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LARVAL INVERTEBRATE WORKSHOP

TIMING OF LARVAL RELEASE BY INTERTIDAL CRABS ON AN EXPOSED SHORE

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ABSTRACT

Semilunar, tidal and diel timing of larval release by four species of intertidal crabs that occur together on exposed cobble beaches on the Pacific coast of Panama was studied to provide comparisons to temporal patterns of hatching known for estuarine species. Ovigerous females, collected periodically and held until their eggs hatched, were observed daily to determine day-to-day variation in the number releasing larvae. Tidal and solar-day timing of hatching were studied by collecting, at 30-min intervals, zoeae released by females held in a box in the intertidal zone. *Xanthodius sternberghii* and *Cataleptodius taboganus* released larvae at night within 1.5 h of high tide and usually during the hour following last light 1–4 days before the quarter moons. *Eurypanopeus planus* released larvae throughout the lunar cycle about 1 h before both daytime and nighttime high tides. *Petrolisthes armatus* also released larvae throughout the lunar month but hatching usually occurred only near the times of high tides that peaked at twilight or at night. The timing of hatching by *X. sternberghii* and *C. taboganus* is closely similar to that exhibited by several intertidal estuarine crabs. In estuaries, such timing may aid escape of larvae from lethal high temperatures and low salinities. Since these environmental factors vary little with the tidal and diel light cycles on exposed coasts they are unlikely to be important mortality factors influencing the timing of hatching in such habitats. Instead the timing of larval release may aid escape of newly hatched larvae from planktivorous fish that locate prey visually. Contrasts in the timing of hatching among the four species are associated with differences in zoeal size and color, features that may affect their visibility to predators.

Precise semilunar, tidal and diel timing of larval release has been reported for several subtidal and intertidal estuarine crabs as well as terrestrial species that migrate to estuarine shores to release larvae (see Christy, 1982 and DeCoursey, 1983, reviews). Hatching in most species occurs on the days of the lunar month that high tides occur near dawn and dusk regardless of lunar phase. In populations exposed to natural diel light cycles, larvae are released only after sunset following the evening high tide. Semilunar periods of larval release often occur when nocturnal ebb tides reach their greatest amplitudes during the semilunar cycle. Consequently, during their first hours of life, zoeae are dispersed by ebb currents at night toward the sea at maximal semilunar rates and may be carried into the coastal ocean (Christy and Stancyk, 1982). High temperatures (Dollard, 1980), reduced salinities (Saigusa, 1981) or both, and intense predation by visually hunting larval and juvenile fish may produce high mortality among larvae released in the upper estuary during the day (Christy, 1982). Hence there might exist selection on females to release larvae when they are most rapidly transported seaward by nocturnal ebb currents. These ideas are difficult to test directly by field experiment because adequate techniques for marking larvae and identifying sources of mortality, even in small estuaries, have yet to be devised. Comparative studies of the timing of larval release by crabs that occur in non-estuarine habitats can, however, provide information helpful in evaluating these ideas.

The purpose of this research was to describe the semilunar, tidal and diel timing of larval release by crabs that occur intertidally on an exposed shore. The xanthid crabs *Xanthodius sternberghii, Cataleptodius taboganus* and *Eurypanopeus planus* were studied to provide comparisons to the estuarine xanthids *Panopeus herbstii*

and *Rhithropanopeus harrisii* for which aspects of the timing of larval release are known (Christy and Stancyk, 1982; Forward et al., 1982). The anomuran porcellanid crab *Petrolisthes armatus,* which occurs sympatrically with the xanthids, was also studied to extend description of the timing of larval release to a non-brachyuran intertidal crab.

Study Site, Animals and Methods

Study Site and Animals.—This study was done at the Naos Marine Laboratory of the Smithsonian Tropical Research Institute, Republic of Panama. Naos Island is located on the east side of the Pacific entrance to the Panama Canal, approximately 2.5 km from the mainland to which it is connected by a causeway. Field sites were located on the east side of the island where boulders and stones occur over sand in the upper and mid-intertidal zones. Tides are semidiurnal. Tidal amplitudes ranged from approximately 2.5 m during the lowest amplitude neap tides to 6 m during the most extreme spring tides during this study. Spring high tides occurred from 0 to 3 days after the full and new moons at approximately 1600–1800 h and 0400–0600 h, Eastern Standard Time.

All four species occurred abundantly in the lower intertidal zone where they sheltered under stones when the area was exposed during low tide. The xanthids usually occurred in crude burrows or hollows in the rock-sand substrate. *P. armatus* simply clung to the undersides of stones. *P. armatus* is a filter feeder. Chela morphology and wear suggests *X. sternberghii* and *C. taboganus* scrape the rock substrate to feed while *E. planus* is a predator. Abele (1976) provides a list of the other common decapods in this habitat.

Semilunar Timing of Larval Release.—Day-to-day variation in the number of females releasing larvae was studied by collecting ovigerous females during diurnal low tides and holding them individually in the compartments of plastic boxes which floated in seawater tables under a translucent roof in an outdoor pavilion. Females rested in approximately 1 cm of raw seawater which was changed daily, but they were not fed. Each morning the compartments in which females were held were examined for zoeae. When zoeae were found, larval release was scored and assigned the previous date. Collection dates and the numbers and species collected are shown in Figures 1–4.

Each collection of ovigerous females produced a record of the number that released larvae each day until the eggs of all females had hatched. If females bred asynchronously then one would expect an equal proportion of females in each collection to release larvae each day. The expected proportion would equal the inverse of the incubation period (time in days from oviposition to hatching). Incubation periods for the xanthids were obtained by collecting nonovigerous females, marking them, maintaining them in simulated habitat in seawater tables and recording daily the reproductive state of each individual. Males were not included, as all three species produced 1–3 clutches of fertilized eggs using stored sperm. The temperature in the seawater tables was recorded twice each day. At least 10 records of the length of incubation were obtained for each species over the range of temperatures to which females in the compartmented boxes were exposed. Incubation periods for *C. taboganus* and *X. sternberghii* ranged from 10 to 13 days. The minimum incubation period of 10 days was chosen for all tests of departure of the observed temporal distributions of larval release by females in each collection from that expected if hatching among females was asynchronous. This choice was made because plots of the number of hatches per day indicated hatching was synchronized among females. Use of the minimum incubation period results in more powerful statistical tests of the null hypothesis of asynchrony among females. The incubation periods for *E. planus* ranged from 9 to 11 days. In this case, the maximum recorded incubation period was chosen to calculate the expected number of hatches per day for the statistical tests because plots of the temporal distribution of larval release indicated hatching by this species was asynchronous among females. This choice results in conservative statistical tests of the null hypothesis of synchrony among females. The length of incubation used in the tests applied to *P. armatus* was the maximum recorded (9–11 days) from the females in each collection, since other estimates were not available.

Tidal and Solar Day Timing of Larval Release.—The timing of larval release relative to tidal stage, time of day and light intensity was studied in the field. Ovigerous females and flat rocks were placed in a rectangular wooden box (92 cm long, 20 cm high, 16 cm deep, inside dimensions) sheathed with fiberglass which was anchored in the intertidal zone at the level at which crabs were collected. The top of the box was made of plexiglass and was removable. The walls and top of the box were perforated with holes screened with 153-μm-mesh Nitex cloth. A pump hose (3.18 cm, internal diameter) was connected to one end of the box and to a large manual diaphragm pump (approximately 4 liters/stroke) positioned in the upper intertidal or supratidal zone. The pump discharged through a hose into a small plankton net (153 μm mesh) mounted obliquely in a second box. Zoeae released by

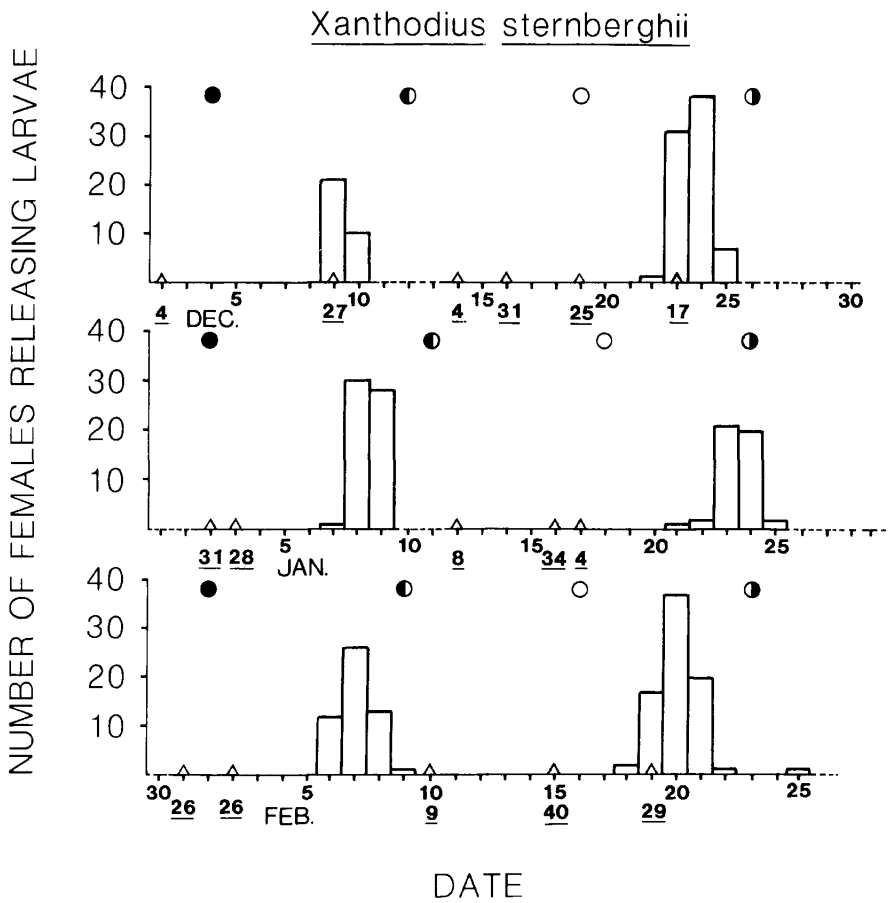

Figure 1. Number of female *Xanthodius sternberghii* releasing larvae per day. Triangles above the X-axis indicate the dates females were collected. Underlined numbers below the triangles give the numbers of females collected. Lunar phases are also indicated with the solid circle representing new moon.

females in the box were collected by operating the pump for a number of strokes sufficient to replace the water inside the box and suction hose from 3.5 to 4.5 times with seawater drawn through the screened openings. Studies with dyes revealed no areas inside the box where water might fail to be removed during a pumping cycle.

Zoeae were collected during two 10-day periods including 19 tidal cycles each and one 2-day period spanning three tidal cycles. (These collection periods are hereafter called sets.) The species and number of ovigerous females used during each set are given in Figures 6–8. Collections were taken every 0.5 h during each tidal cycle of each set, beginning when the water level rose to about 0.5 m above the top of the box containing females and ending 8–9 h later when the water level dropped to the same level. A series of 16–18 sequential collections was obtained for each tidal cycle. (The box was exposed for 3.5–4 h during each low tide period.) Zoeae collected in the net were removed and preserved in 4% buffered formaldehyde solution. All *P. armatus* zoeae were counted in all collections. The xanthid zoeae in each collection were counted when there were about 1,000 zoeae of each species or fewer; when more abundant, their numbers were estimated by diluting the collection and counting zoeae in three to five 8-ml samples taken with a stempil pipet (mean number of zoeae per species per 8 ml sample = 88.5).

Water level was recorded immediately before each collection. Light intensities ($\mu E\ s^{-1}\ m^{-2}$ in the 400–700-nm waveband; $1\ \mu E\ s^{-1}\ m^{-2} = 6.02 \times 10^{17}$ photons $s^{-1}\ m^{-2}$) in air and underwater at the level of the box also were recorded at this time (LI-COR LT 188B meter and LT 192SB quantum

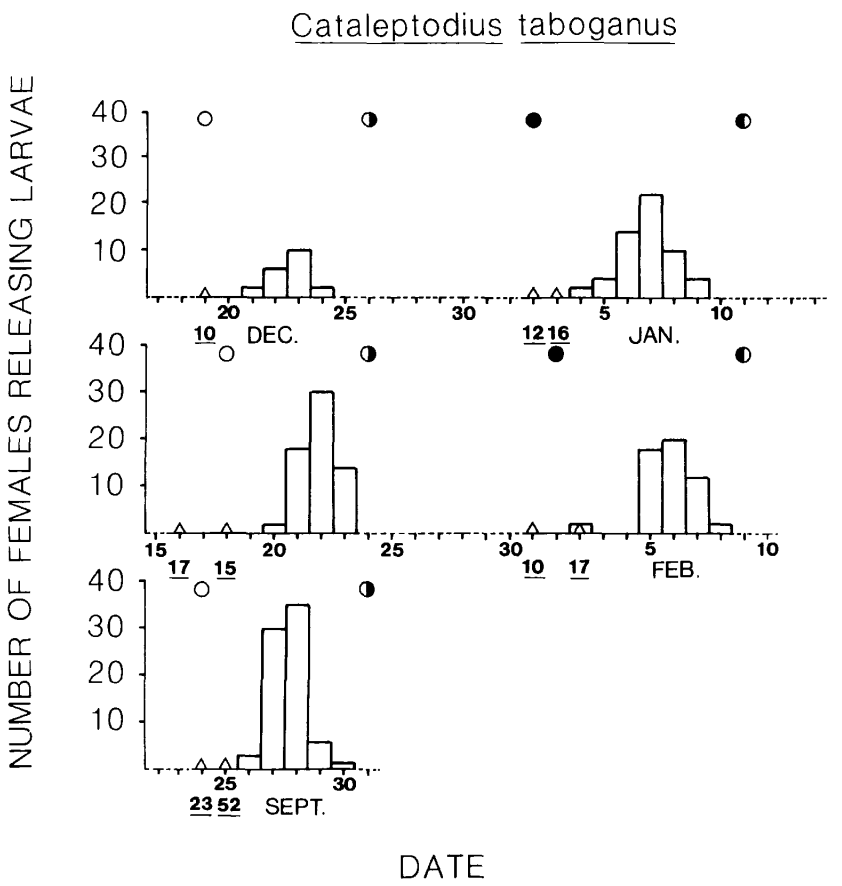

Figure 2. Number of female *Cataleptodius taboganus* releasing larvae per day. Symbols as in Figure 1.

sensor). The times of last and first light were defined as the collection times at which ≤ 1 μE s^{-1} m^{-2} light intensity was recorded at the box. Last light and first light underwater usually occurred about 0.5 h before and 0.5 h after last and first light were recorded in air. The temperature of the water was measured after each collection.

Results

Semilunar Synchrony and Timing of Larval Release.—Hatching by *X. sternberghii* and *C. taboganus* occurred over periods lasting 2–3 days twice each lunar month (Figs. 1 and 2). The temporal distributions of larval release by females in all collections of *C. taboganus* and all but one collection of *X. sternberghii* differed significantly (Kolmogorov-Smirnov tests, Sokal and Rohlf, 1969; $P < 0.01$) from that expected had release been uniform in time. Females collected on different dates less than 10 days apart released their larvae during the same semilunar period (Figs. 1 and 2). Significant differences (Mann-Whitney *U*- or Kruskal-Wallis tests; Sokal and Rohlf, 1969) in timing occurred only among collections of *X. sternberghii* contributing to the second ($P < 0.05$) and final ($P < 0.005$) semilunar hatching periods. In both cases, females in the first collections released larvae about 1 day earlier than the females collected later. These comparisons suggest that collection date and time in captivity had little effect on the timing of larval

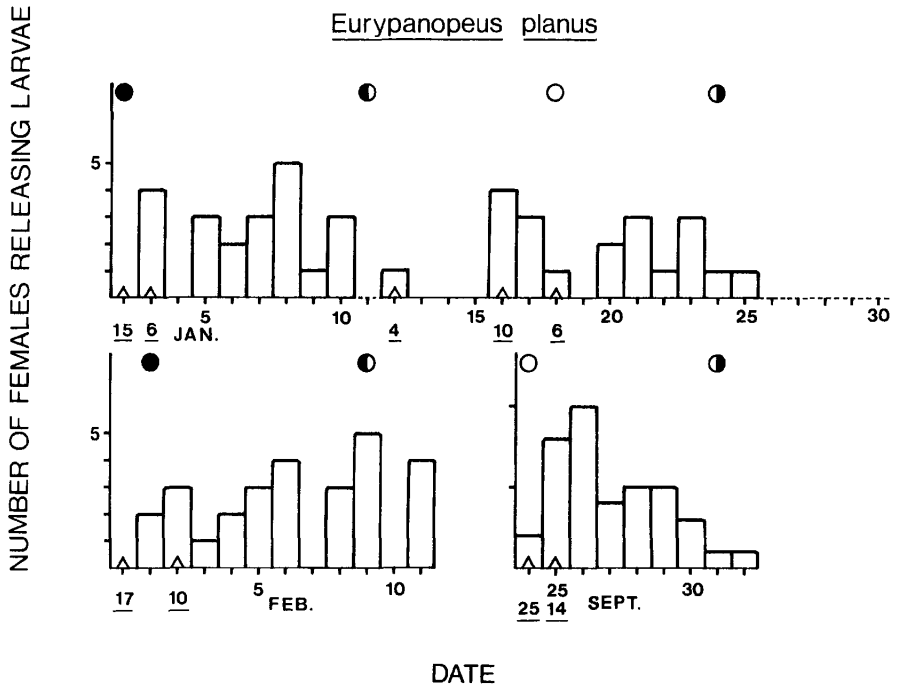

Figure 3. Number of female *Eurypanopeus planus* releasing larvae per day. Symbols as in Figure 1.

release. Further, peaks of release recorded in the seawater tables probably compare closely (<1 day difference) to peaks of release in the field.

The timing of larval release relative to the dates of the quarter moons varied significantly among semilunar release periods (Kruskal-Wallis tests: *X. sternberghii,* H = 149.55, $P < 0.001$; *C. taboganus,* H = 60.12, $P < 0.001$). Mean dates of larval release for *X. sternberghii* ranged from 0.57 ± 0.749 (SD) to 2.92 ± 0.977 days before the quarter moons and were significantly correlated ($r = 0.58$, N = 343, $P < 0.001$) with the number of days before the quarter moons that the evening high tides occurred between 1900 and 2000 h. Mean dates of larval release by *C. taboganus* occurred slightly earlier in the semilunar cycle ranging from 2.13 ± 0.793 to 4.18 ± 1.156 days before the quarter moons. For this species, mean dates of larval release relative to the dates of the quarter moons were significantly correlated ($r = 0.56$, N = 172, $P < 0.001$) with the number of days before the quarter moons that the evening high tides occurred between 1800 and 1900 h.

In contrast, larval release by the females in 5 of the 9 collections of *E. planus* and 9 of the 12 collections of *P. armatus* followed a uniform temporal pattern (Kolmogorov-Smirnov tests, $P < 0.05$) suggesting no consistent trend toward day-to-day hatching synchrony among females or timing of hatching relative to a particular lunar phase (Figs. 3 and 4). In addition, a runs test (Zar, 1974) was used to detect possible trends through time in the percent deviations between the observed and expected (assuming asynchrony among females) frequencies of larval release each day for *P. armatus.* No trends were found, further indicating that larval release was aperiodic.

Diel and Tidal Synchrony and Timing of Larval Release.—The abundances of all species in the sequential 0.5-h collections in a tidal series usually (68 of 70 series

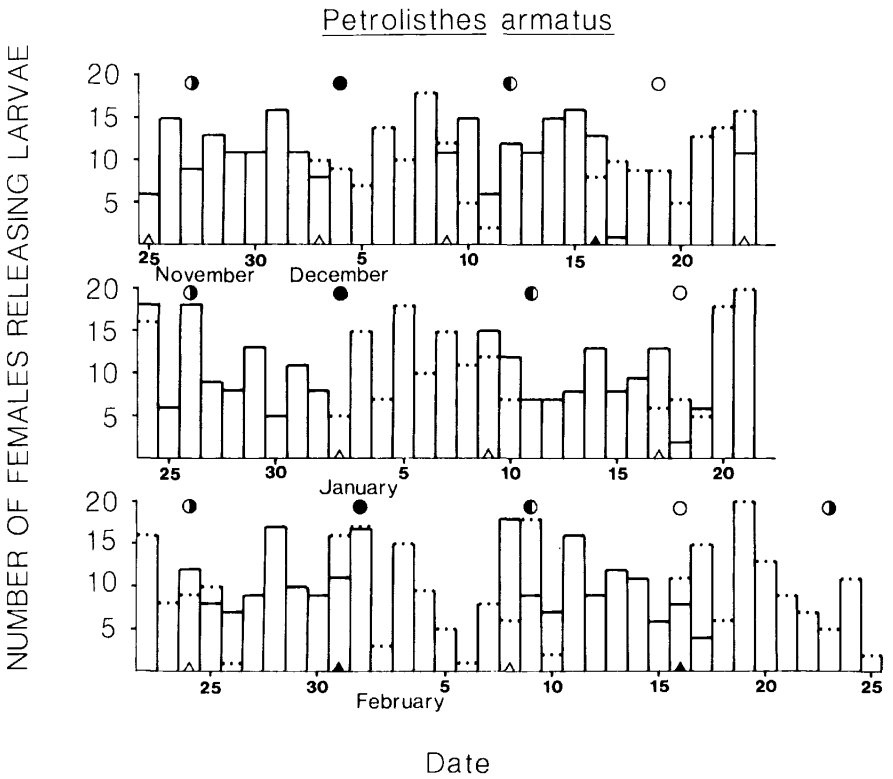

Figure 4. Number of female *Petrolisthes armatus* releasing larvae per day. Bars with solid or broken tops distinguish frequencies recorded in sequential collections. Triangles above the x-axis indicate collection dates. One hundred females were obtained in all but the fifth collection which contained 99 individuals. Black triangles indicate the collections for which the daily frequencies of release were not uniform. Lunar phases as for Figure 1.

total) were unimodal. A single time of larval release was designated for each species and tidal series of collections as the time of the collection at which the cumulative relative frequency of zoeae obtained during the series ≥0.50. From 81 to 90% of the xanthid zoeae and 74% of the zoeae of *P. armatus* obtained in a series were collected during the 1.5-h interval centered on the designated time of larval release (Fig. 5) indicating strong hatching synchrony within and among females during each tidal cycle.

Cataleptodius taboganus and *X. sternberghii* released larvae only during tides in the late afternoon and early evening (Figs. 7 and 8). Zoeae of *C. taboganus* were present in the evening collections taken over a 5-day period, though 95% of the total (100,263) were collected during the first three nights with 45% obtained on the third evening. *Xanthodius sternberghii* zoeae were collected on only two nights with 98% of the total (79,120) obtained on the first evening. Collections of this species were terminated after the second night when it was found that only 1 of the 60 ovigerous females present in the box at the start of the set had not released larvae. With one exception, both species released larvae within 0.5 h of last light (Fig. 9). On the days high tides occurred before last light, hatching occurred after high tide; when tides peaked after last light hatching occurred before

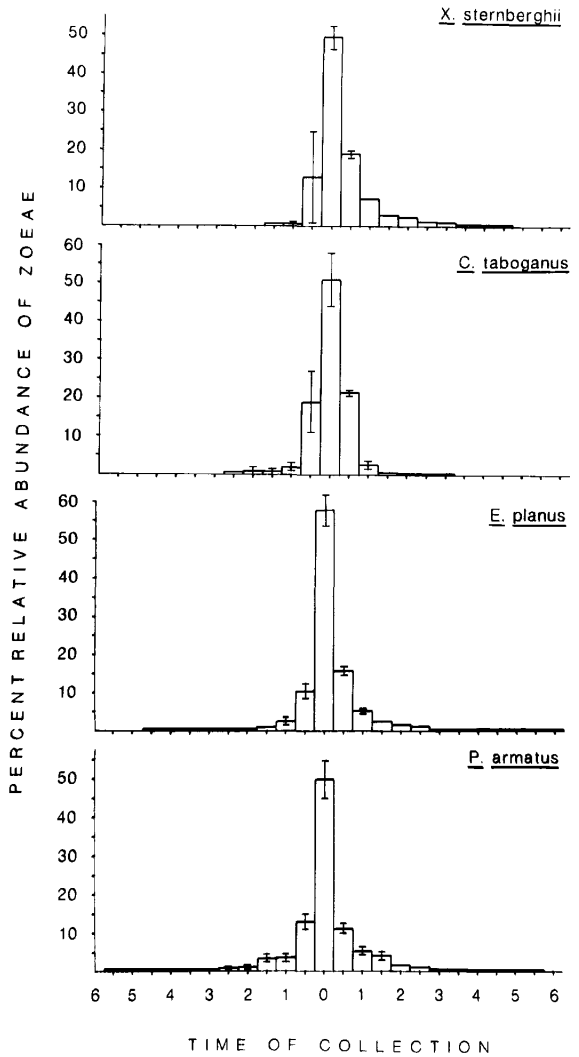

Figure 5. Mean (±SE) percent relative abundance of zoeae per 0.5-h collection averaged over all tidal series of collections that zoeae of each species were present. For each species, collections in a series were aligned with respect to the collection taken at the time designated as the time of larval release (0 on the X-axis). Time of collection given in hours from time of larval release.

high tide, however, deviations between the times of high tide and hatching were small (<1.5 h, Fig. 9).

Eurypanopeus planus released larvae during both of the semidiurnal tides; hatching was not limited to a particular time of the day (Figs. 6 and 7). Larval release occurred from 4 h before to 1 h after the time of high tide averaging 0.95 ± 1.011 h before high tide (Fig. 10). Collections were classified into those taken on days high tide occurred before or at the time of last light, those for which high tide occurred at night and those taken when high tide peaked at or after the time of first light. No differences occurred in the time between release and high tide

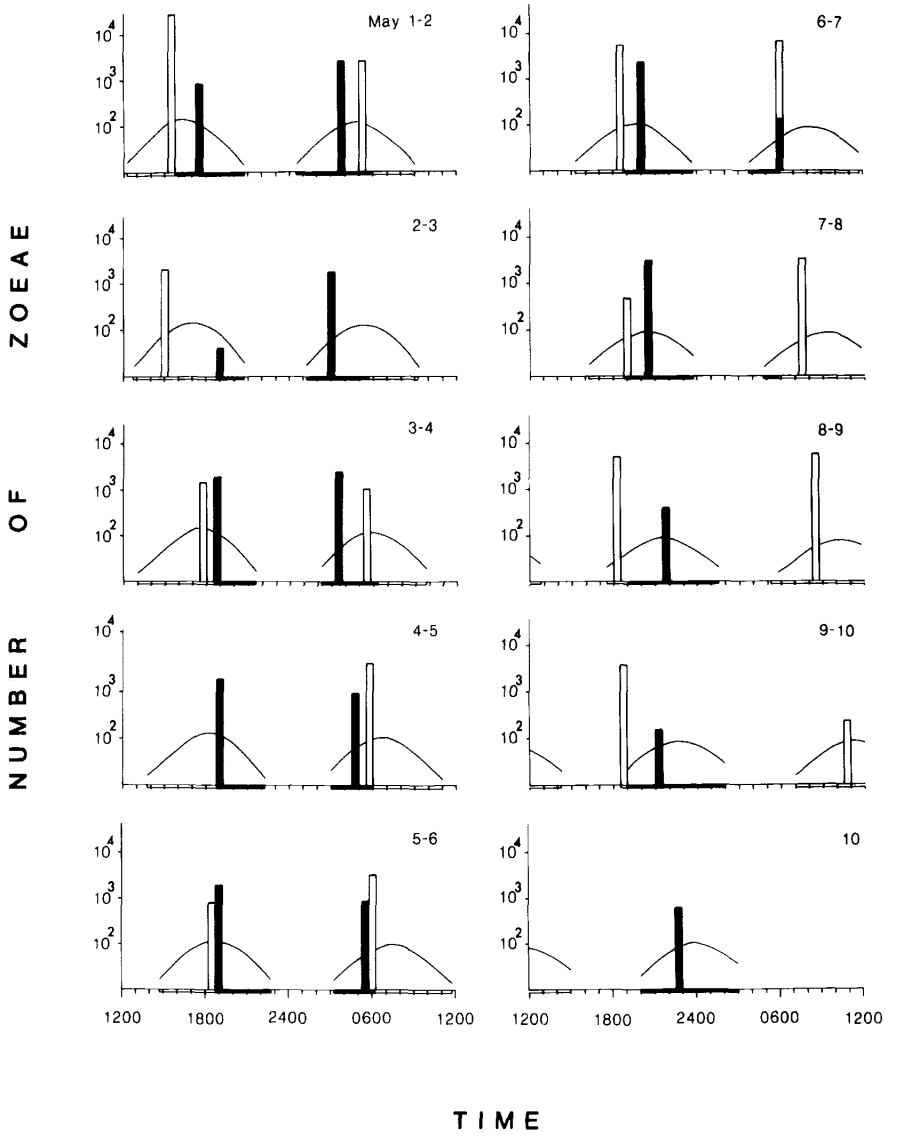

Figure 6. Times of larval release for 32 *E. planus* (open bars) and 150 *P. armatus* (solid bars) during each tidal period from 1 to 10 May 1984. Bar heights indicate the total number of zoeae of each species collected during each tidal series. Horizontal bars on the X-axes delimit the periods collections were made; dark portions show periods of darkness at the box containing females in the intertidal zone. Curves show water heights above the box (maximum height approximately 4 m).

when series of collections so classified were compared (Kruskal-Wallis test, H = 3.58, $P > 0.10$).

Petrolisthes armatus also released larvae during both semidiurnal tides but only when high tides peaked within about 2 h of last and first light (Figs. 6 and 7). On the days the morning high tide occurred more than 2 h after first light, this species released larvae only once a day, during the nighttime tide. Tidal series of collec-

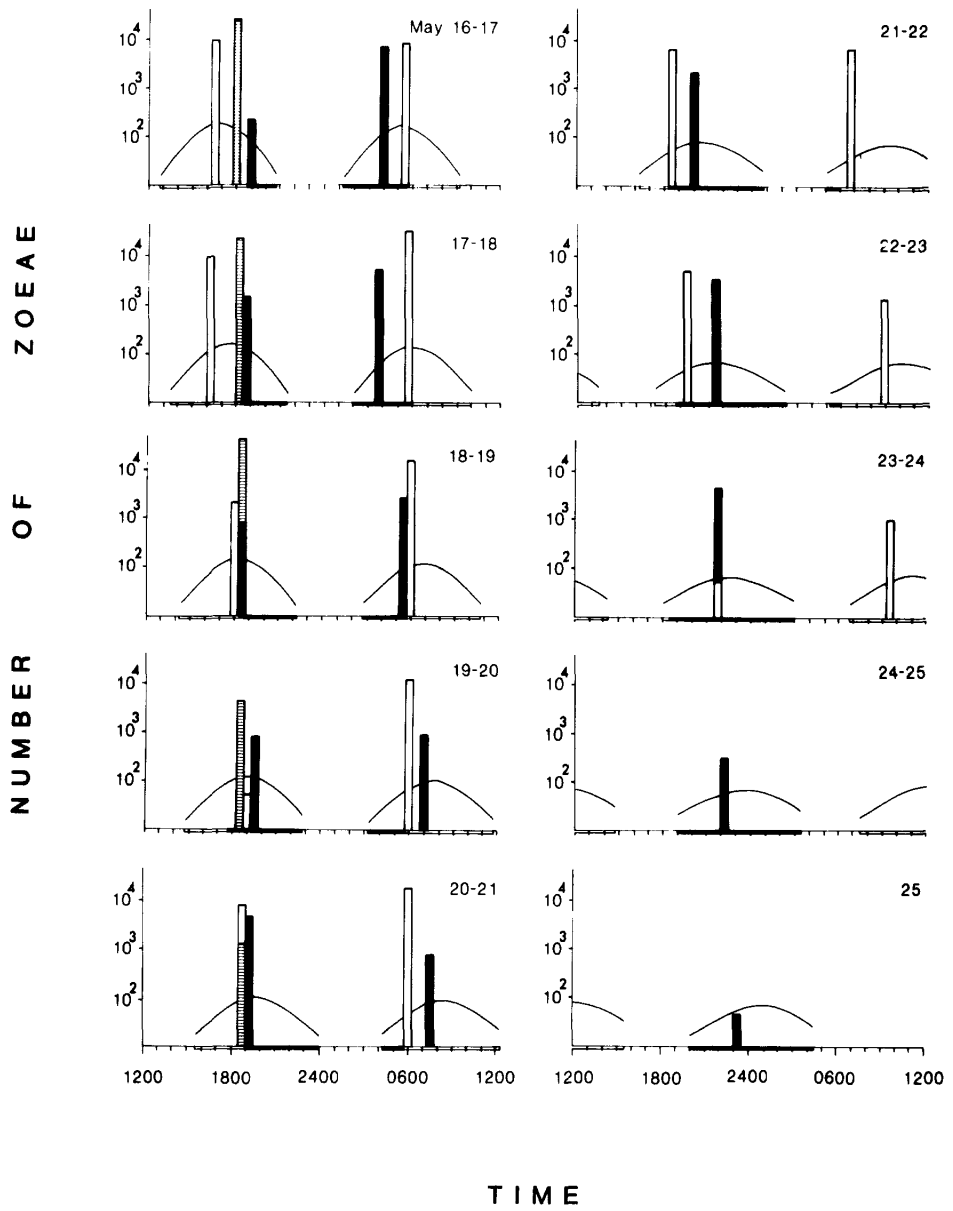

Figure 7. Times of larval release and zoeal abundances for 30 *C. taboganus* (hatched bars), 50 *E. planus* (open bars) and 200 *P. armatus* (solid bars) during each tidal period from 16 to 26 May 1984. Other symbols as for Figure 6.

tions were classified as described above and compared. Larvae were released at different times relative to the time of high tide, depending on when high tide occurred relative to twilight (Kruskal-Wallis test, H = 25.86, $P < 0.001$). The time between hatching and high tide was correlated with the time between last light or first light and high tide (Spearman rank correlation, Zar, 1974; $r_s = 0.809$,

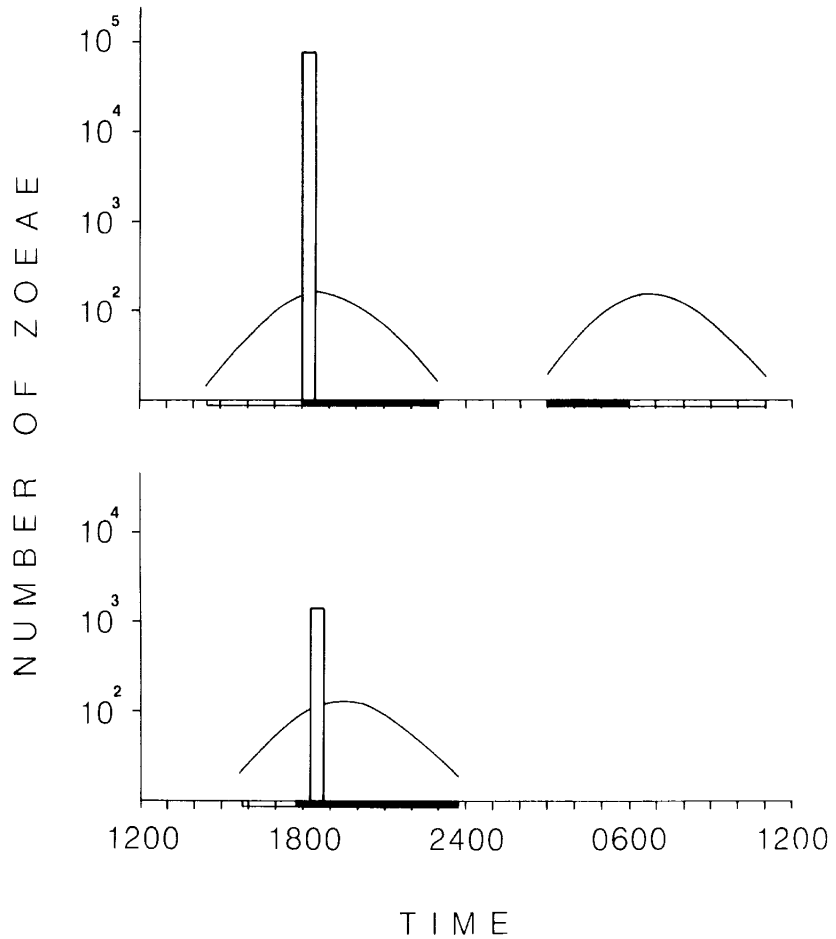

Figure 8. Times of larval release and zoeal abundances for 60 *X. sternberghii* during three tidal periods on 28–29 October. Symbols as for Figure 6.

$P < 0.001$). When high tide occurred before last light, hatching occurred long enough after high tide so that larvae were released during darkness. On those mornings high tide occurred after first light, hatching usually occurred long enough before high tide so that larvae also were released during darkness (Fig. 11).

Major features of the timing of larval release by each species are summarized in Table 1.

Discussion

Timing of Larval Release.—*Xanthodius sternberghii* and *C. taboganus,* held individually under non-tidal conditions, released larvae over 2- to 3-day intervals twice each lunar month when the evening semidiurnal high tides occurred near dusk. Differences between the two species of 1–2 days in the semilunar timing of hatching in the seawater tables probably reflect true differences that occur in the field. In the field, both species usually released larvae immediately after last light. Since *C. taboganus* released larvae 1–2 days before *X. sternberghii,* this species

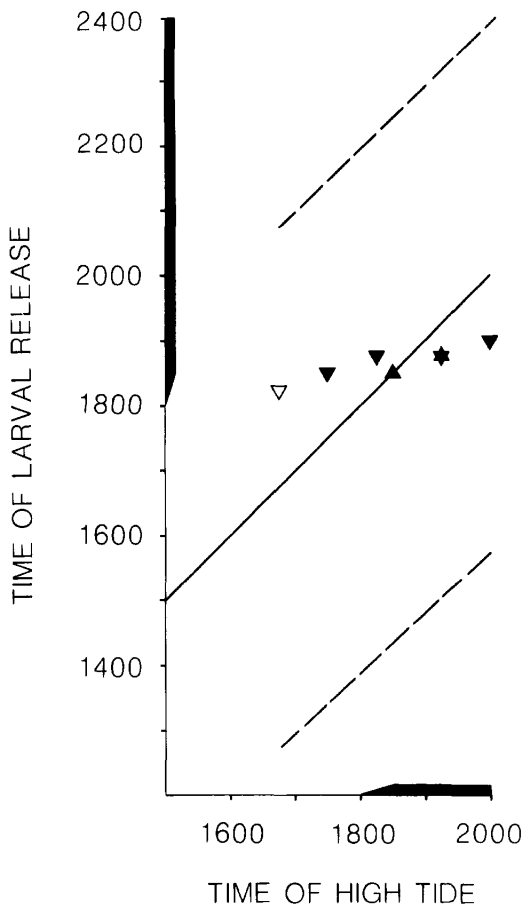

Figure 9. Times of larval release by *C. taboganus* (triangles, points down) and *X. sternberghii* (triangles, points up) relative to the times of high tide. Dark symbols indicate larvae were released at night; open symbols show daytime releases. Nighttime is shown approximately by the heavy bars on each axis. Solid line shows the time of high tide. Dashed lines delimit the interval females were covered by the tide.

more often released larvae after the times of the high tides that peaked before last light (Fig. 9). This suggests that precise timing of hatching to coincide with the time of high tide is less important for *C. taboganus* than for *X. sternberghii.* Although the two species often were found at the same level in the intertidal zone, the upper limit of the distribution of *X. sternberghii* was about 0.5–1 m higher, perhaps explaining why hatching by this species occurred closer to the time of high tide.

Precise tidal and diel timing of larval release may result from responses of females or embryos to cues such as the coincidence of the onset of darkness with a period of stable or slowly changing hydrostatic pressure near the time of high tide. Semilunar timing of larval release by *Panopeus herbstii* (Christy and Stancyk, 1982) and tidal and diel timing of hatching by *Rhithropanopeus harrisii* (Forward et al., 1982), both estuarine xanthids, are consistent with this suggestion. Larval release by *X. sternberghii* and *C. taboganus* ends a period of incubation of about

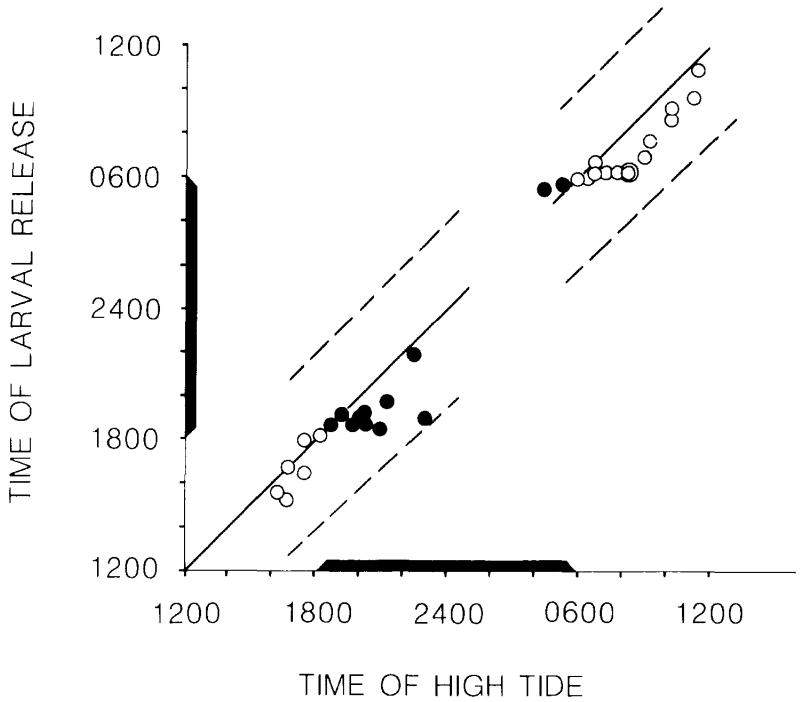

Figure 10. Times of larval release by *E. planus* relative to the times of high tide. Lines and symbol shading as explained for Figure 9.

10–13 days (temperature dependent) which begins with ovulation. Since incubation periods are less than an integral multiple of the semilunar hatching period, the tidal and light cycles are in a different phase relationship when females ovulate than when eggs hatch; the cues used to time ovulation must differ from those used to time hatching.

The timing of larval release by *E. planus* differs from that known for other intertidal brachyuran crabs. Hatching occurred about 1 h before each semidiurnal high tide at all light levels and on all days of the lunar cycle. Hatching during a given tidal cycle was no less synchronous than in the other two xanthids and occurred at approximately the same time when high tides occurred at night.

The temporal pattern of larval release by *P. armatus* differs from that exhibited by intertidal brachyuran crabs. Larvae were released during both semidiurnal tides when high tides occurred during twilight or darkness. On the days high tide occurred before last light, release occurred after high tide during the beginning of the dark period. A similar "delay" is exhibited by *Uca pugilator* (Bergin, 1981) and two species of *Sesarma* (Saigusa, 1981; 1982). *P. armatus* usually released larvae long enough before high tides that occurred after first light so that hatching occurred during darkness.There may exist a tidal component to hatching that establishes a 3- to 4-h interval during which larval release may occur. Hatching may be inhibited by light, resulting in short delays (up to 2.5 h) in the timing of hatching relative to the time of high tide. The mechanism controlling larval release appears less able to produce the "advances" (or delays of about 12 h) in the timing of hatching necessary to adjust for the onset of first light during morning high tides (Figs. 6, 7 and 11).

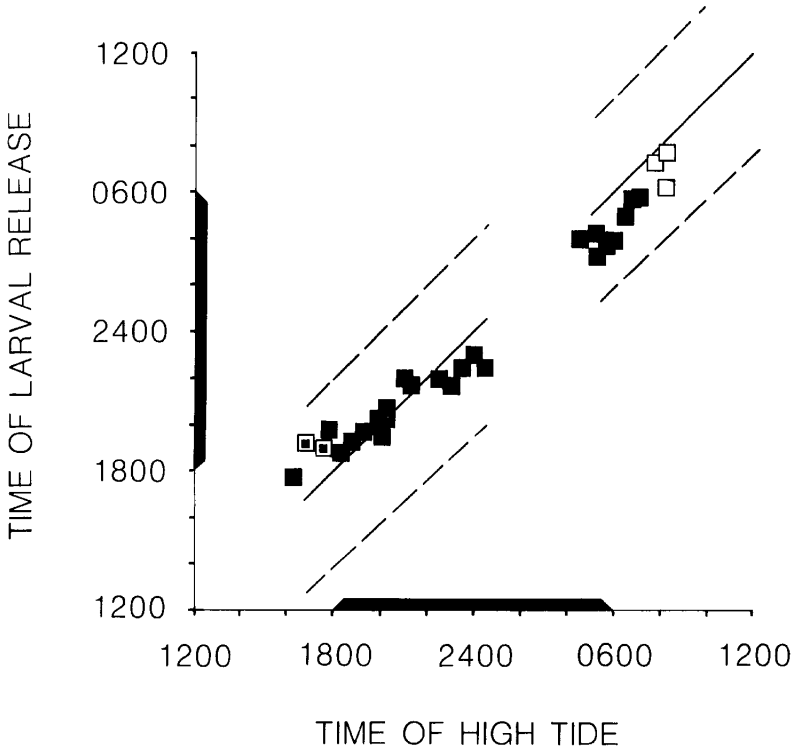

Figure 11. Times of larval release by *P. armatus* relative to the times of high tide. The two small solid squares inside larger ones indicate overlapping points, all nighttime releases. Lines and symbol shading as for Figure 9.

Adaptive Significance.—Semilunar, tidal and diel timing of larval release by *X. sternberghii* and *C. taboganus* is extremely similar to the timing of hatching exhibited by many intertidal estuarine brachyuran crabs. Since temperature and salinity vary little with time of day and tidal phase on the exposed coast, it is not likely that death of newly hatched zoeae due to exposure to temperature or salinity extremes at certain times could select for the observed patterns of hatching in this habitat. Intense predation by diurnally feeding planktivorous fish in the upper estuary has also been invoked as a selective factor leading to the release of larvae when they are rapidly transported seaward at night (Christy, 1982). Could the timing of hatching by *X. sternberghii* and *C. taboganus* also function to place zoeae in the water column when they are least likely to be eaten by planktivorous fish? If so, why do *E. planus* and *P. armatus* release larvae at other times?

Fish communities of the rocky intertidal and near-shore reef habitats in the warm temperate eastern and tropical mid-Pacific contain both diurnal and nocturnal planktivorous species that feed heavily on crustaceans (Hobson and Chess, 1976; 1977). I assume the reef fish communities in the tropical eastern Pacific are similar. Mid-water planktivores probably are more abundant during the day than at night (Hobson, 1965; 1975; Hobson and Chess, 1976; 1977). Rates of predation on planktonic crustaceans are least during the twilight changeover between the diurnal and nocturnal components of the reef fish community (Hobson, 1965).

Table 1. Semilunar, tidal and diel timing of larval release by crabs from exposed rocky beaches, Pacific Coast, Panama

Species	Semi-lunar syn-chrony	Lunar phase	Semi-diurnal tides	Tidal phase*	Time of diel light cycle	Color of zoeae†
Xanthodius sternberghii	yes	0.6 to 3 d before quartermoons	one	HT to 0.5 h before HT	beginning of night	red-orange
Cataleptodius taboganus	yes	2 to 4 d before quartermoons	one	1 h before to 1.5 after HT	dusk, beginning of night	red-orange
Eurypanopeus planus	no	all	both	4 h before to 1 h after HT	night and day	yellow-green
Petrolisthes armatus	no	all	one or both	2 h before to 2.5 h after HT	dusk, dawn, night	some red

* HT is high tide.
† All species also have melanophores and darkly pigmented eyes.

The color of the zoeae of *X. sternberghii* and *C. taboganus* probably makes them conspicuous prey to diurnal planktivores feeding in shallow waters near the shore. Both species appear red-orange to the human eye. The color comes both from numerous chromatophores and from yolk material still present at hatching. Red contrasts strongly with the background spectral radiance of green-yellow coastal waters (Lythgoe, 1979). Both species release larvae during the dusk changeover period when few planktivores are feeding in the water column over release sites. When zoeae are released they must occur as a dense swarm near the bottom. As they expand their exoskeletons or shed their prezoeal skins and gain competence in swimming they must enter the water column where they are further dispersed by currents. By the time their nocturnal predators take up their positions over the rocks they may no longer exist as spatially and temporally predictable patches of prey. There then follows an additional 10–12 h of darkness when they can disperse further from littoral habitats. The importance of this early period of dispersal during darkness may explain why hatching occurs only during the dusk changeover period.

The zoeae of *E. planus* are extremely similar in size (about 1.5 mm from the tip of the rostral to the tip of the dorsal spine) and general morphology to the zoeae of *X. sternberghii* and *C. taboganus*. They differ dramatically, however, in color. Pigments in their chromatophores are yellow-green in hue, a color which probably closely matches the background radiance of near-shore waters. *E. planus* zoeae probably are less apparent to their potential predators in the littoral zone, especially during the day, than are larvae of the other two xanthids. Perhaps as a consequence there is little selection on this species for hatching to occur when few planktivores are active over the rocky intertidal zone.

Petrolisthes armatus released larvae near the times of all nocturnal high tides. The zoeae of this species measure 6.6–6.9 mm from the tip of the telson to the tip of the rostral spine. Melanophores and reddish chromatophores occur sparsely on the carapace, abdomen and appendages. Larvae released during the day probably would be conspicuous to potential predators due to their size. High predation rates during the day are thought to limit entry into the water column of other large crustaceans associated with reefs to the night (Hobson and Chess, 1976). *P. armatus* released larvae in the morning when light would soon penetrate the shallow depths at which zoeae hatched and at times of the night nocturnal planktivores probably were feeding actively. Either the behavior or morphology (4.2-mm barbed rostral spine) of zoeae reduce their susceptibility to predation or

predation on zoeae is not an important selective factor leading to the timing of hatching in this species.

The above explanation of the adaptive significance of the timing of hatching by the xanthids takes zoeal color as given and then shows how precise semilunar, tidal and diel timing of hatching may help visually conspicuous zoeae escape planktivorous fish during their early life. It may be argued to the contrary that breeding synchrony and timing among females may be under selective control by factors affecting adults, or larvae after early dispersal from release sites. Zoeal color may be limited to cryptic hues in species that are not otherwise protected from visual planktivores and for which there are advantages to releasing larvae during both the day and night throughout the lunar cycle. In species that release larvae at dusk, zoeal color may be free to vary to conspicuous hues, whatever advantages such colors may confer on larvae. Specific, testable hypotheses based on broad knowledge of both larval and adult ecology need to be formulated to evaluate these ideas further. At present, the similarity in the timing of larval release between *X. sternberghii* and *C. taboganus* from an exposed shore and that exhibited by several estuarine brachyurans suggests the temporal dynamics of selection (but perhaps not the agents) controlling the timing of hatching are similar in the different habitats.

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