was mounted in a second box above the water line. Larvae released by females in the box were collected by pumping enough water through the screened openings to replace the water inside the box and suction hose by 3.5–4.5 times. Collections were made every 30 min during each tidal cycle, beginning when water covered the suction hoses and ending when suction hoses again were exposed.

Ovigerous *U. beebei* were placed into a box of similar construction except it was larger (100 cm \times 50 cm \times 40 cm) and lacked a bottom. Burrows 20 cm deep and 1.3 cm in diameter were made for crabs, using a coring device. Larvae were collected as described above. Too few ovigerous females were collected in September to use both the tray and pumping techniques. Therefore, the daily volume of larvae hatched in the box, rather than numbers of females releasing larvae in trays, was used to quantify larval release.

The timing of larval release by *U. galapagensis*, *U. oerstedii*, *U. argillicola*, *P. purpureus*, *S. rhizophorae*, and *G. pulchra* could not be determined by pumping because little water covered the upper reaches of tidal creeks where these species lived. Instead, compartmented trays containing crabs were placed inside a rack that was anchored to the creek bed before high tide. The bottom of each compartment was perforated and screened to permit water exchange. The rack was raised to the surface at 30-min intervals, except immediately following high tides, when ovigerous females were checked every 5–10 min. The number of females that had released larvae was counted quickly by using a flashlight. Preliminary observations revealed that all species released larvae only at night. Therefore, trays were kept in outdoor seawater tables at the Naos Laboratories during the daytime to prevent crabs from overheating.

Tidal height was measured every 30 min while monitoring larval release. Larvae were preserved in 5% buffered formaldehyde solution. Hatching was quantified either by counting larvae in each 30-min sample or measuring the amount of larvae volumetrically in graduated test tubes.

Statistics and Data Presentation

All data were analyzed using Rayleigh's test (Batschelet 1981). The *r*-statistic was used to test for nonrandom hatching relative to four environmental cycles. The mean angle and angular deviation of each distribution were calculated to identify peaks and to estimate their dispersion. Bimodal distributions were combined so that they were unimodal before analysis. We determined the timing of larval release relative to a particular environmental cycle at least several times for most species. These samples were combined before analysis, except when different measures of hatching were used or when hatching patterns were compared to tidal amplitude cycles. The periods of the tidal amplitude cycles on the Pacific coast often alternated between 6 and 9 d. Consequently, data were grouped into these two categories before analysis. The total number of crabs examined, number of observational periods, and range of sample sizes for each

environmental cycle are shown in table 4. Observational periods ranged from about 2 wk to 3 mo.

Results of statistical analyses of the hatching patterns for all species are reported in table 4. Graphs of hatching patterns are provided only for species with hatching patterns that have not been published previously. Because hatching patterns remain similar over time, we have summarized hatching relative to lunar and tidal amplitude cycles in a single graph by selecting a representative month for each of the 10 species. Hatching patterns among species relative to tidal and light-dark cycles are unwieldy, and we were not able to summarize these patterns graphically; however, they are readily apparent in table 4. Graphs of these patterns for each species can be found elsewhere (Christy 1986; Morgan and Christy 1994).

RESULTS

High Intertidal Zone

Uca galapagensis, *Uca oerstedii*, *Sesarma rhizophorae*, and the other three species that were combined into a single group all released larvae highly synchronously on or 1 d after full moons when the largest-amplitude tides of the lunar month occurred (fig. 1; table 4). Hatching occurred between 0300 and 0500 hours and began immediately after the higher of the two semidiurnal high tides started to ebb (fig. 2; table 4). Nearly all crabs completed larval release within 10 min. *Uca galapagensis*, *U. oerstedii*, and *S. rhizophorae* all were active reproductively in July, when collecting began, but they stopped reproducing in January, when the study ended. Too few of the other high intertidal species were collected to determine whether they reproduced seasonally.

Middle Intertidal Zone

Hatching by *Eurypanopeus transversus* larvae was less synchronous than that of the high intertidal species but was more synchronous than that of *Pachygrapsus transversus* or *Uca beebei* (figs. 1, 3; table 4). Larvae of *E. transversus* hatched on full moons around the time of maximum-amplitude high tides, as did high intertidal crabs (figs. 1, 2; table 4). We do not know whether *E. transversus* reproduce biweekly, as do *P. transversus* and *Uca beebei*, or monthly, as do species in the high intertidal zone, because we did not collect *E. transversus* later in the month.

Hatching by *E. transversus* occurred on flood tides after midnight rather than on early ebb tides before dawn as for the high intertidal species (fig. 2; table 4). In contrast, *P. transversus* and *U. beebei* released larvae on the higher daytime semidiurnal tide during early ebb. Peaks of release occurred near dusk and dawn for *P. transversus* and soon after dawn for *U. beebei* (fig. 4; table 4).

Pachygrapsus transversus and *U. beebei* reproduced throughout the year. The reproductive season of *E. transversus* was not determined.

Low Intertidal Zone

Cataleptodius taboganus and *Xanthodius sternberghii* released larvae biweekly 1–3 d after maximum-amplitude tides and 3–6 d after full and new moons (fig. 1; table 4). *Petrolisthes armatus* and *Eurypanopeus planus* hatched asynchronously with respect to the tidal amplitude and lunar cycles (fig. 1; table 4).

TABLE 4

TIMING OF LARVAL RELEASE \pm SD RELATIVE TO LUNAR, TIDAL AMPLITUDE, TIDAL, AND LIGHT-DARK CYCLES OF 10 SPECIES OF CRABS THAT INHABIT LOW, MIDDLE, AND HIGH REGIONS OF THE INTERTIDAL ZONE ALONG THE PACIFIC COAST OF THE REPUBLIC OF PANAMA

SPECIES	LUNAR CYCLE			TIDAL AMPLITUDE CYCLE			TIDAL CYCLE			LIGHT-DARK CYCLE		
	Timing	<i>r</i>	<i>n</i>	Timing	<i>r</i>	<i>n</i>	Timing	<i>r</i>	<i>n</i>	Timing	<i>r</i>	<i>n</i>
High intertidal:												
<i>Uca galapagensis</i>	O < 1 d \pm 1.1 d }	.9738	234 (3: 58-97)	MAT } \pm 0.6 d }	.9903	234 (3: 58-97)	HT < 30 min } \pm 13 min }	.9318	137 (2: 58-79)	0400 hours } \pm 15 min }	.9979	137 (2: 58-79)
<i>Uca oerstedii</i>	O < 1 d \pm 0.4 d }	.9954	48	MAT } \pm 0.4 d }	.9954	48	HT < 30 min } \pm 14 min }	.9126	48	0400 hours } \pm 24 min }	.9944	48
<i>Sesarma rhizophorae</i>	O < 1 d \pm 0.7 d }	.9898	55	MAT } \pm 0.7 d }	.9898	55	HT < 30 min } \pm 14 min }	.9161	55	0400 hours } \pm 24 min }	.9943	55
Others	O } \pm 0.3 d }	.9975	8	1 d < MAT } \pm 0.3 d }	.9974	8	HT < 30 min } \pm 3 min }	.9953	8	0330 hours } \pm 20 min }	.9963	8
Middle intertidal:												
<i>Eurypanopeus transversus</i>	O } \pm 0.7 d }	.9530	64	1 d < MAT } \pm 0.7 d }	.9530	64	90 min < HT } \pm 20 min }	.9385	64	0130 hours } \pm 45 min }	.9808	64
<i>Pachygrapsus transversus</i>	2 < O < 5 d \pm 2.3-3.4 d }	.6213-.7457	608 (4: 114-194)	2 < MAT < 2 d \pm 2.3-3.4 d }	.6213-.8582	608 (6: 51-134)	HT } \pm 38 min }	.8848	134	0600 & 1800 hours } \pm 69 min }	.8350	134
<i>Uca beebei</i>	O < 3-6 d \pm 3.3-3.9 d }	.2718-.3842	359 (2: 129, 166)	MAT < 2-3 d \pm 2.9-3.6 d }	.3289-.4830	359 (3: 66, 129)	HT } \pm 39 min }	.8639	129	0730 hours } \pm 180 min }	.7346	129
Low intertidal:												
<i>Cataleptodius taboganus</i>	O < 4 d \pm 1 d }	.9116	172 (5: 10-75)	MAT < 1 d \pm 1.7 d }	.7839	172 (5: 10-75)	HT < 30 min } \pm 48 min }	.8418	30	1830 hours } \pm 33 min }	.9898	30
<i>Xanthodius sternbergii</i>	O < 6 d \pm 1 d }	.9519	344	MAT < 2 d \pm 1.8 d }	.7634	344	HT < 30 min } \pm 42 min }	.8993	60	1900 hours } \pm 45 min }	.9814	60
<i>Eurypanopeus planus</i>	Asynchronous	...	107	Asynchronous	...	107	60 min < HT } \pm 66 min }	.7705	82	0600 & 1800 hours } \pm 87 min }	.7487	82
<i>Petrolisthes armatus</i>	Asynchronous	.0253	1,025	Asynchronous	.0690	1,001 (2: 333, 668)	HT } \pm 93 min }	.5885	150	0630 & 1830 hours } \pm 147 min }	.4415	150

NOTE.—“Others” refers to eight individuals of three species that were combined to determine the collective timing of larval release. Here *n* is the total number of crabs monitored for larval release relative to each environmental cycle. When multiple tests were conducted, the number of sample periods (duration of periods about 2–12 wk) and the range in number of crabs monitored per period is given in parentheses. All values of Rayleigh's *r* were highly significant, except for larval release by *P. armatus* relative to lunar and tidal amplitude cycles and by *E. planus* relative to tidal amplitude cycles. Mean angles were calculated using intervals of 1 d for lunar and tidal amplitude cycles and 30 min for light-dark and tidal cycles. O, new and full moons; MAT, maximum-amplitude tides; HT, high slack tide; dawn, 0600 hours; dusk, 0700 hours.

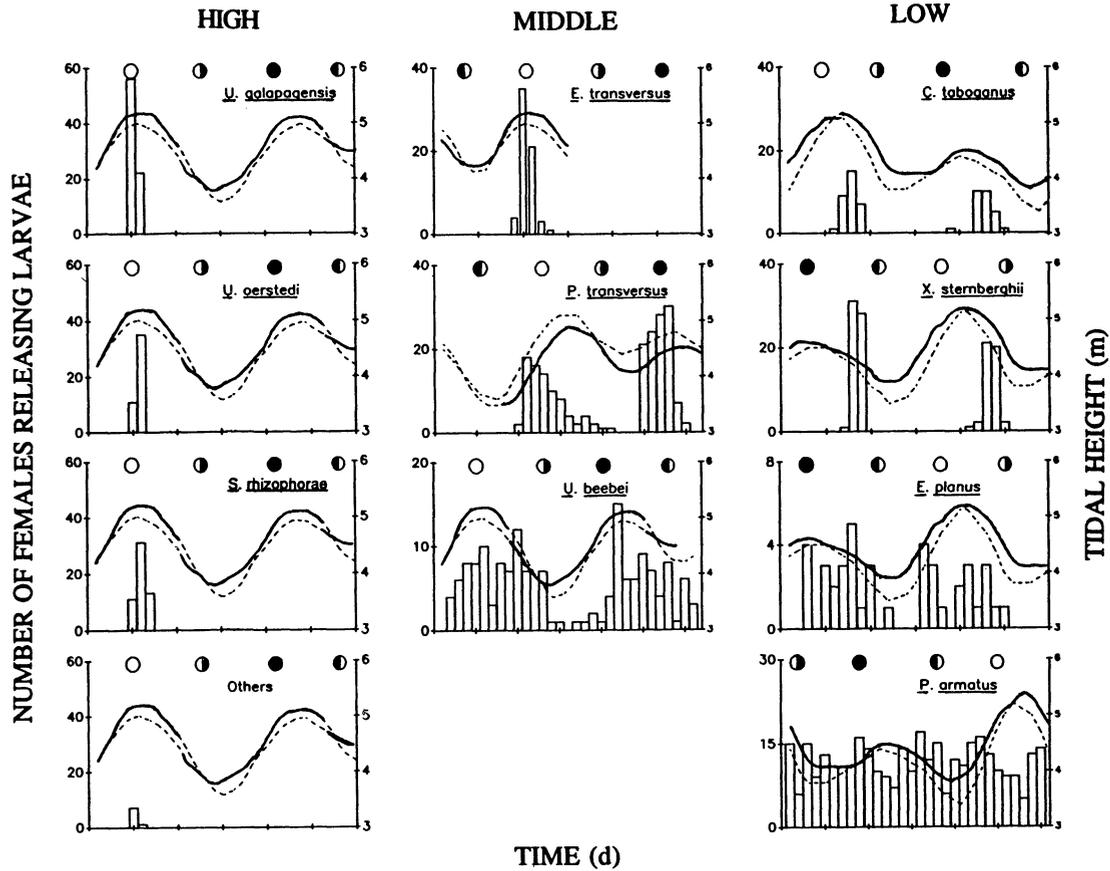


FIG. 1.—Timing of larval release relative to predicted lunar and tidal amplitude cycles by 10 species of crabs from different areas of the intertidal zone along the Pacific coast of Panama. Three high intertidal species (*Uca argillicola*, *Goniopsis pulchra*, *Panopeus purpureus*) formed an eleventh species group called “others.” Numbers of females releasing larvae are shown by bar graphs. Solid and dashed lines represent nighttime and daytime high tides, respectively. Open, solid, and half-filled circles represent full, new, and quarter moons, respectively.

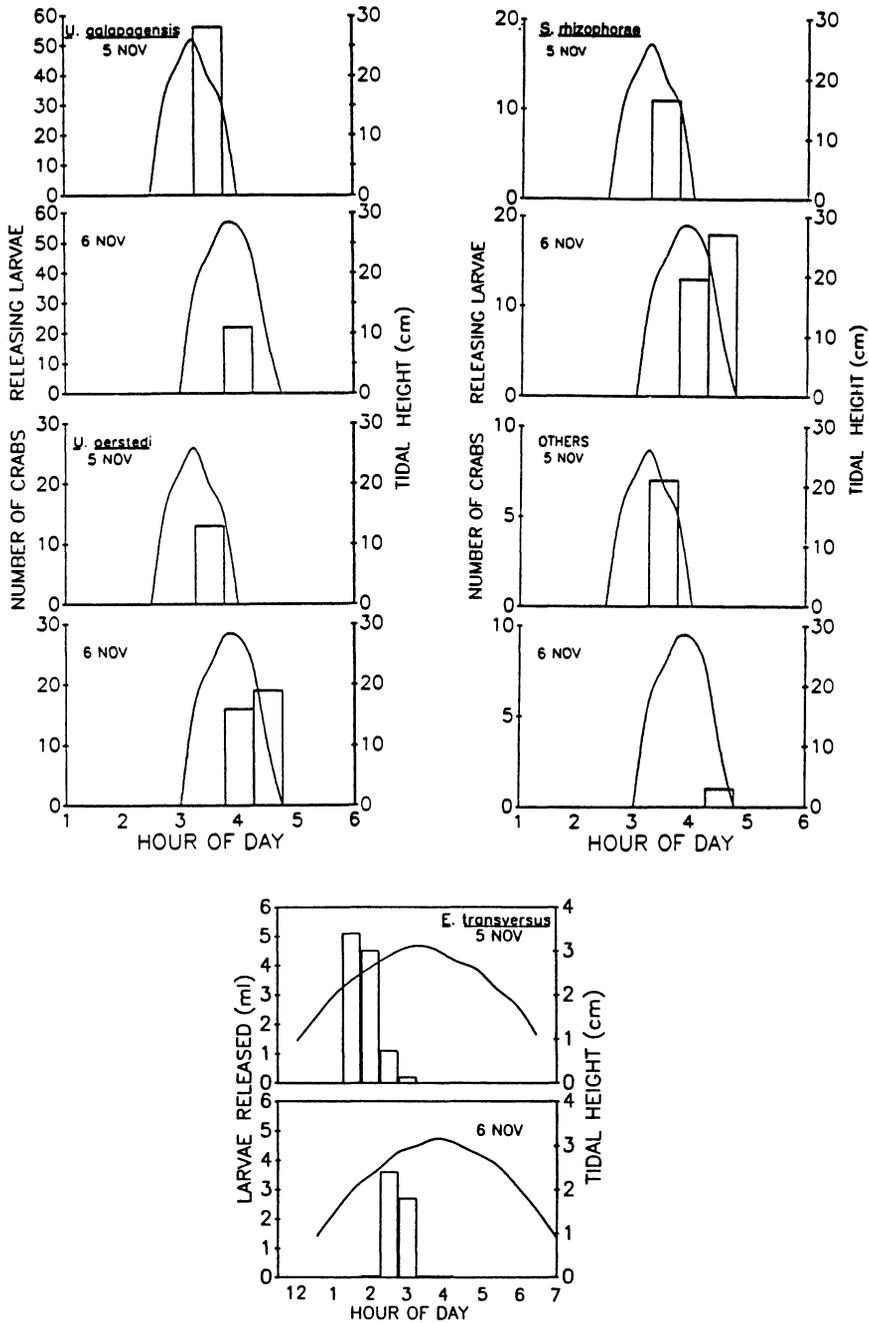


FIG. 2.—Timing of larval release (bar graphs) by three high intertidal species (*Uca galapagensis*, *Uca oerstedii*, *Sesarma rhizophorae*), a group of three high intertidal species (*Uca argillicola*, *Goniopsis pulchra*, *Panopeus purpureus*) called “others,” and one middle intertidal species (*Eurypanopeus transversus*) relative to light-dark and tidal cycles (line graphs) from the Pacific coast of Panama. All crabs released larvae on nocturnal high tides between midnight and 0700 hours during 2 consecutive days.

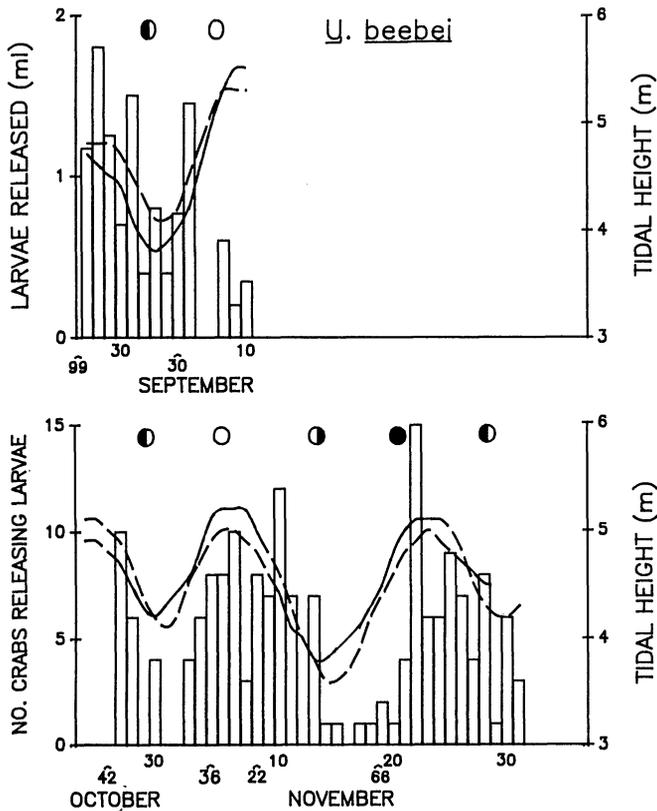


FIG. 3.—Timing of larval release by the middle intertidal crab, *Uca beebei*, relative to predicted lunar and tidal amplitude cycles along the Pacific coast of Panama. Numbers of females releasing larvae are shown by bar graphs. Solid and dashed lines represent nighttime and daytime high tides, respectively. Open, solid, and half-filled circles represent full, new, and quarter moons, respectively. The number of ovigerous females that were added to the experimental chamber on a particular day is indicated on the X-axis by a caret (^).

Except for *E. planus*, crabs from the low intertidal zone released larvae within 30 min of high slack tides. *Eurypanopeus planus* released larvae during flood tides, as did its congener from the middle intertidal zone, *E. transversus* (table 4). *Eurypanopeus planus* released larvae during both diurnal tides, *P. armatus* hatched on nocturnal or crepuscular high tides, and *C. taboganus* and *X. sternberghii* only released larvae when high tides peaked at the onset of darkness (table 4).

We rarely found ovigerous *C. taboganus*, *X. sternberghii*, and *E. planus* from May through August. *Petrolisthes armatus* reproduced at least from November through May.

DISCUSSION

Predatory fishes ultimately may determine the timing of larval release by intertidal crabs from the Pacific coast of Panama. First, fishes may enforce release of

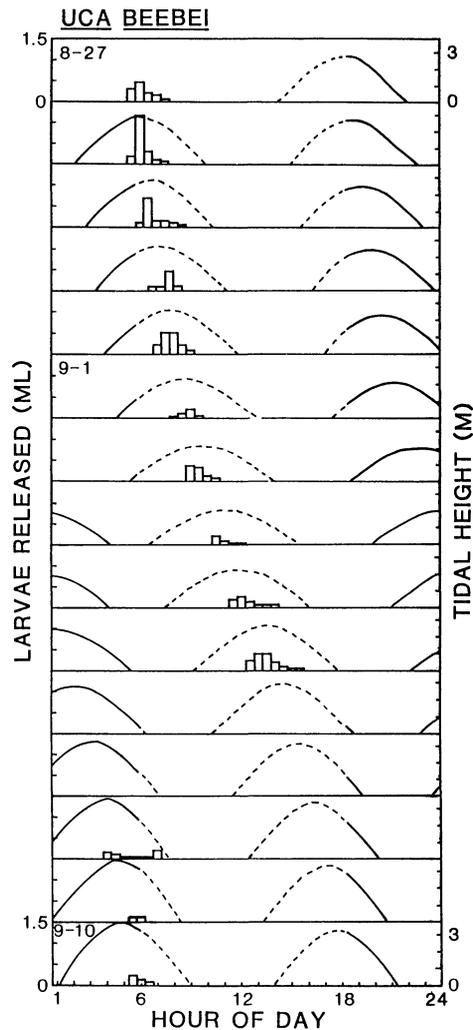


FIG. 4.—Volume of larvae released (*bar graphs*) every 30 min by *Uca beebei* relative to light-dark and tidal cycles. Solid and dashed lines represent nighttime and daytime high tides from August 27 to September 10, 1987, along the Pacific coast of Panama. Hour of the day is based on a 24-h clock.

larvae near refuges, and therefore the vertical position of adults on the shoreline indirectly affects reproductive timing. Second, reproductive timing also is influenced by interspecific differences in vulnerabilities of larvae to planktivorous fishes.

Vertical Zonation

The distribution, abundance, and life histories of intertidal organisms are profoundly influenced by the frequencies and amplitudes of tides (Palmer 1974; De-

TABLE 5

SUMMARY OF HATCHING RHYTHMS OF 10 SPECIES AND ONE GROUP OF THREE SPECIES OF CRABS FROM THE PACIFIC COAST OF PANAMA RELATIVE TO LUNAR, TIDAL AMPLITUDE, TIDAL, AND LIGHT-DARK CYCLES

VERTICAL DISTRIBUTION	TIDAL AMPLITUDE/LUNAR			TIDAL		LIGHT-DARK	
	Monthly	Biweekly	Asynchrony	High	Low	Night	Day
High	4	0	0	4	0	4	0
Middle	0	3	0	3	0	1	2
Low	0	2	2	4	0	3	1

Coursey 1983). Residents of the high intertidal zone must endure severe environmental fluctuations, because they are immersed less often and for less time than those living lower on the shore. Consequently, organisms inhabiting the upper intertidal zone time activities differently and are more resistant to environmental fluctuations than those lower on the shore (Jansson 1967; Barnwell 1968; Frith and Brunenmeister 1980).

Many intertidal crabs are active on the surface during low tide. However, ovigerous females remain in burrows and crevices except to release larvae during high tide (Christy 1978; Saigusa 1982; Salmon 1987; Henmi 1989a). Nonovigerous crabs in the high intertidal zone emerge from their refuges, change color to thermoregulate, and reach their maximum metabolic rate sooner during each tidal cycle than crabs at the lower level (Fingerman 1960; Barnwell and Brown 1963; Wilkens and Fingerman 1965). They also may be more active at night than those from the lower shore (Barnwell and Brown 1963). Reproductive traits also may differ for species inhabiting the upper and lower regions of the shore. High intertidal species may have shorter breeding periods (Pillay and Ono 1978; Sastry 1983; Henmi 1989b) and produce fewer broods of fewer, larger eggs during breeding seasons (Bliss 1968; Pillay and Ono 1978; Henmi 1989b).

Reproductive seasons of high intertidal species in Panama were synchronized and were shorter than for species that inhabit the lower shore, as has been noted for crabs elsewhere (Pillay and Ono 1978; Sastry 1983; Henmi 1989b). Reproduction by the high intertidal species occurred during the wet season and ceased abruptly with the onset of the dry season. The reproductive seasons of low and middle intertidal species were not as synchronous. At least three of the seven species residing low on the shore reproduced throughout the year. Furthermore, the refractory period of three species (*Cataleptodius taboganus*, *Xanthodius sternberghii*, *Eurypanopeus planus*) occurred from May to August instead of the dry season as for high intertidal species.

In accordance with the predictions from table 1, the timing of larval release was correlated with the location of adults in the intertidal zone. All crabs released larvae on high tides, and the timing of larval release was most synchronous among high intertidal species and asynchronous in some low intertidal crabs (table 5). Hatching by all species that were situated at the extreme upper end of the intertidal zone occurred for a few minutes on one or two consecutive days each month

when the higher of the two biweekly sets of maximum-amplitude nocturnal high tides reached their habitat. Residents of the middle intertidal zone are covered by both of the monthly tidal maxima but may not be inundated during neap tides. Consequently, middle intertidal species reproduced biweekly (table 5). Based solely on vertical distributions, species from the lower intertidal zone would be expected to release larvae asynchronously, because they are immersed on all high tides. However, both asynchronous and biweekly hatching patterns were observed among these species (table 5).

Intertidal crabs may release larvae only when refuges are immersed to minimize encounters with predators, such as birds and raccoons that prey on crabs during low tide and fishes that eat crabs during high tides (Crane 1947; Engstrom 1984; Omori et al. 1984; Sasekumar et al. 1984; Abele et al. 1986; Wilson 1989; Warren 1990). All 10 species released larvae when their habitats were immersed regardless of the considerable differences in size, thickness of the exoskeleton, spination, coloration, speed, clutch size, egg color, and phylogeny. Egg-bearing females may remain near burrows during low tides because they are slower than nonovigerous females and may be less able to escape birds and raccoons (S. G. Morgan and J. H. Christy, personal observations). Female crabs release larvae by extending to their full height and vigorously pumping their abdomens for several minutes to fan larvae into surrounding waters (DeCoursey 1983; Forward 1987) and are likely to attract predators while in this exposed posture. Females that attract the attention of predatory fishes and crabs while releasing larvae during high tides could quickly retreat to refuges, wait until predators lose interest, and resume releasing larvae after predators depart.

Planktivory

Another selective force must influence hatching patterns because some low intertidal species released larvae on maximum-amplitude tides contrary to the predictions of table 1. Larval release by crabs throughout the intertidal zone may have converged on maximum-amplitude high tides if ensuing ebb tides transport larvae most expeditiously from shorelines where the risk of predation by planktivorous fishes is greatest (Christy 1982*b*, 1986; Morgan 1987*a*, 1990). Although larval survival of species from all levels of the intertidal zone may be enhanced by hatching on maximum-amplitude tides, only low intertidal species are immersed by all tides and therefore have the flexibility to release larvae at other times during the tidal amplitude cycle.

We selected several species from the low and middle intertidal zones that hatch either asynchronously or synchronously relative to the tidal amplitude cycle to determine whether planktivory may influence the timing of larval release. We then compared preferences of fish for newly hatched larvae of these species (S. G. Morgan and J. H. Christy, unpublished manuscript). Of the three xanthid crabs that reside sympatrically in the low intertidal, *C. taboganus* and *X. sternberghii* release larvae highly synchronously near the time of maximum-amplitude tides and *E. planus* releases larvae throughout the tidal amplitude cycle. During feeding trials in the Bay of Panama, silversides, *Hubbesia gilberti*, ate fewer *E. planus* larvae than *C. taboganus* and *X. sternberghii* larvae. Furthermore, silversides preferred larvae of

two middle intertidal species (*Pachygrapsus transversus*, *Uca beebei*) that hatch with moderate synchrony on maximum-amplitude tides to *E. planus* larvae, but not *C. taboganus* and *X. sternberghii* larvae. Therefore, larvae that are transported most rapidly from shorelines on maximum-amplitude ebb tides were preferred to larvae that often hatch on tides of lesser amplitude. These experiments suggest that planktivory ultimately may determine the timing of larval release relative to the tidal amplitude cycle by both middle and lower intertidal species.

Feeding trials also indicated that diurnally foraging planktivorous fish may influence the timing of larval release relative to the light-dark cycle (S. G. Morgan and J. H. Christy, unpublished manuscript). Silversides preferred two species that hatch only at night (*C. taboganus*, *X. sternberghii*) to three species that hatch both during the day and the night (*E. planus*, *U. beebei*, *P. transversus*). Thus, preferences of fish for crab larvae exactly matched predictions that were based on their hatching patterns (table 2). Larvae that hatch quite synchronously near nocturnal maximum-amplitude high tides (*C. taboganus*, *X. sternberghii*) were most vulnerable to planktivorous fish. Larvae that hatch moderately synchronously on maximum-amplitude high tides during the day and night (*U. beebei*, *P. transversus*) were eaten less often, and larvae that hatch during the day and night on high tides of any amplitude (*E. planus*) were least preferred.

The risk of predation to newly hatched larvae of intertidal crabs is primarily determined by the amount and color of pigments and secondarily determined morphologies or behaviors of larvae (S. G. Morgan and J. H. Christy, unpublished manuscript). For instance, larvae of *C. taboganus*, *X. sternberghii*, and *E. planus* have similar responses to attacks by fishes and are virtually identical morphologically; however, they are colored differently (table 6). Larvae of *C. taboganus* and *X. sternberghii* have red yolk and chromatophores, and *E. planus* larvae have a pale yellow-green appearance that reduces contrast with surrounding waters (Lythgoe 1979). Larvae of the other two species that often hatch during the day also are relatively inconspicuous to silversides, but they are small and have short spines that make them more vulnerable than *E. planus* larvae. Like *C. taboganus* and *X. sternberghii*, *P. armatus* release larvae crepuscularly or nocturnally and have red yolk and chromatophores, which presumably render these larvae highly vulnerable to planktivorous fish despite their long spines.

Hatching Rhythms of Crabs Worldwide

Patterns of larval release by 46 species of crabs worldwide (table 7) are similar to the 10 species of intertidal crabs from the Pacific coast of Panama (table 5). This condition suggests that predation may shape the hatching rhythms of crabs worldwide, including supratidal and subtidal species. Supratidal crabs must leave burrows to release larvae and therefore should be free to release larvae on tides of any amplitude. Similarly, subtidal crabs always are covered by water and should be able to release larvae independently of tides. However, all supratidal crabs and some subtidal crabs release larvae on maximum-amplitude high tides. This further supports the conclusion that releasing larvae on maximum-amplitude high tides facilitates offshore transport of vulnerable larvae and that planktivory

TABLE 6
MORPHOLOGY, COLOR, AND VULNERABILITY TO PLANKTIVOROUS FISHES OF NEWLY HATCHED LARVAE OF 10 SPECIES OF CRABS
FROM THE PACIFIC COAST OF PANAMA

SPECIES/VERTICAL ZONATION	MORPHOLOGY			COLOR			Risk
	Body Size	Spine Length	Spine Number	Chromatophores	Yolk	Larva	
High intertidal:							
<i>Uca galapagensis</i>	Small	Short	2	Brown	Yellow	Brown	High
<i>Uca oetzedi</i>	Small	Short	2	Yellow brown	Yellow	Light ocher	Moderate
<i>Sesarma rhizophorae</i>	Small	Short	3	Dark brown	Yellow	Brown	High
Middle intertidal:							
<i>Eurypanopeus transversus</i>	Medium	Long	4	Black	Yellow	Pale yellow	Moderate
<i>Pachygrapsus transversus</i>	Small	Short	3	Dark brown/ yellow-green	Yellow-green	Dark brown or yellow-green	Moderate
<i>Uca beebei</i>	Small	Short	2	Brown-yellow	Yellow	Light ocher	Moderate
Low intertidal:							
<i>Eurypanopeus planus</i>	Medium	Long	4	Black	Green	Pale green	Low
<i>Cataleptodius taboganus</i>	Medium	Long	4	Red	Red	Red	High
<i>Xanthodius sternberghii</i>	Medium	Long	4	Red	Red	Red	High
<i>Petrolisthes armatus</i>	Medium	Very long	3	Red	Red	Red	High

NOTE.—The maximum number of larval spine types is four: one dorsal, one rostral, one pair of antennal, and one pair of lateral spines.

TABLE 7

SUMMARY OF A WORLDWIDE SURVEY OF THE HATCHING RHYTHMS OF 46 SPECIES OF CRABS WITH RESPECT TO VERTICAL ZONATION OF FEMALES AND LUNAR, TIDAL AMPLITUDE, TIDAL, AND LIGHT-DARK CYCLES

VERTICAL DISTRIBUTION	TIDAL AMPLITUDE/LUNAR				TIDAL		LIGHT-DARK	
	Annually	Monthly	Biweekly	Asynchrony	High	Low	Dark	Light
Supratidal-high intertidal	1	2*	6	0	7	0	7	0
High intertidal	0	5	0	0	5	0	5	0
Intertidal	0	0	11	0	10	0	8	2
Low intertidal-subtidal	0	0	8	7	9	0	8	5
Subtidal	0	0	2	4	1	2

* Different populations of the two species hatch monthly or biweekly. See Morgan (1995) for references.

may be the primary force influencing the timing of larval release by crabs from nearshore habitats.

As with high intertidal crabs, supratidal crabs only appear to release larvae at night. These crabs commonly release larvae in tidal creeks, marshes, and mangroves, where fishes may be especially abundant (Weinstein 1979; Boesch and Turner 1984; Thayer et al. 1987; Morgan 1990; Sogard and Able 1991; Ayyvazian et al. 1992; Rountree and Able 1992; Sasekumar et al. 1992; Baltz et al. 1993). The likelihood of broods and clouds of even inconspicuous, well-armed larvae being detected simply may be too great for hatching to occur during the daytime in these shallow productive areas (S. G. Morgan and S. T. McAfee, unpublished manuscript).

Densities of fishes around subtidal species may be less than those encountered by supratidal crabs, and therefore well-defended larvae of some subtidal species may hatch safely during the daytime. Thus, flexibility in the timing of larval release relative to tidal amplitude and light-dark cycles increases inversely with the risk of predation from the supratidal to the subtidal zones. However, all crabs examined release larvae on high tides presumably to export larvae from coastlines where planktivorous fishes may be more prevalent than farther offshore (Morgan 1987a, 1990).

Alternative Hypotheses

Energetic considerations are unlikely to explain the hatching patterns shown by the 10 species of crabs from Panama. Although it is conceivable that the high intertidal species considered here may release larvae near burrows simply to avoid walking a long distance to the water, it is difficult to believe that this is significant for many other species that forage throughout the intertidal zone daily. Furthermore, energetic considerations cannot explain why the large majority of crabs only release larvae at night.

Avoidance of larval stranding (Salmon et al. 1986) also cannot entirely explain why intertidal crabs hatch on high tides and many hatch on maximum-amplitude high tides. It is unlikely that some species from subtidal and low intertidal zones release larvae on maximum-amplitude high tides because their larvae are more

prone to stranding along shorelines than neighboring species that hatch on low-amplitude high tides.

Physiological stress also has been invoked to explain the hatching patterns of crabs (Dollard 1980; Saigusa 1981), but evidence for this hypothesis is not compelling. By hatching on nocturnal maximum-amplitude high tides, larvae that are released in tidal creeks and estuaries may minimize exposure to high temperatures and low salinities. Maximum temperatures in shallow waters usually occur during afternoons, so that larvae released at night experience lower temperatures until they are carried to deeper waters on the next ebb tide. Hatching on maximum-amplitude high tides would expose larvae to cooler, higher-salinity waters, which may be especially important when rainfall is heavy and salinities are low.

However, we expect that larvae of crabs living in the high intertidal zone in Panama and elsewhere are well adapted physiologically to this demanding environment. First, larvae of the fiddler crab, *Uca minax*, which typically are released into tidal creeks and shallow water habitats, survived very well when exposed to stressful temperature and salinity conditions for two days (Morgan 1987a). Indeed, *U. minax* larvae, which quickly disperse downstream to the sea, survived much better than larvae of the subtidal crab, *Rhithropanopeus harrisi*, which are retained in low-salinity waters throughout development. Second, even subtidal crabs from diverse habitats commonly hatch larvae at night (Morgan 1995), which suggests that thermal stress may not be the primary force selecting for nocturnal larval release by intertidal crabs. Third, intertidal crabs that live on exposed coasts, where water temperatures and salinities vary little, also release larvae on nocturnal maximum-amplitude high tides (Christy 1986).

It has been hypothesized (Christy 1978) that larvae are released by fiddler crabs when reinvasion of adult habitats weeks later is facilitated by spring flood tides, but the settlement-timing hypothesis has since been rejected (Christy 1982b). Therefore, the selective advantage of releasing larvae on high-slack spring tides probably operates as tides ebb in the first 6 or 12 h of hatching in semidiurnal and diurnal tidal regimes, respectively.

Ultraviolet radiation (UV) may kill crab larvae that remain in surface waters for even less than a day and could influence the timing of larval release (S. G. Morgan and J. H. Christy, unpublished manuscript). If so, then larvae with few UV-absorbing pigments should hatch only at night and heavily pigmented larvae may hatch during the day. However, the relative vulnerability of various species of crab larvae to UV did not match patterns of larval release (S. G. Morgan and J. H. Christy, unpublished manuscript).

Predatory invertebrates also are unlikely to entirely explain complex hatching patterns, such as widespread hatching at night. Because they do not rely on light to capture prey, predatory invertebrates could enforce nocturnal larval release only if they were more abundant during daytime than nighttime. However, such strong patterns from various habitats worldwide likely would have been noticed. Furthermore, spines, the primary defensive structures of crab larvae, appear to have evolved specifically to deter planktivorous fishes rather than predatory invertebrates (Morgan 1989, 1992), which suggests that fishes may be the primary predators of crab larvae.

None of these alternative hypotheses satisfactorily explains why many crabs release larvae on nocturnal spring high tides despite differences in evolutionary history, nor can they explain the diversity of hatching patterns shown by crabs.

CONCLUSIONS

Predation by visual predators may best explain the hatching patterns of crabs. Egg-bearing females, embryos, and larvae all risk predation during larval release, and the hatching patterns of supratidal, intertidal, and subtidal crabs may reduce predation on all three life stages. Larvae most likely are released near refuges, which thereby reduces predation by marine predators, such as fishes and other crabs, on embryos or females. Consequently, the vertical zonation of species largely determines the synchrony of larval release relative to the tidal cycle. Hatching is highly synchronous for species from the high intertidal zone because these crabs are inundated by fewer tides than those from the lower shore. Another benefit accrues from releasing larvae on maximum-amplitude high tides. Larval survival may be enhanced by hatching on these tides because larvae are transported most rapidly from shorelines where planktivorous fishes abound. Therefore, even some low intertidal and subtidal species with larvae that are particularly vulnerable to predation may hatch biweekly even though crabs are inundated daily. Other low intertidal and subtidal species with larvae that are better defended from planktivorous fishes release larvae daily. Supratidal crabs that must walk to the water to release larvae also may release larvae on maximum-amplitude tides to expedite transport of larvae from shorelines.

Planktivory may be the driving force behind diel hatching patterns of intertidal crabs. Only species with larvae that were relatively inconspicuous to fish hatched during the day and night, whereas highly conspicuous larvae hatched only at night, which thereby minimized exposure to diurnally foraging planktivores. Furthermore, the occurrence of daytime hatching appeared to be unrelated to interspecific differences in attributes of adults or embryos.

Thus, selection for avoidance of visual predators can explain the complex hatching patterns of intertidal crabs. Avoidance of larval strandings, physiological stress and predatory invertebrates, facilitation of larval settlement, and energetic considerations alone cannot account for the diversity of hatching patterns shown by intertidal crabs.

Some coral reef fishes, intertidal fishes, and other marine invertebrates also release larvae or spawn gametes on nocturnal maximum-amplitude high tides. This hatching pattern may have evolved independently among diverse groups of shallow-water animals primarily in response to predatory fishes. However, specific predictions of our paradigm may need to be modified for other groups of animals due to fundamental differences in life histories.

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