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HATCHING RHYTHMS OF FIDDLER CRABS AND ASSOCIATED SPECIES AT BEAUFORT, NORTH CAROLINA

Michael Salmon, William H. Seiple, and Steven G. Morgan

ABSTRACT

Estuarine crabs usually show hatching periodicities closely synchronized with tidal, lunar, or solar day periodicities. To define their timing, we monitored hatching activity either directly (by observing females during hatching) or indirectly (by measuring larval densities during nocturnal ebbing tides).

Larval densities in the Newport River, at a site (Beaufort) near the ocean, revealed two patterns. Intertidal species (*Uca* spp., *Panopeus herbstii*) showed highest densities twice monthly, during the spring tides. Subtidal species (*Neopanope* spp., three pinnotherids, the blue crab *Callinectes sapidus*) showed larval densities which, on the average, were similar during all ebbing tides. We speculate upon the selection pressures that may have shaped these differences and propose a hypothesis to explain why the patterns are adaptive.

Fiddler crabs were used to determine when, in relation to high tide (HT), hatching occurred. Most larval release in the laboratory and under field conditions occurred within 1 h after HT.

To determine what environmental cue might synchronize semimonthly hatching rhythms in fiddler crabs, we compared the timing of larval release at two local sites where tidal amplitude pattern was identical but HT time differed each night by an average of 1.92 h. The results suggested that fiddler crabs respond to tidal amplitude and not the time interval between HT and the onset of darkness.

Most estuarine crabs produce large numbers of small larvae (zoeae), which disperse and complete development within a few weeks (Thorson, 1950). Recent evidence (reviewed in DeCoursey, 1983) suggests that the moment of hatching occurs in synchrony with tidal, lunar, or solar day periodicities. To evaluate the biological significance of this timing, it is essential that the relevant synchronizing cues and responses to them are accurately described.

Fiddler crabs (genus *Uca*) are the most abundant macrobenthic crustacean inhabitants of North American estuaries (Montague, 1980) and their larvae, during peak periods of hatching, can reach densities of 100,000/m^3 in tidal creeks (DeCoursey, 1979). Many aspects of reproduction in these animals are closely synchronized with the semidiurnal and semilunar tidal cycles including courtship (Barnwell, 1968; von Hagen, 1970; Zucker, 1976; Christy, 1978; Salmon and Hyatt, 1983), female receptivity (Christy, 1978), egg maturation (Feest, 1969; Salmon and Hyatt, 1983), and hatching (Wheeler, 1978; Bergin, 1981; Christy and Stancyk, 1982).

The peak period of hatching varies geographically. Crabs located along the west coast of Florida (Charlotte Harbor) hatch their larvae during the neap high tides (HT) which occur an hour or two after sunset (Christy, 1978), but not during HT of greater height which sometimes occur toward the early morning (Christy, personal communication). In South Carolina estuaries, peak hatching also occurs shortly after sunset and is closely associated with the early evening maximum amplitude spring high tide (spring maximum HT) (Christy and Stancyk, 1982). Four other species (*Sesarma cinereum, S. reticulatum, Panopeus herbstii,* and *Pinnixa chaetopterana*) were reported to show identical responses. These data suggest that it is advantageous to release larvae during HTs associated with the

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early evening. However, hatching on the east coast might be synchronized with the spring maximum HT, diel periodicities, or both.

The exact timing of hatching in relation to HT is also uncertain. DeCoursey (1979) found that laboratory populations of fiddler crabs (*Uca pugilator, U. minax, U. pugnax*) released larvae between 50–250 min after HT at their collection site. However, Bergin (1981), working with laboratory-held *U. pugilator,* found hatching was broadly synchronized (±2 h) with HT. In the field, DeCoursey (1979) found that larvae reached peak densities in creeks about 3 h before HT. In 1983, she repeated her field measurements (her fig. 8). The data indicated that larvae were most abundant from 2–6 h before some, but not all, spring HTs. Thus, no consistent pattern, either within or between these measurements, has emerged.

Here, we attempt to answer the following three questions: (1) Is hatching in the early evening the "rule" among east coast crabs or do other species show different patterns? (2) Do east coast fiddler crabs synchronize hatching with the spring maximum HT (a tidal amplitude periodicity) or with HTs occurring within some interval after sunset (a diel-tidal periodicity)? (3) When, in relation to HT, do fiddler crabs hatch their larvae, and why is this timing adaptive?

Materials and Methods

Larval Density Patterns

Larval densities of crab species were monitored within surface waters beginning after every high tide that occurred between 1730 and 0450 h, 20 June through 26 August 1983. Preliminary observations showed that peaks in larval density at this site occurred about 1 h after HT. Therefore, sampling began 30 min after each high tide and lasted 1.5 h. Water samples (1.8–2.7 m^3) were obtained from the Duke University Marine Laboratory sea-water system at Beaufort, North Carolina. The pumps were located at the end of a 25-m long pier and within a channel of the Newport River (Fig. 1). Floats attached to the intake line kept its opening within 30 cm of the surface. A tide gauge adjacent to the pump house, maintained by the National Oceanographic and Atmospheric Administration, was used to measure amplitude changes between evening high tide and the low tide that followed. We also measured water temperature at HT. The laboratory provided data on the daily range of temperature and salinity at the dock site.

Each sample was filtered through a 1-m long plankton net (General Oceanics, 153 μm mesh) mounted next to the pier, chilled over night, then preserved in buffered formaldehyde. Larval densities were estimated by concentrating the sample to 100 ml, mixing it, withdrawing 4 or 5 5-ml subsamples, and counting all the larvae of each decapod species in every subsample. These values were summed and densities for each species in the entire sample were estimated by extrapolation. Zoeae were identified from published (Sandifer, 1972) and unpublished (Kurata, 1970) morphological descriptions. We were unable to separate the fiddler crab larvae (*U. pugilator, U. minax,* and *U. pugnax*); these were combined as "*Uca* species." Three xanthid morphs, all resembling *Neopanope sayi,* were termed "*Neopanope* species."

To determine how density patterns of each species varied over each semilunar cycle, we aligned our records at the syzygies and calculated the mean ± SD of density estimates for evenings with HTs in phase. A total of 4.6 semilunar cycles was sampled. Thus, average densities for samples obtained on the first 8 days of each semimonthly cycle were based upon 5 observations (evening plankton samples) while those for the remaining 6 days were based upon 4 observations. We assumed that on evenings when larval densities were highest, females showed peaks of hatching activity. However, a small (but unknown) number of first stage larvae could have been released a day or more in advance of that evening, then transported to our net over several tidal cycles.

Fluorescene dye, which traced surface currents on in- and outgoing neap tides, was used to determine minimum distance between the sampling site and habitats serving as sources for zoeae.

Hatching in Relation to High Tide

Ovigerous fiddler crabs (*U. pugilator,* 1.20–1.83 cm in carapace width; *U. pugnax,* 0.8–1.65; *U. minax,* 1.81–2.60) were placed in vertically suspended incubation tubes, each end of which was bissected by a rod to prevent escape. Small diameter incubation tubes (20 cm long × 15 mm inside diameter) were made of grey polyvinyl chloride (PVC) tubing; larger tubes (20 cm × 25 mm), which

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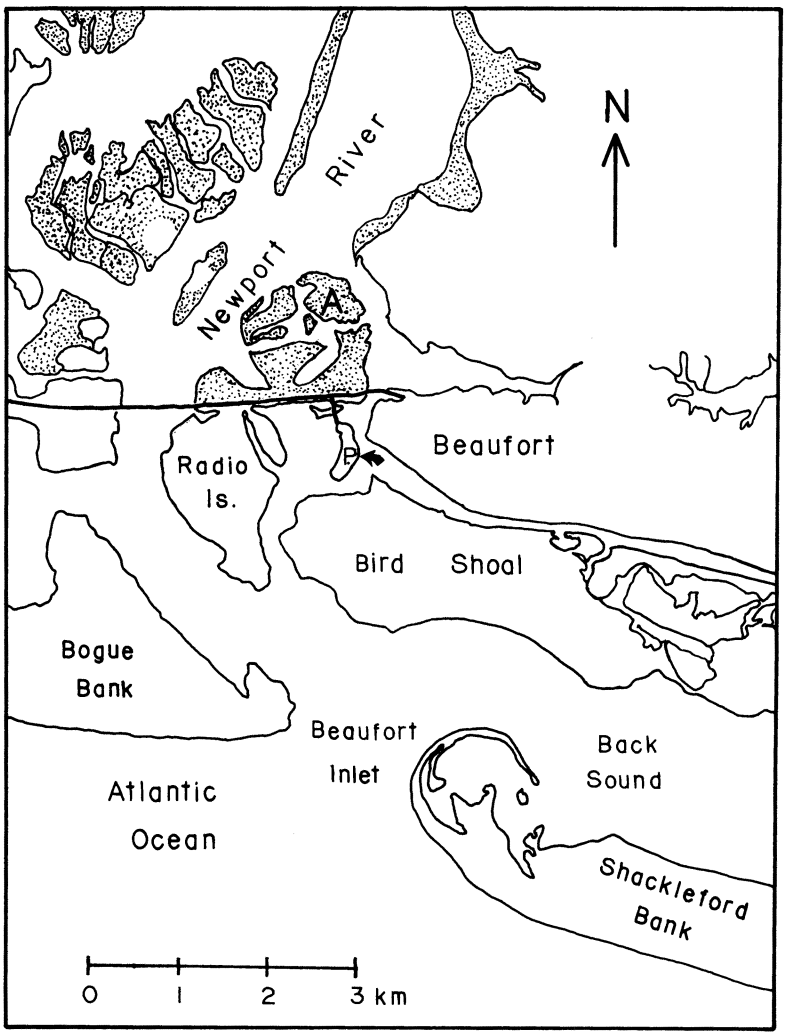

Fig. 1. Map of the Newport River area. Samples were collected at Pivers Island (P.), approximately 3 km from Beaufort Inlet. Stippled areas = marshes. Arrow indicates location of pier in channel.

housed *U. minax,* were made of clear Plexiglas. Both sets of tubes were kept within the same light-tight cabinet in a non-air conditioned room. A timer was used to provide a 14L:10D photocycle, with lights (2 cool white 100 watt fluorescent tubes) off at 2000 h. Cabinet temperature ranged from 23°C (day) to 21°C (night) during observations (June–July 1984).

Each tube was immersed to a depth of 1.0 cm in a beaker of sea water; the sea water was changed daily. Hatching always occurred during the dark period. To determine when hatching occurred, beakers were visually checked for the presence of larvae at 15 min intervals with a dim flashlight, beginning 2 h before and ending 3 h after HT at the collecting site. For *U. pugilator* collected adjacent to Pivers Island, HT was recorded at the laboratory dock. *Uca minax* and *U. pugnax* were collected at the North River, about 10 km from Beaufort, where previous observations showed HT occurred an average of 1.92 h later.

The North River site was used to measure hatching by fiddler crabs before, during, and after HT in the field. This small, nearly rectangular marsh was bissected by Highway 70 across its long (east–west) axis. Tidal waters from the river entered by a single long (about 400 m), shallow creek (≤0.8 m at HT) no more than 3.0 m wide that flowed under the highway through two concrete drainage

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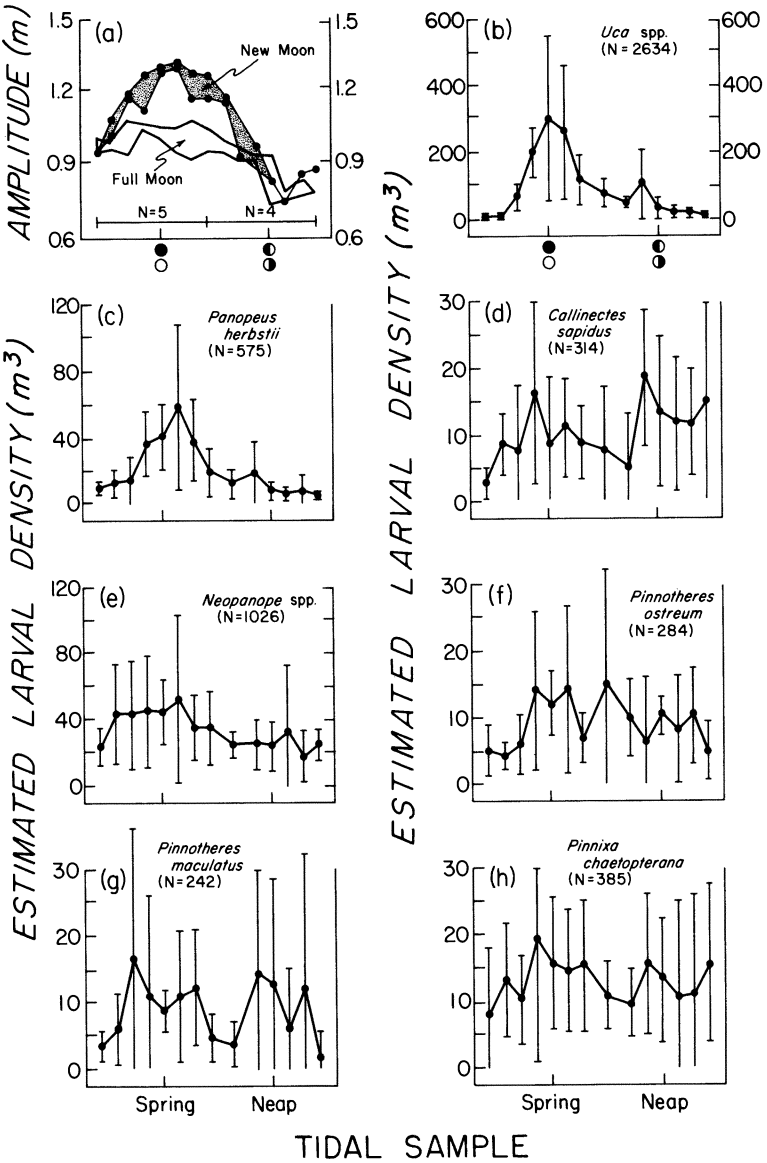

Fig. 2. (a), Amplitude changes between high tide and the low tide that followed as recorded at Pivers Island 20 June–26 August 1983. Shading indicates range of values for new moon semimonthly cycles; open areas indicate full moon cycles. High tides fell between 1730 and 0450 h. (b)–(h), Estimated mean larval densities (per m³) in the surface waters for the seven most abundant species. Brackets indicate SD. Values are based upon 5 samples over the first 8 days and 4 samples for the remaining 6 days of the semimonthly cycle. N = actual number of first stage zoeae counted.

tiles, then continued westward toward a woods. Ovigerous females of *U. minax* and *U. pugnax* were most common within burrows along the entire stream bank.

At 20–30 min intervals, a 100-l surface water sample was taken at the highway. Each sample was filtered through a plankton net and stored in jars for later counting. Eight samples were obtained each evening, beginning about 1 h before HT. Sample number 3 was usually obtained at HT (no current flow). Water level each evening was measured with a calibrated stick, fixed to the bottom for the

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Table 1. Highest water temperatures (°C) recorded during late afternoon or evening high tides at the two study sites (1984).

Date	North River	Beaufort
30 June	28.0	26.5
16 July	32.0	27.3
7–10 August	29.0–32.0	29.0–29.5
14 August	31.5	29.0
22–25 August	26.5–29.0	26.5–28.0

duration of the study. Temperature and salinity readings were made at HT with a YSI salinometer (Model 33). Larval densities, especially during evenings of peak hatching, were too high for direct counts. Subsampling techniques, as described above, were used to estimate densities.

Cues Synchronizing Hatching Responses

Since HT at the North River averaged 1.92 h later each evening than at Beaufort, crabs located at the 2 sites were compared with regard to the evenings when most crabs hatched. If crabs at both sites responded only to tidal amplitudes, then peaks should occur on the same evening but at different times. However, if peak hatching periods were selected on the basis of some interval following sunset, crabs at the North River should show hatching peaks about 2 days in advance of those at Beaufort, since the time of HT at the 2 sites would then differ only by about 15 min. To distinguish between these alternatives, we compared the time of hatching peaks (greatest larval densities per evening) exhibited by Beaufort *Uca* species (mostly *U. pugilator* and *U. pugnax*) during June–August 1983, and August 1984, with those shown by the North River *Uca* species (mostly *U. pugnax* and *U. minax*) in 1984. We assumed, based upon our results (see below) and others (DeCoursey, 1983), that there were no species differences in larval release time in relation to HT.

At Beaufort and the North River, there were differences in the seasonal occurrence and magnitude of highest water temperatures at afternoon and early evening HT. Since these could affect developmental rates of embryos, and hence the duration of incubation, we recorded HT temperatures at both sites in late June, mid-July, and early, mid-, and late August.

Results

Physical Measurements

Tidal patterns at Beaufort were semidiurnal with changes in amplitude strongly associated with the lunar phase (Fig. 2a). Semimonthly cycles associated with the new moon showed the maximum amplitude difference between high tide and the low tide that followed (about 1.3 m). During the neap tides, differences averaged 0.7 m. Water temperature at HT ranged from 26.5°C in late June to 29°C in August 1983. In 1984, they ranged from 26.5° to 29.5°C (Table 1).

Current-borne dye indicated that over the 1.5-h sampling period, we sampled ebbing waters originating no less than 0.7 km north (upcurrent) of the laboratory pier. Zoeae released from the Beaufort marsh (A in Fig. 1) were within this zone and probably accounted for many of our subjects. However, other larvae, released at locales farther up the estuary, could have been transported to our net over several tidal cycles.

At the North River, HT water temperatures ranged from 26.5° to 32°C. They were consistently higher than those recorded at Beaufort (Table 1).

Density Patterns

Eighteen species of first stage zoeae were identified (Table 2). *Uca* and *Neopanope* accounted for 64% of all zoeae seen. The density patterns of these and the remaining five most abundant species (Fig. 2b–h) relative to semilunar cycles revealed two categories of response. *Uca* spp. and *P. herbstii* were always most

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Table 2. First stage zoeae found in plankton samples taken at Beaufort, June–August 1983 (N = 5,755).

Species	Number	Cumulative percentage
Uca spp.	2,634	46
Neopanope spp.	1,026	64
Panopeus herbstii	575	74
Pinnixa chaetopterana	385	81
Callinectes sapidus	314	86
Pinnotheres ostreum	284	91
Pinnotheres maculatus	242	95
Panopeus sp.	123	97
Pinnixa cylindrica	67	98
Sesarma cinereum	37	–
Menippe mercenaria	18	–
Eurypanopeus depressus	18	–
Persephona punctata	14	–
Pinnixa sayana	12	–
Heterocrypta sp.	3	–
Macrocoeloma sp.	2	–
Pachygrapsus transversus	1	100

abundant on nights of the spring maximum HT. On these nights, HT occurred during the early evening. Christy and Stancyk (1982) found an identical pattern in their samples at a South Carolina estuary.

The remaining species (three pinnotherids, *Neopanope* spp., and the blue crab *Callinectes sapidus*) showed responses in which larval density was apparently unrelated to either HT time or to HT amplitude change. In general, density estimates from one day to the next exhibited consistently low, species-typical levels upon which one–four day "bursts" of unusually high densities were superimposed. The bursts occurred at any phase of the semimonthly cycle and were inconsistent across consecutive cycles. For example, the two "peaks" in the record for *P. maculatus* (Fig. 2g) were caused by single bursts in two different cycles and contributed to the obviously greater variability associated with means during those days.

Hatching in Relation to High Tide

Most fiddler crabs kept in incubation tubes released their larvae after HT at their collection site. Most did so within three h after HT (Fig. 3). Freshly collected crabs (those in which larval release occurred within 24 h of capture) appeared more synchronous with HT. Females of *U. minax,* kept in tubes for more than 8 days, became particularly variable in hatching time.

Field measurements at the North River in June, July, and early August also indicated that most hatching occurred after, not before HT (Fig. 4). No larvae were present in the first sample (1 h before HT) and were either rare or absent 20–30 min before HT. Typically, densities rose from zero to low levels at slack tide, reached their highest levels 20–40 min later, then fell to low levels.

Cues Correlated with Semimonthly Timing

The temporal relations between semimonthly hatching peaks and environmental periodicities are shown in Table 3. Beaufort crabs showed a close correspondence between the time of the spring maximum HT and the time of peak hatching

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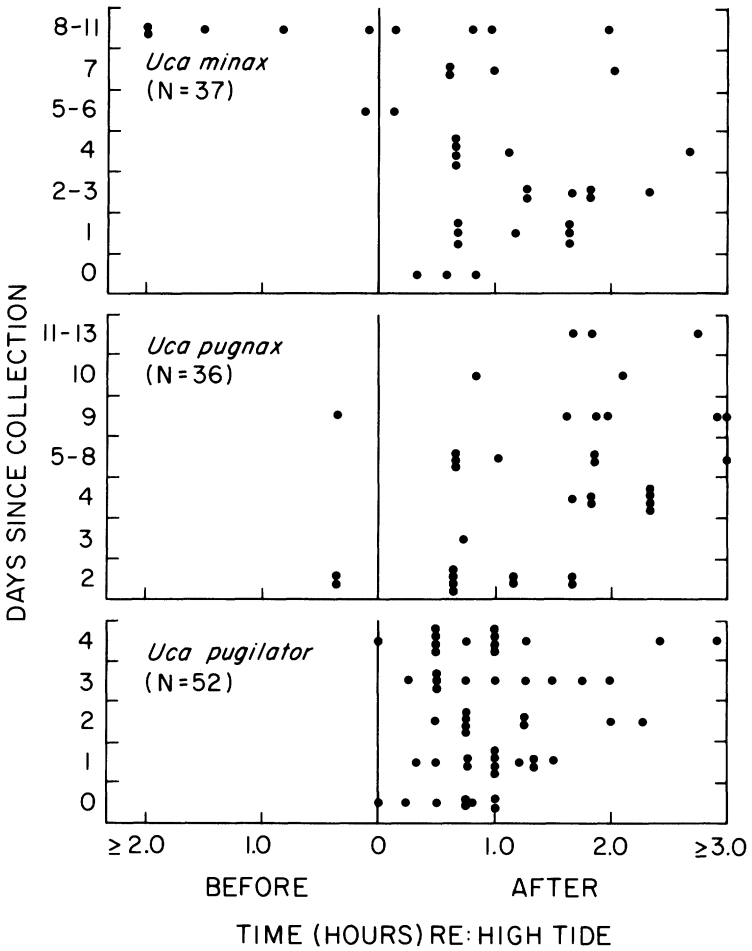

Fig. 3. Hatching time in relation to the predicted time of high tide at the collecting site for fiddler crabs held in incubation tubes, June–July 1984. Each point is one female.

activity (see also Fig. 2b). For example, the mean selected HT time (2105 h, when larval densities were highest) differed from the mean spring maximum HT time (predicted, 2108 h) by only 3.0 min. Similarly there was a close correspondence (10.7 min) between the mean interval separating sunset from the selected ($\bar{x}$ = 60.3 min) and predicted (71.0 min) HT time when larval densities reached semimonthly highs.

In contrast, the North River crabs were inconsistent in their temporal choices. Their mean selected HT time (2146 h) varied from that predicted in response to tidal amplitude (2252 h) by over 1 h (66 min too early), while the mean time interval between sunset and the HT when most hatching occurred was almost

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Fig. 4. Semimonthly hatching profiles at the North River site, late June, early July, early August, and late August. Hatched record indicates temporal pattern of density each evening in relation to the

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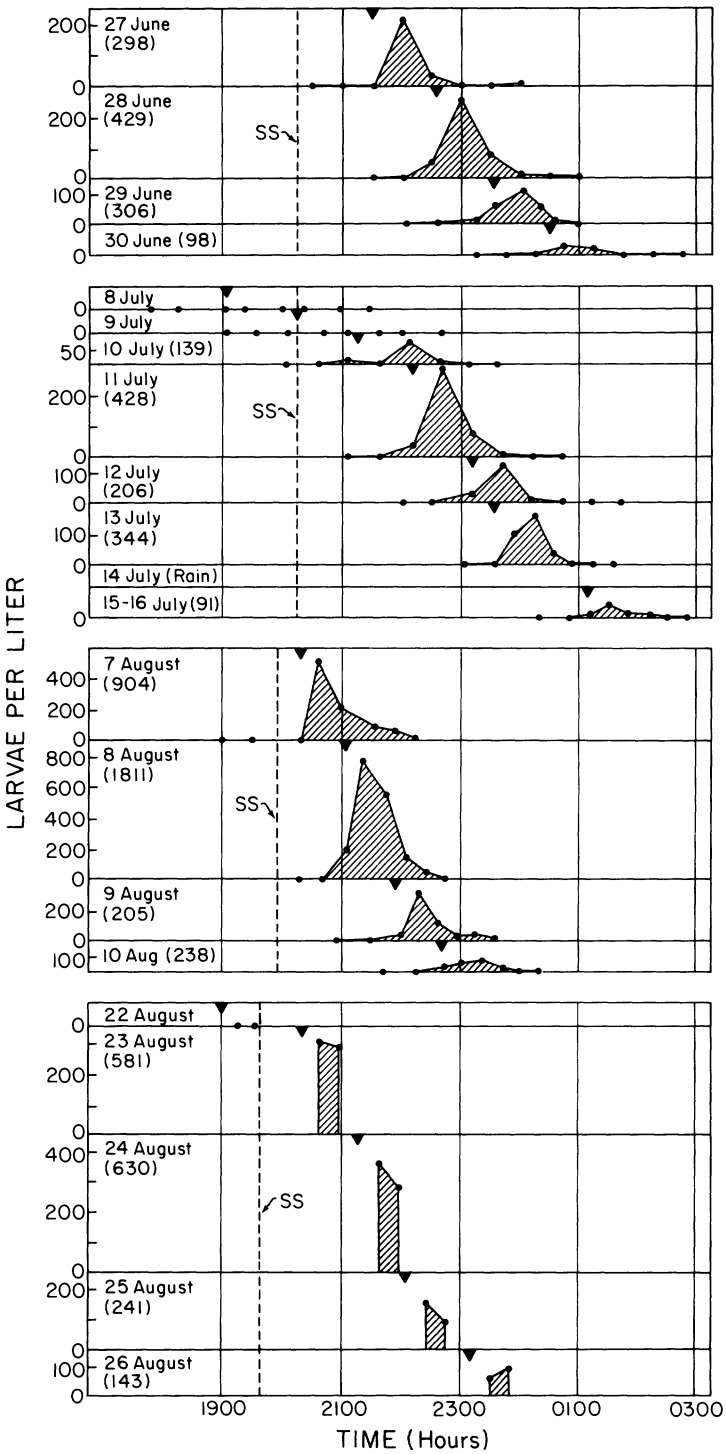

time of high tide (inverted solid triangle). Data based upon eight 100-l samples/evening except for 22–26 August, when only two 100-l samples (20 and 40 min after high tide) were taken. Values in parentheses indicate total zoeae/evening. SS indicates time of sunset.

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Table 3. Times of peak semimonthly hatching in Beaufort and North River *Uca* spp. in relation to the time of sunset and the highest (spring) amplitude tides.

Location	Observed peak hatching	Predicted peak hatching[1]	Time: selected HT	Maximum amplitude HT	Difference (min)[2]	Time of sunset (SS)	Difference (min): selected HT-SS	Difference (min): predicted HT-SS
Beaufort	25 June	24 June	2131	2051	40	2015	76	36
(1983)	10 July	10 July	2112	2112	0	2014	58	58
	23 July	23 July	2030	2030	0	2006	24	24
	8 August	9 August	2100	2149	49	1954	66	115
	24 August	23 August	2152	2119	33	1937	135	102
(1984)	10 August	10 August	2030	2030	0	1955	35	35
	25 August	27 August	2003	2142	99	1935	28	127
		Mean:	2105	2108		$\bar{x} \pm$ SD	60.3 ± 38.44	71.0 ± 42.68
North River	28 June	29 June	2235	2320	45	2016	139	
(1984)	11 July	11 July	2210	2210	0	2015	115	
	8 August	10 August	2105	2227	82	1955	70	
	24 August	27 August	2115	2332	137	1935	100	
		Mean:	2146	2252		$\bar{x} \pm$ SD	106.0 ± 28.88	

[1] Evening of maximum amplitude HT.
[2] Time difference between HT of peak hatching and HT of maximum amplitude.

twice as long as that shown by the Beaufort crabs (106.0 versus 60.3 min; $t = 2.0829$, $P < 0.05$, 9 *d.f.*). Thus, North River crabs did not, on the average, show semimonthly peaks of hatching consistent with either of the two environmental variables presumed to be important: tidal amplitude or the time of sunset. An inspection of Fig. 4 suggests that in late June and early July, semimonthly hatching peaked late in the evening and at about the time of the predicted spring maximum HT. In August, hatching occurred earlier than predicted by response to tidal amplitude, but later in time relative to sunset than by Beaufort crabs during the same year (Table 3).

Discussion

Hatching of Fiddler Crabs in Relation to High Tide

Our laboratory data (Fig. 3) indicate that hatching occurs most commonly after HT and thus agrees with the original results of DeCoursey (1979). These data suggest that captive females, their developing clutches, or both can remain synchronized to the time of HT at their home beach for as long as 14 days. Similar results were obtained by Bergin (1981) with *U. pugilator*. Our data extend these findings to *U. pugnax* and *U. minax*. The latter, for unexplained reasons, failed to remain synchronized as long as *U. pugnax*.

In our study, we compared the timing of larval release by laboratory-held crabs to those of crabs in the field, using short observation intervals (20–30 min). The hatching profiles exhibited by North River crabs (Fig. 4) confirmed the phase relationships between HT and hatching. However, they also suggest that crabs in the field are more strongly synchronized with HT than those kept in incubation tubes, especially after several days of confinement. While the specific cue or cues responsible remain to be identified, responsiveness to such stimuli may enable females to compensate for slight daily variation (commonly, ± 15 min at the North river) in the time of HT at local habitats.

Why should hatching occur 20–40 min after HT, rather than at HT or an hour

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or two later? Christy (1982) pointed out that shallow creeks often are nursery areas for small fishes, many of which are visually hunting planktivores. While nocturnal hatching should reduce the impact of planktivores, at Beaufort killifish (*Fundulus heteroclitus*), spot (*Leistomos xanthurus*), and anchovy (*Anchoa mitchelli*) contained fresh zoeae of *Uca* in their stomachs (M. Dame, unpublished observations), even when captured during HTs occurring several hours after sunset. Thus, synchronous larval release on nocturnal ebbing, rather than nocturnal high tides may have two advantages: (1) rapid removal of larvae from the area, minimizing their exposure time to predators, and (2) "swamping" of predators (DeCoursey, 1983), which minimizes the likelihood that the progeny of any one female will suffer disproportionately from the predation that occurs.

It may be detrimental to wait too long after the tide ebbs for other reasons, relating to creek depth. First, we found that after HT current velocities at the North River increased for about 1 h, then actually decreased, presumably due to bottom friction. Second, 1 h after HT many small fishes (among them killifish) moved out of shallow water into the creek and began to migrate toward open river waters. These might consume larvae if they were also present. Thirdly, during the spring tides when most hatching occurs, portions of the creek bottom were actually exposed within 3 h after HT. These observations suggest that at our study site, hatching was adaptively timed so as to minimize the risks of predation and stranding within the marsh.

In some areas (e.g., Charlotte Harbor, Florida; Christy, 1980), females incubate clutches in supratidal burrows. Females are therefore exposed to potential predators when walking to the water's edge to hatch their eggs. DeCoursey (1983) suggested that nocturnal hatching might occur to minimize this risk. At the North River, females most commonly incubate their clutches along the creek bank, an area inundated at HT. We saw no females emerge from underwater burrows to release their larvae. Thus, we presume that most hatching occurs from within burrows, after entrances have been opened. Such females should be relatively safe from predators. Female *U. pugilator* at another local site (Shackleford Bank; Fig. 1) have been observed releasing larvae from underwater burrows (D. Colby, personal communication). Interestingly, Colby (unpublished observations) found larval density profiles much like those at the North River, i.e., release and larval transport from the site were completed within 1 h after HT.

Cues Synchronizing Semimonthly Peaks

The results of this study, as well as others (Christy and Stancyk, 1982), indicate that Atlantic Coast fiddler crabs most commonly hatch their larvae in the early evening, at about the time of the spring maximum HT (Fig. 2b). Our comparisons between crabs at the North River and Beaufort sites were made to determine whether populations respond to HTs occurring at some interval after darkness or to tidal amplitude per se. The results (Fig. 3, Table 2) indicate that early in the summer, both Beaufort and North River crabs may have responded to tidal amplitudes, but that later in the season, North River crabs failed to do so. These data, while preliminary, provide no support for the hypothesis that crabs rely upon some narrow interval between sunset and HT, since crabs from the two sites showed significiant diel differences in these time intervals.

We found differences between low tide subsurface substrate temperatures (where females incubate clutches) to be negligible at all habitats. However, at both locations incubating females may differ in the extent to which their clutches are periodically cooled by flooding tides, especially late in the summer. Coolest mid-

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summer daily water temperatures at both sites were always associated with flooding tides. At the North River, higher summer water temperatures could have accelerated embryonic development, causing hatching to occur before the evenings of the highest amplitude tides. Differences (Table 1) between summer HT temperatures and their seasonal arrival at both sites are probably a consequence of Beaufort's closer proximity to oceanic waters, which heat more gradually. Because our site at the North River was located some 10 km inland, mixing with ocean water was less complete. For example, HT salinities in the creek varied between 20–25 ppt, but at Beaufort the range was typically 29–34.5 ppt.

Semimonthly Density Patterns

Our records (Fig. 2) revealed that species differed in their larval density patterns (population hatching responses) over the summer months. Some, like *Uca* spp. and *P. herbstii,* tend to concentrate hatching during early evening HTs, a response which along the east coast places their larvae in the water column during the spring tides. Christy and Stancyk (1982) showed that because hatching in these and other species (*Sesarma cinereum, S. reticulatum, P. chaetopterana*) occurs at about the time of HT, larvae are quickly exported by ebb tides from adult habitats to lower estuarine or oceanic areas where further development occurs (Pinschmidt, 1963; Goy, 1976). Other species (*Neopanope* spp., *C. sapidus, P. maculatus, P. sayana*) also complete larval development in these regions (Goy, 1976; Dittel and Epifanio, 1982). Yet, they do not "pay attention" to tidal amplitude fluctuations or the specific time of night when HT occurs. It therefore seems unlikely that differences in when hatching occurs are a function of where these nursery areas are located.

The second pattern might represent an artifact resulting from sampling error. Numbers of zoeae for the blue crab and for pinnotherid crabs were low and thus might not accurately reflect hatching activity in nature. While this possibility cannot be dismissed, we feel it is unlikely for the following reasons. First, *Neopanope* spp. were nearly twice as abundant as *P. herbstii,* yet failed to show a semimonthly peak in hatching. Thus, the response itself appears "real." Secondly, *P. herbstii,* though represented by only 575 zoeae, showed a consistent correlation between peak hatching activity and the occurrence of the spring maximum HT. Indeed, this pattern was evident for *each* of the 4.6 semimonthly cycles, suggesting our sampling method was sensitive to such trends when they existed. It therefore seems unlikely that a failure to find a similar response in the blue crab and in pinnotherid crabs was solely a function of their low numbers.

On the other hand, the differences between species were correlated with hatching site. Hatching at about the time of early evening spring HT is now known to occur in three intertidal genera (*Uca, Panopeus, Sesarma*). (In North and South Carolina, *P. herbstii* is especially common in intertidal burrows; Williams, 1965; personal observation.) We therefore hypothesize that species in these three genera show convergence in their hatching rhythms because of the selection pressures (predation pressures upon the larvae; dangers of shallow-water stranding) associated with such habitats. In contrast, species whose larvae were released during all nocturnal high tides may typically be found in subtidal waters where larval stranding should not occur. The adults may also be located in the lower estuary when they release their larvae. Thus, distances separating hatching site from areas where further larval development occurs may be short. These factors may mean that *all* ebbing currents, even those associated with the neap tides, may be sufficient for relatively "safe" larval transport.

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The natural history of the above mentioned species tends to support this hypothesis. For example, all tend to occupy subtidal habitats. Adult *N. sayi* are usually located between the intertidal zone and 15 fathoms (27.4 m) (Williams, 1965). Beach (1969) found that subtidal oysters were more frequently infested with *P. ostreum* than intertidal oysters. Williams (1965) listed the depth ranges for pinnotherids as intertidal to 8.5 fathoms (15.5 m) (*P. chaetopterana*) and to 25 fathoms (45.7 m) (*P. maculatus*).

Most adults also occur in the lower zones of estuaries. In Delaware Bay, *P. ostreum* most commonly infests oysters found in more saline waters (Flower and McDermott, 1952). Adult *P. maculatus* in North Carolina are most abundant at lower estuarine sites (Kruczynski, 1973). In Chesapeake Bay, adult *N. sayi* are most common at intermediate to high salinities (Goy, 1976). Blue crabs typically migrate to lower estuarine areas before releasing their larvae (Williams, 1965; Provenzano *et al.*, 1983).

Why did our samples contain species showing two semimonthly density patterns, while those from South Carolina (Christy and Stancyk, 1982) showed only one? At their study site, shallow marsh areas dominated and may have led to a preponderance of intertidal species. *Uca,* for example, accounted for 93.8% of their larvae but only 46% of ours (Table 1). Larvae of both *S. reticulatum* and *S. cinereum* were also found in their samples; we found only the latter, and at much lower densities. Because our site was adjacent to both intertidal marsh and deeper (channel) areas, we sampled several subtidal species in numbers amenable to analysis. These data provided an opportunity to reveal their contrasting hatching pattern. The results also suggest that still other hatching patterns may be revealed by different estuarine species, or the same species when ecological settings vary from those that we found.

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