Reference: *Biol. Bull.* **163:** 251–263. (October, 1982)

ADAPTIVE SIGNIFICANCE OF SEMILUNAR CYCLES OF LARVAL RELEASE IN FIDDLER CRABS (GENUS *UCA*): TEST OF AN HYPOTHESIS

JOHN H. CHRISTY

Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, SC 29208

ABSTRACT

The hypothesis that semilunar timing of larval release by fiddler crabs (genus *Uca*) results in transport of the final larval stage (megalopa) by spring tide currents to substrates in the upper estuary occupied by adults was tested and rejected. Water temperatures in the North Inlet estuary, South Carolina, increased from approximately 20°C to 28°C and the length of larval life decreased during the May–September breeding season. Nevertheless, ovigerous female *U. pugilator, U. pugnax,* and *U. minax*, collected bimonthly and maintained in the laboratory, released larvae ±1.5 d of the full and new moons throughout most of the breeding season. Megalopae of *Uca* spp. were most abundant in a small tidal creek in the upper estuary during nocturnal flood tides and near the bottom about 5 d before and after the spring tides in September. *Uca* spp. and several other estuarine crabs appear to release larvae near the times of the high tides that are followed by the nocturnal ebb tides of greatest amplitude during the semilunar cycle. At North Inlet, such timing results in rapid seaward transport of newly hatched zoeae and subsequent export into coastal waters. Convergence among estuarine brachyurans in the timing of larval release probably reflects a shared adaptive response to selective factors, such as lethal combinations of high temperatures and low salinities, or predation by diurnal planktivors, that cause high larval mortality during the day in the upper estuary.

INTRODUCTION

Semilunar cycles of larval release have been reported for several estuarine crabs (Christy and Stancyk, 1982). Such cycles can be inferred for 17 species of fiddler crabs (genus *Uca*) from cycles of male courtship activity (Crane, 1958; von Hagen, 1970; Christy, 1978; Zucker, 1978) female sexual receptivity, mate choice, and incubation behavior (Christy, 1978), ovarian and egg development (von Hagen, 1962, 1970; Feest, 1969; Zucker, 1973; DeCoursey, 1981) and variation in the density of newly hatched zoeae in the plankton (Christy and Stancyk, 1982). Direct evidence of a semilunar hatching rhythm has been obtained for *U. pugnax* under laboratory conditions (Wheeler, 1978) and for *U. pugilator* in both the laboratory and the field (DeCoursey, 1981). Tidal and diel timing of larval release has been well described for *Uca pugilator* (DeCoursey, 1979, 1981; Bergin, 1981), *U. pugnax*, and *U. minax* (DeCoursey, 1979); all three species release larvae at night near the time of high tide.

Hypotheses concerning the ecological consequences and the adaptive significance of semilunar cycles of larval release in *Uca* spp. and other estuarine crabs fall into two classes: those that invoke semilunar variation in factors such as food avail-

Received 6 February 1982; accepted 16 July 1982.
Contribution Number 458 of the Belle W. Baruch Institute for Marine Biology and Coastal Research.

ability, susceptibility to predation, and tidal exposure that may effect the reproductive success of adult males and females (Bergin, 1978, 1981; Zucker, 1978; DeCoursey, 1979) and those that rely on semilunar variation in factors that effect the dispersal, survival, and settlement rates of larvae (von Hagen, 1970; Bergin, 1978; Christy, 1978; Wheeler, 1978; Zucker, 1978; DeCoursey, 1979; Saigusa, 1981). Although supporting evidence for some of these hypotheses has been sought in interspecific comparisons of adult (Zucker, 1978) and larval (Saigusa, 1981) ecology, no hypothesis has been critically tested.

This paper presents a test of the hypothesis that the timing of larval release by female fiddler crabs results in transport of the final larval stage (megalopa) by spring tide currents to substrates suitable for settlement (Christy, 1978). This hypothesis is based on the following observations and argument. Vertical migration within or between larval stages relative to tidal and residual currents may aid retention of crab larvae in estuaries (Sandifer, 1975; Cronin, 1979). However, *Uca* megalopae have been found tens of kilometers from habitats occupied by adults in stratified estuaries where larval vertical migration should be most effective in reducing seaward transport (Dudley and Judy, 1971; Sandifer, 1973). To return to adult habitats, which extend commonly to the heads (*sensu* Carriker, 1967) of estuaries (Crane, 1975), megalopae often must move many kilometers up-estuary before they settle and molt to crabs. They might do this by remaining on or near the bottom during ebb tides where currents are weak, then rising in the water column into stronger currents during flood tides (Carriker, 1967; Christy, 1978). Given these patterns of transport and behavior, megalopae that could settle during spring tides, when current velocities are at a maximum, would return to adult habitats faster than those that were ready to settle at other times. If larval mortality is proportional to the time spent in the water column (Thorson, 1946, 1950; Vance, 1973), more megalopae that were ready to settle during spring tides would reach adult habitats than those moving into the upper estuary at other times; selection might favor females that release zoeae that become megalopae during spring tides. This idea appears consistent with the timing of larval release by *U. pugilator* on the southwest coast of Florida (Christy, 1978).

The hypothesis requires that the time between larval release and a spring tide must equal an integral multiple of the length of larval development. Development rates of brachyuran larvae depend strongly on temperature (*e.g.*, Costlow *et al.*, 1960, 1962, 1966; Vernberg and Vernberg, 1975). On the east coast of the United States *Uca* spp. begin breeding when water temperatures are cool and end breeding when temperatures are considerably higher (Crane, 1943). If the hypothesis is correct, and if larval development rates are temperature dependent in the field, then there should be a change in the phase relationship between the semilunar cycles of larval release and the spring tides as water temperature increases seasonally, and megalopae should be transported to adult habitats only during spring tides. Therefore, the hypothesis was tested by monitoring when female *Uca* spp. release larvae throughout a breeding season and by determining when megalopae colonize adult habitats.

Materials and Methods

This study was conducted at the North Inlet estuary and the Field Laboratory of the Belle W. Baruch Institute for Marine Biology and Coastal Research, Georgetown County, South Carolina (Fig. 1). This is a high salinity, homogeneously mixed estuary in which the currents are dominated by the semidiurnal partial tide (Kjerfve and Proehl, 1979).

may effect the reproduc-
1981; Zucker, 1978; De-
in factors that effect the
gen, 1970; Bergin, 1978;
1979; Saigusa, 1981). Al-
has been sought in inter-
aigusa, 1981) ecology, no

iming of larval release by
tage (megalopa) by spring
y, 1978). This hypothesis
rtical migration within or
may aid retention of crab
ver, *Uca* megalopae have
dults in stratified estuaries
n reducing seaward trans-
to adult habitats, which
f estuaries (Crane, 1975),
efore they settle and molt
bottom during ebb tides
nn into stronger currents
these patterns of transport
les, when current velocities
han those that were ready
l to the time spent in the
megalopae that were ready
an those moving into the
les that release zoeae that
consistent with the timing
f Florida (Christy, 1978).
l release and a spring tide
evelopment. Development
ture (*e.g.*, Costlow *et al.*,
e east coast of the United
are cool and end breeding
If the hypothesis is correct,
ent in the field, then there
semilunar cycles of larval
seasonally, and megalopae
ring tides. Therefore, the
. release larvae throughout
colonize adult habitats.

and the Field Laboratory
Coastal Research, George-
ity, homogeneously mixed
diurnal partial tide (Kjerfve

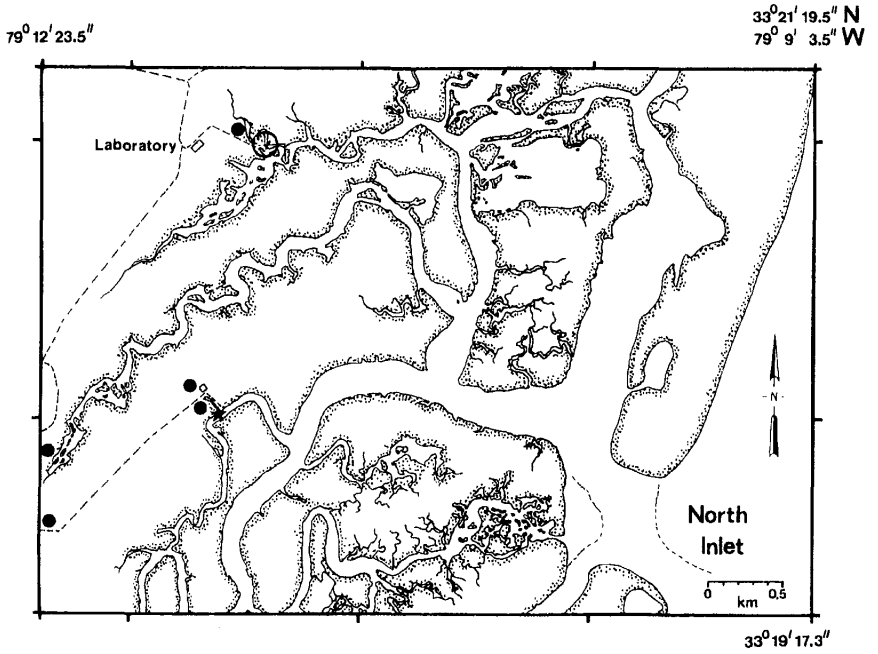

FIGURE 1. Northern portion of the North Inlet estuary. Solid circles indicate the sites where ovigerous female *Uca* were collected. The open circle shows the site where the plankton was sampled for crab megalopae. The star shows the location of the tide gauge. The approximate boundaries of the flood and ebb deltas are indicated by the dashed lines. (After the North Inlet quadrangle map, United States Geological Survey, 1942. Inlet morphology is approximate.)

Larval release in the laboratory

Cycles of larval release were determined by maintaining sequential collections of ovigerous females under controlled conditions and counting daily the number that released larvae. Ovigerous female *U. pugilator* and *U. pugnax* were dug from intertidal substrates (Fig. 1) during low tide at approximately 2-week intervals from 28 July to 12 September 1978, and from 4 May to 18 September 1979. Ovigerous female *U. minax* were collected concurrently with the other species in 1978 only. Approximately 100 females of each species were collected in each sample. Female crabs were maintained in the dark in incubation tubes suspended in filtered sea water (1 μm, 34‰ salinity) in an insulated fiberglass tank supplied with four under-gravel filters, two 500-watt immersion heaters controlled by a thermoregulator, and an opaque lid. The incubation tubes allowed females to rest in about 0.5 cm of water and retained larvae after hatching (Fig. 2). From 28 July to 22 September 1978 the temperature in the tank was 28°C. During 1979, the tank temperature was 24°C from 4 to 31 May, 26°C from 1 June to 29 July, and 28°C from 30 July to 2 October. These temperatures corresponded closely to the substrate temperatures at the depths at which females were collected.

Each morning the number of females of each species that released larvae was recorded and assigned to the date of the previous night. Every female released all her larvae in a single night. The criteria for scoring release were the absence of eggs on the pleopods of females and the presence of zoeae in the incubation tubes. The

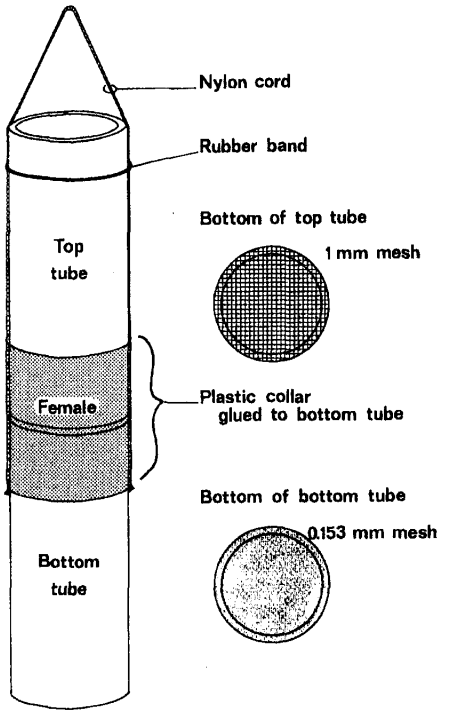

FIGURE 2. Incubation tube used to house ovigerous female *Uca* in a temperature-controlled seawater tank.

latter criterion was necessary because females occasionally, though rarely (5 out of 3,015 females), ate their eggs before they hatched.

Larval development rates

To test the assumption that larval development rates depend on temperature, *U. pugilator* larvae were reared at 22 and 28°C. About 1 h after hatching, zoeae obtained from females in the incubation tubes were mixed in a glass bowl, concentrated in a light beam, and transferred by pipette into filtered sea water (0.45 μm, 34‰ salinity) in the compartments of plastic boxes fitted with hinged lids. Ten zoeae were placed into 100 ml of water in each compartment. Zoeae were transferred daily to fresh seawater in clean compartments and fed a surfeit of 1- to 3-h old *Artemia salina* nauplii. All zoeae were reared under a 14L:10D cycle in an environmental chamber. The 22°C experiment was begun on the night of 11 May 1979 with 230 zoeae from 9 females. The 28°C experiment was begun on 2 September 1978 with 160 zoeae from 12 females. Zoeae from several females were pooled so that estimates of development rates would include components of variation due to differences among broods. The water temperatures at high tide in the marsh matched the rearing temperatures on the dates the experiments were begun.

Plankton samples

To determine when megalopae reach the upper estuary, plankton samples were collected during day and night flood tides at a single station near the head of a small

tidal creek (1–1.5 m deep at mid-tide) (Fig. 1). All three species of *Uca* occur abundantly on the creek banks and in the marsh adjacent to the sampling site. Samples were taken by hand from a foot bridge with a conical net (0.5 by 2 m, 800-μm mesh Nitex cloth) fitted with a flowmeter.

From 31 August to 7 September 1978, two to four 5-min samples were taken at 10-min intervals beginning at mid-flood tide (3 h after slack low water). For the first 2.5 min of each sample, the net was suspended just above the creek bottom; for the remaining 2.5 min, the net was raised so that it was just under the surface of the water. From 7 to 11 September, two separate 5-min top and bottom samples were taken at each mid-flood tide. From 12 to 23 September, one top and one bottom sample were taken. Finally, on 20 and 21 September, one top and one bottom sample were taken during mid-ebb tide (3 h after slack high water) at night. From 10 to 25 m^3 (mean $\pm$ SD = 15.44 $\pm$ 4.90 m^3) of water was filtered during each 5-min sample. All *Uca* megalopae were counted in each sample. Megalopal densities are the means of the densities of the sequential samples collected during each sampling period.

Physical measurements

From 19 July to 4 October 1978 and from 11 January to 23 July 1979 surface water temperatures were measured within 1 h of the time of a high tide at or near the site where the plankton samples were taken. From 11 January to 30 April 1979 water temperatures were recorded during the day. At all other times temperatures were taken at night. On two occasions temperatures were measured within 30 min of slack high water at several points along a transect from the mouth of North Inlet to the upper marsh and were found to vary less than 1.5°C.

Tide heights and amplitudes were obtained from a tide gauge located in the North Inlet estuary (Fig. 1). This paper relates semilunar cycles of larval release to semilunar cycles in the amplitude of nocturnal ebb tides. A nocturnal ebb tide is defined as one that follows a high tide that occurs between the hours of sunset and sunrise. When both high tides occurred during daylight, the one closest to sunrise or sunset was designated as the nocturnal high tide for that day.

RESULTS

Breeding seasonality and water temperatures

Crab activity was observed daily during low tide throughout the 1979 breeding season. Male *U. pugilator* first courted on 13 March. By the end of March, both *U. pugilator* and *U. pugnax* were courting, and both species fed during low tide in aggregations in the lower intertidal zone. Courtship activity declined rapidly after the full moon on 16 September 1978 and after the new moon on 21 September 1979, and ended for the year about 5 d after both dates.

Water temperature increased rapidly in the spring from a low of about 7°C in February to about 20°C by late April and early May. Temperatures continued to rise to about 28°C in the late summer (Fig. 3).

The length of incubation in summer for several species of *Uca* is from 12 to 15 d (Feest, 1969; von Hagen, 1970; Greenspan, 1975; Christy, 1978). If females mated and began incubation in late March and cool spring temperatures no more than double the period of incubation, then females may have first released larvae in late April. Larval release by *U. pugilator* first occurred during the period of 2 to 6 May in 1981 (J. Christy, unpublished). Stage I *Uca* zoeae were common in plankton

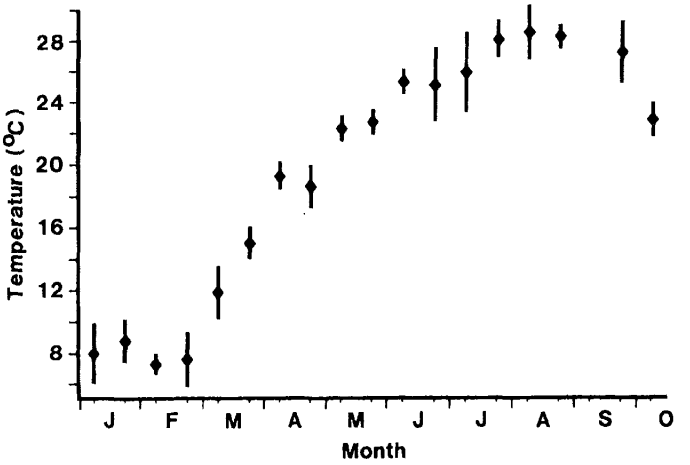

FIGURE 3. Bimonthly means of daily water temperatures in the North Inlet estuary recorded within 1 h of diurnal (11 January–30 April) or nocturnal (1 May–4 October) high tides. Temperatures were recorded in 1978 (19 July–4 October) and in 1979 (11 January–23 July). The bars indicate two standard errors above and below each mean.

samples taken at the study site in mid-May, 1979 (Christy and Stancyk, 1982). At the beginning of the breeding season, *Uca* larvae probably develop in water averaging 20 to 22°C.

Larval development rates

Development of *U. pugilator* zoeae was significantly slower at 22°C (mean ± SD = 19.4 ± 2.47 d, range = 16–27 d, $N = 230$, 76% survival to megalopa) than at 28°C (mean ± SD = 14.7 ± 2.39 d, range = 12–20 d, $N = 160$, 59% survival to megalopa) ($t_{267} = 19.013$, $P \ll 0.001$). These experiments confirm that development rates of *Uca* larvae are temperature dependent in the laboratory (Vernberg and Vernberg, 1975). On the assumption that larval development rates also depend on temperature in the field, it seems justified to expect, if the hypothesis is correct, a seasonal change in the timing of larval release relative to the spring tides as water temperatures increase during the breeding season.

Larval release in the laboratory

During August and September 1978, *U. pugilator, U. pugnax*, and *U. minax* displayed marked semilunar cycles of larval release (Fig. 4) as did *U. pugilator* and *U. pugnax* during most of the 1979 breeding season (Fig. 5). Females of all three species released larvae (mean ± SD) 0.06 ± 1.116 d before the date of a full or new moon (Table I). In 1978 the average deviations of the mean dates of release from the dates of the syzygies were 0.24 d for *U. pugilator*, −0.09 d for *U. pugnax*, and −0.80 d for *U. minax*. In 1979 *U. pugilator* released larvae, on average, 0.19 d and *U. pugnax* 0.41 d after a full or new moon. There was no significant correlation between the mean date of larval release for each cycle relative to the date of the full or new moon and the sequential rank of the date of each syzygy during the breeding season for either *U. pugilator* [Kendall's coefficient of rank correlation (Sokal and Rohlf, 1969); $\tau = 0.36$, $N = 8$, $P > 0.05$] or *U. pugnax* ($\tau = 0.27$, $N = 8$, $P > 0.05$). The expected seasonal change in the timing of larval release relative to the full and new moons and spring tides did not occur.

ɔrth Inlet estuary recorded within
·) high tides. Temperatures were
). The bars indicate two standard

ty and Stancyk, 1982). At
develop in water averaging

ly slower at 22°C (mean
survival to megalopa) than
$N = 160$, 59% survival to
confirm that development
laboratory (Vernberg and
ment rates also depend on
he hypothesis is correct, a
o the spring tides as water

U. pugnax, and *U. minax*
4) as did *U. pugilator* and
g. 5). Females of all three
re the date of a full or new
nean dates of release from
0.09 d for *U. pugnax*, and
ae, on average, 0.19 d and
no significant correlation
ative to the date of the full
syzygy during the breeding
ınk correlation (Sokal and
· = 0.27, $N = 8$, $P > 0.05$).
ase relative to the full and

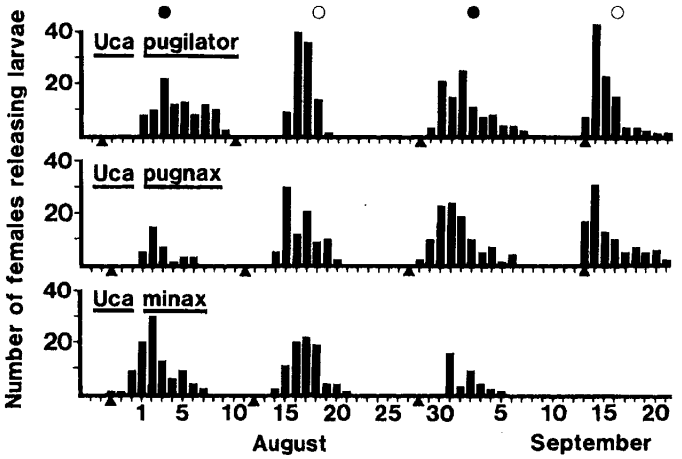

FIGURE 4. Cycles of larval release by *Uca* spp. in the laboratory in 1978. The triangles show the dates on which each sample of ovigerous females was collected. The dates of the full and new moons are indicated by the open and solid circles, respectively.

Variation in the density of Uca *megalopae*

Uca megalopae were significantly more abundant in the water column during the night than during the day [Fig. 6; Wilcoxon's signed ranks test comparing the

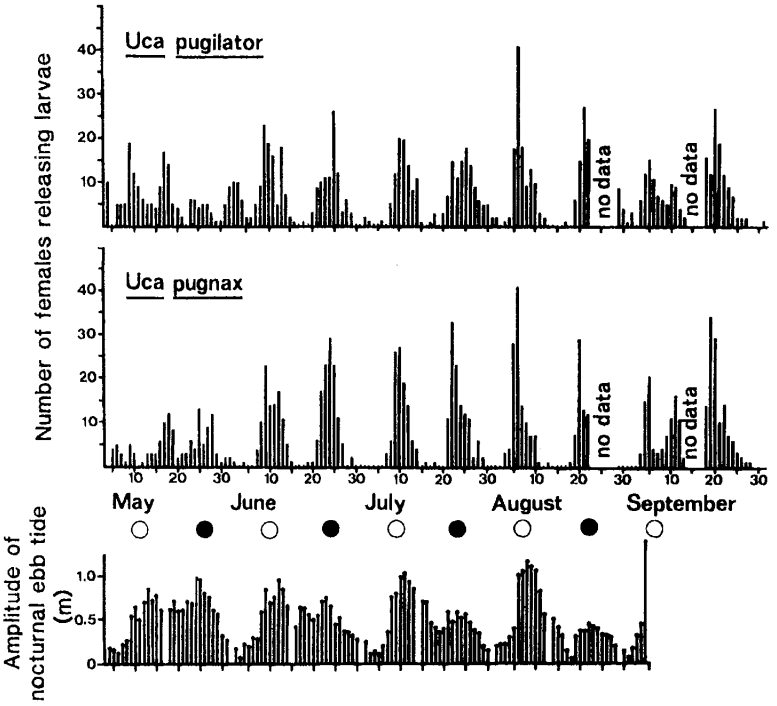

FIGURE 5. Cycles of larval release by *Uca* spp. in the laboratory in 1979 and the amplitudes of the nocturnal ebb tides at North Inlet. Dots on the x-axis indicate that ovigerous females were present in the laboratory but none released larvae. Moon phases are indicated as in Figure 4.

TABLE I

Deviation of the mean date (±SD, days) of larval release in the laboratory from the date of a full or new moon.

Date of syzygy	*U. pugilator*		*U. pugnax*		*U. minax*	
	Mean date	*N*	Mean date	*N*	Mean date	*N*
1978						
Aug. 3	1.40 ± 2.29	99	−0.26 ± 1.46	34	−0.65 ± 1.75	95
Aug. 18	−1.42 ± 6.90	100	−1.58 ± 1.60	89	−1.06 ± 1.46	83
Sept. 2	−0.69 ± 2.20	100	−1.43 ± 2.10	100	−0.69 ± 1.48	35
1979						
May 11	−0.38 ± 4.28	99	1.82 ± 5.21	51		
May 25	−0.30 ± 6.80	100	−1.29 ± 4.26	82		
June 10	−0.62 ± 2.07	110	0.12 ± 2.53	102		
June 24	−0.54 ± 3.20	100	−0.37 ± 2.06	116		
July 9	1.41 ± 2.95	97	1.24 ± 2.40	109		
July 23	2.27 ± 7.08	115	0.57 ± 2.03	114		
Aug. 7	0.06 ± 1.96	118	−0.63 ± 1.61	115		
Sept. 6	−0.20 ± 3.98	104	1.84 ± 3.14	96		

density of megalopae in each nocturnal flood tide and subsequent diurnal flood tide (Sokal and Rohlf, 1969); $T = 11$, $N = 17$, $P < 0.005$] and significantly more (80% on average) were moving in the lower 50 cm of the water column at mid-flood tide than near the surface (Wilcoxon's signed rank test comparing densities each night in surface and bottom samples; $T = 50$, $N = 38$, $P < 0.005$). On 19 and 20 September densities of megalopae were 2.02 and 3.31 per m^3 during nocturnal flood tides. In contrast, approximately 6 h later during nocturnal ebb tides, densities had dropped to 0.09 and 0.02 megalopae per m^3 on the two nights, respectively. Megalopae were most abundant about 5 d before and after the spring tides (Fig. 6), not during the spring tides as would be expected if the hypothesis were correct.

DISCUSSION

Semilunar cycles of larval release by *U. pugilator* and *U. pugnax* in the laboratory in 1979 corresponded closely to semilunar cycles in the density of newly hatched stage I zoeae in the upper estuary (Christy and Stancyk, 1982 This indicates that the timing of larval release in the laboratory probably accurately estimates the timing of larval release in the field.

Neither *U. pugilator* nor *U. pugnax* exhibited a semilunar cycle of larval release during May 1979. Wheeler (1978) reported a similar aperiodicity in June for *U. pugnax* collected in Delaware and maintained in the laboratory. *Sesarma cinereum* from North Inlet also lacked cycles of reproduction and hatching in the field and laboratory during May and June in both 1978 and 1979, though this crab exhibited marked semilunar cycles of larval release at other times (Dollard, 1980). The causes and consequences of aperiodic larval release by these crabs in the early breeding season are unknown.

The timing of larval release by *U. pugilator* and *U. pugnax* changed little during the 1979 breeding season even though water temperatures increased at least 5°C. The rearing experiments confirmed that the length of larval development decreases with an increase in temperature. If the larval lifespan in the field decreased as the water temperature increased from May to September, then it is clear that females

atory from the date

	U. minax	
N	Mean date	*N*
34	−0.65 ± 1.75	95
89	−1.06 ± 1.46	83
100	−0.69 ± 1.48	35
51		
82		
102		
116		
109		
114		
115		
96		

ıbsequent diurnal flood tide
.nd significantly more (80%
er column at mid-flood tide
ıparing densities each night
5). On 19 and 20 September
ng nocturnal flood tides. In
tides, densities had dropped
espectively. Megalopae were
.des (Fig. 6), not during the
e correct.

U. pugnax in the laboratory
e density of newly hatched
k, 1982 This indicates that
urately estimates the timing

ilunar cycle of larval release
aperiodicity in June for *U.*
oratory. *Sesarma cinereum*
ıd hatching in the field and
), though this crab exhibited
(Dollard, 1980). The causes
crabs in the early breeding

ugnax changed little during
ures increased at least 5°C.
ırval development decreases
in the field decreased as the
then it is clear that females

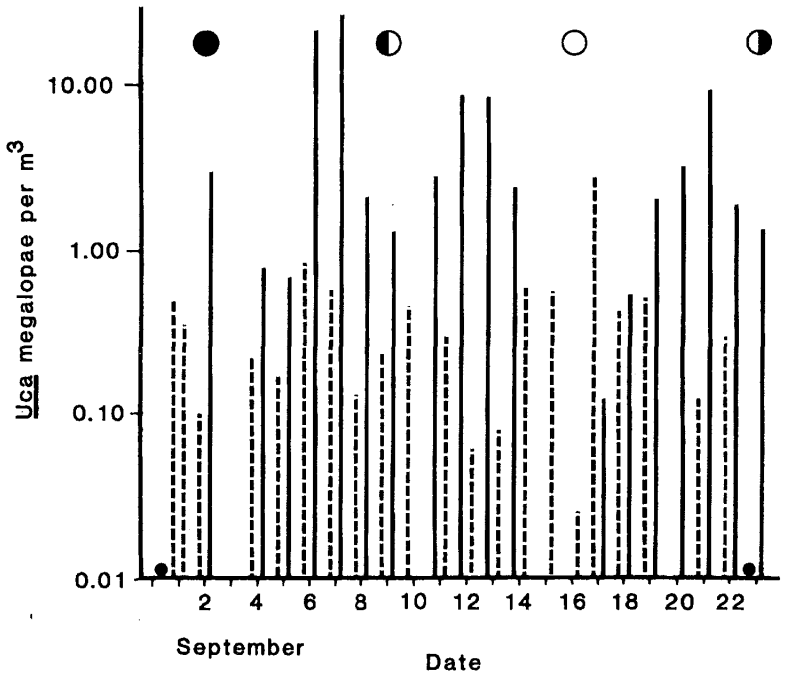

FIGURE 6. Temporal variation in the density of *Uca* spp. megalopae during September 1978. Samples were collected during daytime (broken bars) and nighttime (solid bars) flood tides in a tidal creek in the upper estuary (Fig. 1). Densities of 0 megalopae per m^3 are indicated by dots on the x-axis. Full and new moons are indicated as in Figure 4. First and last quarter moons are indicated by half-solid circles.

did not time release so that megalopae would be present and ready to settle during spring tides at all times in the breeding season.

Megalopae were expected to reach the upper estuary during spring tides, but little movement occurred at such times. The observed bimodal distribution of the abundance of megalopae during the semilunar cycle may reflect differential rates of larval development or transport among the three species of *Uca*, or temporal variation in hydrographic features that affected the transport of all species equally. Megalopae may have been rare during the syzygies because the tide ebbs during most of the night around the time of the full and new moons in the North Inlet estuary and because megalopae entered the water column primarily during nocturnal flood tides. Any hypothesized selective advantage to megalopae that move up the estuary during spring tides must be less than the advantages to megalopae that move only during the night.

During each summer tide cycle there is a net export of approximately 15% of the brachyuran crab larvae (99% stage I) that are entrained in the water that is tidally pumped across the boundaries of the North Inlet estuary (Christy and Stancyk, 1982). Crab larvae that develop in the ocean may enter the estuary by being transported landward by currents near the bottom (Scheltema, 1975; Sulkin *et al.*, 1980). This study suggests that once *Uca* megalopae occur in tidal creeks, they selectively ride flood tides at night, perhaps moving in a saltatorial fashion to substrates in the upper estuary. *Uca* megalopae were common on intertidal substrates during diurnal low tides following nights of peak abundance, but they were rare when few were

caught the previous night. Megalopae that moved past the sampling site at night probably were seeking substrates on which to settle.

The results of this study do not support the hypothesis that cycles of larval release by *Uca* spp. result in maximum rates of transport of megalopae by spring tide currents to substrates in the upper estuary. Rather, the timing of larval release appears to result in rapid seaward transport of newly hatched zoeae on nocturnal ebb tides.

At North Inlet, the amplitude of nocturnal ebb tides is correlated with the semilunar cycle. High tides occur just after sunset during the full and new moons and the subsequent ebb tides are greater in amplitude than those that occur at other times in the semilunar cycle (Fig. 5). Since *U. pugilator, U. pugnax*, and *U. minax* release larvae only at night near the time of high tide, and since peak hatching occurred near the time of the full and new moons, these crabs were releasing larvae at the time in the semilunar cycle when stage I zoeae would be transported most rapidly at night toward the ocean. It is impossible to judge whether larval release occurs in response to factors that vary with the phases of the moon or in response to factors that vary with the amplitude of nocturnal ebb tides because these two cycles coincide at North Inlet. To distinguish between these alternatives, one needs to know when larval release occurs at a site where nocturnal ebb tides of greatest amplitude occur sometime other than during the syzygies.

Reproductive cycles have been described for 17 species of *Uca* (von Hagen, 1962, 1970; Feest, 1969; Zucker, 1973, 1978; Christy, 1978; Wheeler, 1978; DeCoursey, 1981) at sites ranging from the east coast of India to the mid-Atlantic coast of the United States. With one exception, both larval release and the greatest amplitude nocturnal ebb tides during the semilunar cycle occur within about three days of the full and new moons. However, in Charlotte Harbor on the west coast of Florida, both larval release by *U. pugilator* and nocturnal ebb tides of maximum amplitude usually occur during the quarter moons (Christy, 1978; NOAA tide tables). This exception, which provides the only data of use to distinguish between the above alternatives, suggests larval release is timed to occur during large amplitude ebb tides at night, not during a particular phase of the moon.

Semilunar cycles of larval release have been described for 5 species of grapsid crabs (Warner, 1967; Saigusa and Hadaka, 1978; Seiple, 1979; Dollard, 1980), 2 gecarcinids (Gifford, 1962; Henning, 1975; Klaasen, 1975), a xanthid and a pinnotherid (Christy and Stancyk, 1982). All these estuarine crabs release larvae on large amplitude nocturnal ebb tides near the time of the full and new moons. It is unlikely that convergence in such a fundamental feature of the reproductive ecology of these terrestrial, semiterrestrial, and benthic crabs is a fortuitous result of similar adaptive responses to selective factors that operate differently in the diverse habitats of the adults (*e.g.*, Zucker, 1978; DeCoursey, 1979; Bergin, 1981). Convergence among these species more likely reflects a shared adaptive response to mortality factors experienced in common by their meroplanktonic larvae (but see Saigusa, 1981). This study suggests such selective factors must cause higher larval mortality during the day and in the upper estuary than during the night and in the lower estuary or offshore. The following mortality factors may meet these criteria.

On the Atlantic and Gulf Coasts of the United States, larval, postlarval, and juvenile stages of many marine and estuarine spawned fish use the upper reaches of tidal creeks as "nurseries," moving seaward as they grow and mature (*e.g.*, Chao and Musick, 1977; Bozeman and Dean, 1979; Shenker and Dean, 1979; Weinstein, 1979). Planktivorous species such as menhaden (*Brevoortia tyrannus*), silversides

.e sampling site at night

ıat cycles of larval release
ıegalopae by spring tide
timing of larval release
:hed zoeae on nocturnal

ɔrrelated with the semilu-
and new moons and the
:hat occur at other times
ax, and *U. minax* release
peak hatching occurred
re releasing larvae at the
transported most rapidly
:r larval release occurs in
or in response to factors
these two cycles coincide
one needs to know when
greatest amplitude occur

:ies of *Uca* (von Hagen,
978; Wheeler, 1978; De-
to the mid-Atlantic coast
:ase and the greatest am-
ır within about three days
ɔor on the west coast of
l ebb tides of maximum
:ty, 1978; NOAA tide ta-
:e to distinguish between
ur during large amplitude
oon.
d for 5 species of grapsid
1979; Dollard, 1980), 2
5), a xanthid and a pin-
: crabs release larvae on
full and new moons. It is
f the reproductive ecology
ortuitous result of similar
ıtly in the diverse habitats
·gin, 1981). Convergence
ıve response to mortality
: larvae (but see Saigusa,
se higher larval mortality
e night and in the lower
meet these criteria.
es, larval, postlarval, and
ısh use the upper reaches
w and mature (*e.g.*, Chao
d Dean, 1979; Weinstein,
rtia tyrannus), silversides

(*Menidia menidia*) and the bay anchovie (*Anchoa mitchilli*) are abundant in the upper estuary during the entire crab breeding season. Other common species such as spot (*Leiostomus xanthurus*) and pinfish (*Lagodon rhomboides*) are planktivorous only when small, in the spring, when crabs begin to breed (Thayer *et al.*, 1974; Kjelson *et al.*, 1975; Chao and Musick, 1977). In general, such species feed on planktonic crustaceans only during the day (*e.g.*, Kjelson *et al.*, 1975; Robertson and Howard, 1978). Predation in the upper estuary by diurnally feeding planktivores may produce powerful selection on when estuarine crabs release larvae. Zoeae that are rapidly transported seaward following release near the peaks of large amplitude nocturnal tides may better escape such predation than those released at other times (see also Bergin, 1978). If true, one would expect crab larvae that complete development in the upper estuary to possess traits that reduce predation.

Rhithropanopeus harrisi is found in the extreme upper-reaches of tidal creeks and along rivers at the headwaters of estuaries from New Brunswick to Brazil (Williams, 1965). This xanthid crab releases larvae continuously, its zoeae display patterns of vertical migration that minimize seaward transport, and it completes larval development in the estuary (Williams, 1971; Cronin, 1979). *R. harrisi* zoeae are striking among the xanthid larvae that are common in estuaries on the western Atlantic coast because they possess extremely long rostral and antennal spines (Chamberlain, 1962; Kurata, 1970). Recent experiments demonstrate that these spines, together with the dorsal spine, deter ingestion by small planktivorous fish because they make zoeae too large (approximately 2 mm) to enter their buccal cavities (Morgan, 1981).

Dollard (1980) suggested that larvae released on nocturnal high tides might escape lethal high temperatures. Maximum temperatures are likely to occur during late afternoon low tides in shallow tidal creeks in the upper estuary. At North Inlet in July and August such temperatures commonly exceed 40°C (Dollard, 1980), while maximum temperatures in deeper channels in the middle and upper estuary remain around 30 to 32°C (Bergin, 1978).

Survival rates at high temperatures of first stage *Uca* sp. zoeae depend on salinity (Vernberg and Vernberg, 1975). Fifty percent of stage I *U. pugilator* zoeae die within 1 h, while fifty percent of *U. pugnax* zoeae die within 5 h at 40°C and 20‰. At 35‰ and 40°C, fifty percent mortality of *U. pugilator* and *U. pugnax* zoeae occurs at 12.5 and 6.5 h, respectively. At 38°C zoeae of both species survive over 2.5 d at 20‰ and about 3.5 d at 35‰. Comparable data for the other crabs discussed above are not available.

During summer low tides, larval mortality will be highest in hot, low salinity water in pools and shallow creeks in the upper marsh. Zoeae that are released at high tide just after dark would be transported seaward and might experience relatively high salinities and cool morning temperatures during their first low tide. By migrating vertically with respect to flood- and ebb-directed currents, zoeae might be further displaced seaward into cool high-salinity water during subsequent tidal cycles. Larvae that are released at the peak of large amplitude tides that occur after sunset may best escape lethal combinations of salinity and temperature in both space and time (see also Saigusa, 1981).

I emphasize that future hypotheses about the adaptive significance of the timing of larval release in *Uca* spp. and many other estuarine brachyurans must explain why these crabs release larvae at high tide at night when the amplitude of the nocturnal ebb tides are at a semilunar maximum and zoeae are most rapidly transported away from the upper-reaches of the estuary.

ACKNOWLEDGMENTS

I thank Drs. D. Allen, P. Feeny, M. Salmon, and S. Stancyk for their comments on a draft of this paper. Dr. Pat DeCoursey assisted with the initiation of this research and shared her knowledge and unpublished data on tidal and diel timing of larval release by *Uca* sp. The staff of the Baruch Institute provided frequent and capable assistance. This research was supported by Grant OCE77-20960 from The National Science Foundation.

LITERATURE CITED

BERGIN, M. E. 1978. *Hatching rhythms in* Uca pugilator *(Bosc) (Decapoda, Brachyura) from North Inlet, South Carolina.* Masters thesis, University of South Carolina, 46 pp.

BERGIN, M. E. 1981. Hatching rhythms in *Uca pugilator* (Decapoda: Brachyura). *Mar. Biol.* **63:** 151–158.

BOZEMAN, E. L., AND J. M. DEAN. 1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek. *Estuaries* **3:** 89–97.

CARRIKER, M. R. 1967. Ecology of estuarine benthic invertebrates: a perspective. Pp. 442–487 in *Estuaries,* G. H. Lauff, Ed. Amer. Assoc. Adv. Sci. Pub. No. 83, Washington.

CHAMBERLAIN, N. A. 1962. Ecological studies of the larval development of *Rhithropanopeus harisi* (Xanthidae, Brachyura). *Chesapeake Bay Inst. Johns Hopkins Univ. Tech. Report* **28:** 1–47.

CHAO, L. N., AND J. A. MUSICK. 1977. Life history, feeding habits and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. *Fish. Bull.* **75:** 657–702.

CHRISTY, J. H. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator:* a hypothesis. *Science* **199:** 453–455.

CHRISTY, J. H., AND S. E. STANCYK. 1982. Movement of larvae from North Inlet estuary, S. C., with special reference to crab zoeae. In *Estuarine Comparisons,* V. Kennedy, Ed. Academic Press, New York.

COSTLOW, J. D., JR., C. G. BOOKHOUT, AND R. MONROE. 1960. The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. *Biol. Bull.* **118:** 183–202.

COSTLOW, J. D., JR., C. G. BOOKHOUT, AND R. MONROE. 1962. Salinity and temperature effects on the larval development of the crab *Panopeus herbstii* Milne-Edwards, reared in the laboratory. *Physiol. Zool.* **35:** 79–93.

COSTLOW, J. D., JR., C. G. BOOKHOUT, AND R. MONROE. 1966. Studies on the larval development of the crab *Rhithropanopeus harrisi* (Gould) I. The effect of salinity and temperature on larval development. *Physiol. Zool.* **39:** 81–100.

CRANE, J. 1943. Display, breeding and relationships of fiddler crabs (Brachyura, Genus *Uca*) in the Northeastern United States. *Zoologica* **28:** 217–223.

CRANE, J. 1958. Aspects of social behavior in fiddler crabs with special reference to *Uca maracoani. Zoologica* **43:** 113–130.

CRANE, J. 1975. *Fiddler crabs of the world, Ocypodidae: genus* Uca. Princeton University Press, Princeton.

CRONIN, T. W. 1979. *Factors contributing to the retention of larvae of the crab* Rhithropanopeus harrisi *in the Newport River estuary, North Carolina.* Ph.D. thesis, Duke University. 206 pp.

DECOURSEY, P. J. 1979. Egg-hatching rhythms in three species of fiddler crabs. Pp. 399–406 in *Cyclic phenomena in marine plants and animals,* E. Naylor and R. G. Hartnoll, Eds. Pergamon Press, Oxford.

DECOURSEY, P. J. 1981. Cyclic reproduction of fiddler crabs, *Uca*: a model for estuarine adaptation. *Estuaries* **4:** 263.

DOLLARD, H. A. 1980. *Larval release patterns in the wharf crab,* Sesarma cinereum, *from North Inlet, South Carolina.* Masters thesis, University of South Carolina. 34 pp.

DUDLEY, D. L., AND M. H. JUDY. 1971. Occurrence of larval, juvenile and mature crabs in the vicinity of Beaufort Inlet, North Carolina. *Tech. Report, NMFS, Special Scientific Report, Fisheries* **673:** 1–10.

FEEST, J. 1969. Morphophysiologische Untersuchungen zur Ontogeneses und Fortpflanzungsbiologie von *Uca annulipes* and *Uca triangularis* mit Vergleichsbefunden an *Illyoplax gangetica. Forma Functio* **1:** 159–225.

GIFFORD, C. A. 1962. Some observations of the general biology of the land crab, *Cardisoma guanhumi* (Laterielle) in South Florida. *Biol. Bull.* **123:** 207–223.

GREENSPAN, B. N. 1975. *Male reproductive strategy in the communal courtship system of the fiddler crab* Uca pugnax. Ph.D. thesis, Rockefeller University. 195 pp.

ancyk for their comments
e initiation of this research
l and diel timing of larval
ded frequent and capable
20960 from The National

da, Brachyura) from North Inlet,
46 pp.
Brachyura). Mar. Biol. 63: 151–

rval and juvenile fish in a South

perspective. Pp. 442–487 in Es-
, Washington.
nent of Rhithropanopeus harisi
Univ. Tech. Report 28: 1–47.
nctional morphology of juvenile
75: 657–702.
he fiddler crab Uca pugilator: a

North Inlet estuary, S. C., with
. Kennedy, Ed. Academic Press,

ffect of salinity and temperature
the laboratory. Biol. Bull. 118:

y and temperature effects on the
vards, reared in the laboratory.

ies on the larval development of
inity and temperature on larval

(Brachyura, Genus Uca) in the

ial reference to Uca maracoani.

eton University Press, Princeton.
he crab Rhithropanopeus harrisi
uke University. 206 pp.
ler crabs. Pp. 399–406 in Cyclic
. Hartnoll, Eds. Pergamon Press,

model for estuarine adaptation.

ma cinereum, from North Inlet,
34 pp.
and mature crabs in the vicinity
l Scientific Report, Fisheries 673:

und Fortpflanzungsbiologie von
an Illyoplax gangetica. Forma

land crab, Cardisoma guanhumi

urtship system of the fiddler crab

HENNING, H. G. 1975. Kampf-, Fortpflanzung- und Hautungsverhalten-Wachstum und Geschlechtsreife von *Cardisoma guanhumi* Latreille (Crustacea, Brachyura). *Forma Functio* **8:** 463–510.

KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON. 1975. The general feeding ecology of postlarval fishes in the Newport River estuary. *Fish. Bull.* **73:** 137–144.

KJERFVE, B., AND J. A. PROEHL. 1979. Velocity variability in a crossection of a well-mixed estuary. *J. Mar. Res.* **37:** 409–418.

KLAASEN, F. 1975. Oekologische und ethologische Untersuchungen zur Fortpflanzungsbiologie von *Gecarcinus lateralis* (Decapoda, Brachyura). *Forma Functio* **8:** 101–174.

KURATA, H. 1970. *Studies on the life histories of decapod Crustacea of Georgia.* Unpublished manuscript, Marine Institute, University of Georgia, Sapelo Island, Georgia.

MORGAN, S. G. 1981. Larval spines as an anti-predator device in *Rhithropanopeus harrisi* (Decapoda, Xanthidae). *Am. Zool.* **21:** 1004 (Abst. No. 518).

ROBERTSON, A. I., AND R. K. HOWARD. 1978. Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. *Mar. Biol.* **48:** 207–213.

SAIGUSA, M. 1981. Adaptive significance of a semilunar rhythm in the terrestrial crab *Sesarma. Biol. Bull.* **160:** 311–321.

SAIGUSA, M., AND T. HADAKA. 1978. Semi-lunar rhythm of the zoeae-release activity of the land crabs *Sesarma. Oecologia* **37:** 163–176.

SANDIFER, P. A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia. *Chesapeake Sci.* **14:** 235–257.

SANDIFER, P. A. 1975. The role of pelagic larvae in recruitment to populations of adult crustaceans in the York River estuary and lower Chesapeake Bay, Virginia. *Estuarine and Coastal Mar. Sci.* **3:** 269–279.

SCHELTEMA, R. S. 1975. Relationship of larval dispersal, gene-flow, and natural selection to geographic variations of benthic invertebrates in estuaries and along coastal regions. *Estuarine Research* **1:** 372–391.

SEIPLE, W. 1979. Distribution, habitat preference, and breeding periods in the crustaceans *Sesarma cinereum* and *Sesarma reticulatum* (Brachyura: Decapoda: Grapsidae). *Mar. Biol.* **52:** 77–86.

SHENKER, J. M., AND J. M. DEAN. 1979. The utilization of an intertidal salt marsh creeks by larval and juvenile fishes: abundance, diversity and temporal variation. *Estuaries* **2:** 154–163.

SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry.* W. H. Freeman and Co., San Fransisco.

SULKIN, S. D., W. VAN HEUKELEM, P. KELLY, AND L. VAN HEUKELEM. 1980. The behavioral basis of larval recruitment in the crab *Callinectes sapidus* Rathbun: a laboratory investigation of ontogenetic changes in geotaxis and barokinesis. *Biol. Bull.* **159:** 402–417.

THAYER, G. W., D. E. HOSS, M. A. KJELSON, W. F. HETTLER, JR., AND M. W. LACROIX. 1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. *Chesapeake Sci.* **15:** 6–19.

THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the plankton larvae in the sound (Oresund). *Medd. Komm. Dan. Fisk. Havendersog. Copenhagen Series Plankton* **4:** 1–523.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev. of Camb. Philos. Soc.* **25:** 1–45.

VANCE, R. R. 1973. On reproductive strategies in marine benthic invertebrates. *Amer. Natur.* **107:** 339–352.

VERNBERG, F. J., AND W. B. VERNBERG. 1975. Adaptations to extreme environments. Pp. 165–180 in *Physiological ecology of estuarine organisms,* F. J. Vernberg, Ed. University of South Carolina Press, Columbia.

VON HAGEN, H. O. 1962. Freilandstudien zur Sexual und Fortpflanzungsbiologie von *Uca tangeri* in Andalusien. *Zeit. Morph. Oekol. Tiere* **51:** 611–725.

VON HAGEN, H. O. 1970. Anpassungen an das spezielle Gezeitenzonen-Niveau bei Ocypodiden (Decapoda, Brachyura). *Forma Functio* **2:** 361–413.

WARNER, G. F. 1967. The life history of the mangrove tree crab *Aratus pisoni. J. Zool.* **153:** 321–335.

WEINSTEIN, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fish. Bull.* **77:** 339–357.

WHEELER, D. 1978. Semi-lunar hatching periodicity in the mud fiddler crab *Uca pugnax* (Smith). *Estuaries* **1:** 268–269.

WILLIAMS, A. B. 1965. Marine decapod crustaceans of the Carolinas. *Fish. Bull.* **65**(i–xi): 1–298.

WILLIAMS, A. B. 1971. A ten-year study of meroplankton in North Carolina estuaries: annual occurrence of some brachyuran developmental stages. *Chesapeake Sci.* **12:** 53–61.

ZUCKER, N. 1973. *Social behavior in the tropical fiddler crab* Uca terpsichores. Ph.D. thesis, University of Illinois. 150 pp.

ZUCKER, N. 1978. Monthly reproductive cycles in three sympatric hood-building tropical fiddler crabs (genus *Uca*). *Biol. Bull.* **155:** 410–424.