

TIMING OF LARVAL PRODUCTION AND FLUX OF INVERTEBRATE LARVAE IN A WELL-MIXED ESTUARY

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Abstract: Flux of invertebrate larvae between an estuary and coastal waters and the effect of the timing of larval production by estuarine crabs on larval transport were studied in North Inlet estuary, South Carolina. Invertebrate larvae were sampled from three transects across the entrances to this well-mixed estuary during spring and neap tidal periods in each season in 1979. Crab zoeae also were sampled nightly throughout the summer at a single station in the upper reaches of the estuary. The net flux of most larval groups corresponded to the net flux of water and was not different from zero. Six of the 20 larval groups sampled (e.g. echinoderm plutei, barnacle cyprids) showed significant imports to the estuary during one or more sampling periods. Only crab zoeae were exported significantly from the estuary. Such exports occurred during spring tidal periods in the summer when the densities of stage I zoeae of the seven dominant estuarine species were 6 to 57 times greater in the lower estuary and 100 to 10,000 times greater in the upper estuary than during neap tidal periods. Maximum zoeal densities occurred when female crabs released larvae. The timing of larval release may result in rapid seaward transport of newly hatched zoeae on nocturnal ebb tides of greatest amplitude during the semilunar cycle, leading to significant net export from the estuary.

Introduction

Larvae of several taxa of estuarine invertebrates hatch or are liberated only at specific times in the diel, tidal, and semilunar or lunar cycles (Naylor 1976; Saigusa and Hadaka 1978; Clark 1979; DeCoursey 1979). However, most models of mechanisms leading to retention of larvae of estuarine organisms ignore the potentially important effects of the timing of larval entry into the water column on larval dispersal and eventual settlement in ap-

appropriate habitats (but see Carriker 1961; Russell-Hunter et al. 1972). Instead, such models invoke either larval responses to salinity gradients, patterns of nontidal circulation and tidal currents (Bousfield 1955; Carriker 1967; Sandifer 1975) or the effects of currents and eddy diffusion alone (Ayers 1956; de Wolf 1974) to explain patterns of larval distribution and abundance. In addition, models of retention rarely have been tested directly by measuring the net flux of larvae across the boundaries of an estuary.

This paper presents the results of a study of the seasonal and annual flux of invertebrate larvae between a well-mixed estuary and coastal waters and a concurrent study of the semilunar timing of larval production by brachyuran crabs common in the upper-reaches of this estuary. The major objectives of this research were (1) to determine the possible effects of the timing of larval release by crabs on larval retention as measured by the net flux of crab zoeae, and (2) to compare the signs and magnitudes of the net fluxes of the different larval groups.

Materials and Methods

North Inlet estuary encompasses approximately 3200 ha of salt marsh near Georgetown, South Carolina (Fig. 1). This estuary has a single inlet to the sea at the confluence of three major tidal creeks (Debidue, Town, and Jones Creeks) that average about 3 m deep at mean tide level. The mean tidal range is 1.7 m and peak current velocities of 2.3 m s^{-1} have been recorded in Town Creek. Salinities in the northern portion of the marsh typically are above 32 ppt because the only freshwater input is in the form of runoff, which usually is a very minor component of the tidal prism (Kjerfve and McKeller 1980). In contrast, the southern portions of the marsh receive brackish water from Mud Bay and salinities are generally lower and more variable than in the northern portions (Schwing and Kjerfve 1980).

Larval Flux

Samples were collected in 1979 from anchored boats at two stations on transects near North Inlet across Town and North Jones Creeks, and from one station in South Jones Creek (Fig. 1). Detailed discussions of station placement and materials sampled can be found in Kjerfve et al. (1981) and Chrzanowski et al. (1979). Samples were collected every two hours for 25 h during both neap and spring tide periods in May, July, and October–November, and during mid and neap tide periods in February. Two complete tidal cycles occurred during each 25 h sampling period, but there was no replication of day and night cycles within periods.

Zooplankton were collected with $153 \mu\text{m}$ mesh, 30 cm mouth diameter nets which had 1 m long cylindrical sleeves to prevent clogging. Paired, sequential, vertical oblique tows were made from the stationary boats by lowering closed nets to the bottom, opening them, and bringing them to the surface. Vertical oblique tows were taken from a moving boat in South Jones

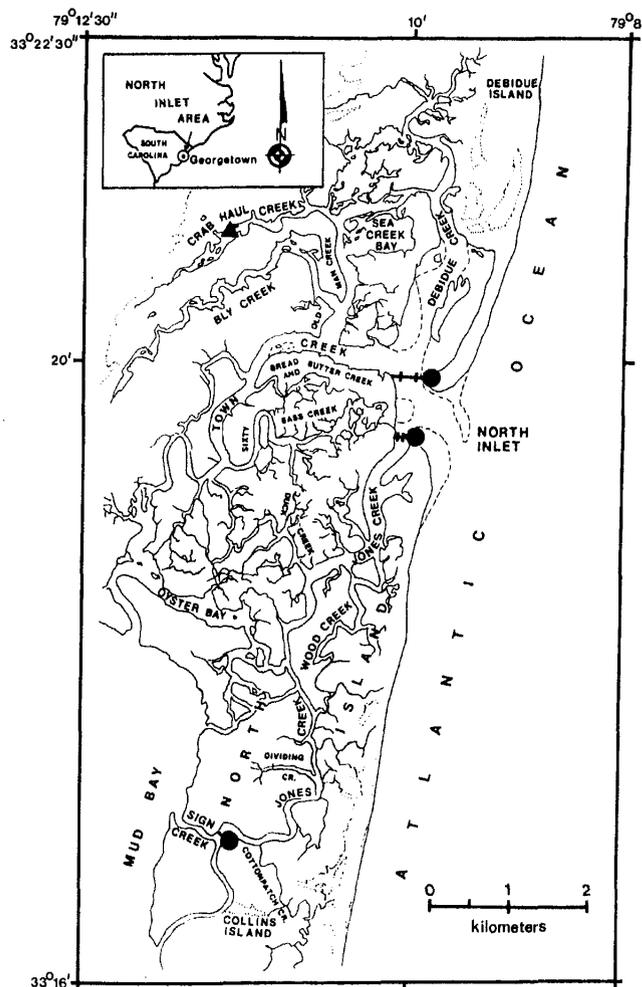


Figure 1. Map of North Inlet estuary showing locations of transects used in the study of the flux of invertebrate larvae (circles) and the sampling station used in the study of production of brachyuran larvae (triangle).

Creek because current velocities were too low for stationary sampling. The amount of water filtered was quantified with General Oceanics flowmeters in the net mouths. Between 0.6–7.6 m³ of water was filtered during tows lasting 1.5–5 min, depending upon current velocity.

Samples were diluted or concentrated so that at least 400 organisms were present in a 2 ml Stemple pipette subsample. Organisms were identified to species (copepods) or larval group and enumerated. All counts were adjusted to yield numbers of organisms per m³. A residual analysis showed that samples of less than 0.6 m³ of water did not accurately estimate zooplankton abundance, so such samples were excluded from the analysis of larval flux. In all, 1173 samples were collected over the year, and 92% (1077) were used in flux calculations. Water velocity measurements were taken concurrently at each station with biplane current crosses (Pritchard and Burt 1951).

The instantaneous flux of zooplankton was calculated from:

$$F = \sum_{j=1}^n [\bar{V}_j W_j D_j \bar{C}_j] \quad (1)$$

where F is the transport or flux; n is the number of sampling stations; \bar{V}_j is the depth-averaged instantaneous velocity at station j ; W_j and D_j are width and depth of the partial cross-section represented by station j ; and \bar{C}_j is the concentration of zooplankton at station j . Integration of velocity over depth is possible in these flux calculations because instantaneous velocity varies little with depth (Kjerfve and Proehl 1979; B. Kjerfve, Baruch Institute, pers. comm.). Although samples were collected over two tidal cycles, single tidal cycle transports were calculated by summing the instantaneous fluxes for each tidal cycle to permit comparison with other studies (e.g. Carlson 1978). Tidal cycle estimates calculated in this manner ignore natural rhythms in the data and exaggerate estimates of variance. By our sampling two consecutive tide cycles, sustained rhythms were detected, mathematically defined, and incorporated in an equation to calculate flux. This method supplied an estimate of variance, was not affected by a small number of missing observations, and allowed statistical evaluation of the mean net transport relative to zero transport. Since zooplankton were collected only for two tidal cycles, the method may underestimate variability, but it still provides a reasonable approximation of flux. The net transport calculated for each tidal series (two tidal cycles) was obtained by modelling the instantaneous flux (F) (eq 1) as a function of time (T). The model was

$$\begin{aligned} F_T = & \mu + \alpha_1 \text{Sin}(2\pi T/24.84) + \beta_1 \text{Cos}(2\pi T/24.84) \\ & + \alpha_2 \text{Sin}(2\pi T/12.42) + \beta_2 \text{Cos}(2\pi T/12.42) \\ & + \alpha_3 \text{Sin}(2\pi T/6.21) + \beta_3 \text{Cos}(2\pi T/6.21) \\ & + \alpha_4 \text{Sin}(2\pi T/24.00) + \beta_4 \text{Cos}(2\pi T/24.00) + \epsilon \end{aligned} \quad (2)$$

where μ is the mean instantaneous flux; $\alpha_1, \alpha_2, \alpha_3, \alpha_4, \beta_1, \beta_2, \beta_3, \beta_4$ are coefficients; and ϵ is a random error term. The mean flux per tidal cycle was calculated by multiplying μ by the length of a tidal cycle in the appropriate time units. More detailed discussions of this model may be found in Chrzanowski et al. (in press a, b).

Least squares estimates of $\mu, \alpha_1, \alpha_2, \alpha_3, \alpha_4, \beta_1, \beta_2, \beta_3, \beta_4$ were made using the general linear model procedures of the SAS computing package (Helwig and Council 1979). A complete development of the statistical theory of the general linear model is available in Graybill (1976). The standard t-test from the general linear model was used to test ($\alpha = 0.05$) the null hypothesis $\mu = 0$ versus the two-sided alternative where μ is the average instantaneous flux (eq 2) for each larval group. About one out of every 20 such tests should be significant at the $\alpha = 0.05$ level by chance alone; whether such significant

fluxes are ecologically meaningful can be judged using other criteria (see below). A more conservative multiple comparisons test would lack the sensitivity to reveal some of the significant fluxes seen in this study.

Brachyuran Larval Production

Brachyuran zoeae were collected nightly near the time of high tide from 18 May to 10 October, 1979, at a station in a shallow (about 1.7 m at mean high tide) tidal creek in the upper marsh (Fig. 1; Miller and Gardner 1981). This sampling time was chosen because the fiddler crabs, *Uca pugilator*, *Uca pugnax* and *Uca minax*, which are among the numerically dominant brachyurans in the marsh, release larvae only at night near the time of high tide (DeCoursey 1979; Bergin 1981).

Two sampling methods were used. From 18 May to 23 July, three 10-min samples were taken each night with a centrifugal pump powered by a gasoline engine. The intake of the suction line (1.6 cm diameter) was lowered to 10 cm above the creekbed for the first 5 min of each sample and then raised to 10 cm below the surface for the remaining 5 min. The three nightly samples were taken at 30 min intervals, the first beginning (mean \pm SD) 1.5 ± 0.56 h after high tide. An average of 0.224 m^3 of water was filtered for each sample. Nightly zoeal densities are the averages of the three nightly samples.

From 24 July to 10 October, one 1.5 h sample was taken each night by drawing water with an electric centrifugal pump through a $153 \mu\text{m}$ mesh net mounted vertically in a plastic pipe (15.25 cm diameter) fitted to the intake of the suction line of the pump. The net and pipe were bouyed so that the mouth of the net remained about 20 cm below the surface at all tide heights. Sampling began 0.09 ± 0.25 h after high tide. An average of $2.25 \pm 0.12 \text{ m}^3$ of water was filtered each 1.5 h sample. Zoeae collected each night were preserved as single samples.

Zoeae in samples were identified by comparison with larvae hatched in the laboratory (*Uca* spp., *Sesarma cinereum*, *Sesarma reticulatum*) and from published descriptions. All zoeae were counted in samples containing up to about 200 individuals of the most abundant species. At higher densities, three to five aliquots were taken with 5 ml Stemple pipette and density estimates were based on the average count per aliquot when this number exceeded 20. This procedure resulted in counting the number of zoeae of the most abundant species in a volume of sample equal to a minimum of 38 l of water in the marsh and the number of zoeae of the rarest species in a volume of sample equal to at least 114 l of creek water. The coefficient of variation among aliquots with counts of 20 or more individuals was $9.4 \pm 1.0\%$. Sampling error could not be estimated because simultaneous replicate samples were not taken.

Results

Larval Flux

Estimates of mean net flux of twenty different larval categories during

spring, mid, or neap tides were calculated for each sampling period (Table 1). Variation about these estimates was large (coefficients of variation up to 200%) because larval densities varied greatly between paired sequential samples and day and night cycles were not replicated. Few of the net fluxes were significantly different from zero. Copepodids and copepod nauplii, including those of the dominant copepod *Acartia tonsa*, showed occasional significant import, especially during neap tides in July and October. There was significant import of barnacle cyprids on spring tides in February and May. Hydrozoan larvae (November), pilidium larvae (May, July) and pluteus larvae (July) also were imported significantly on some spring tides. Had observation of significant fluxes been due to chance alone there should have been an approximately equal number of imports and exports. However, 8 of the 10 significant fluxes were imports even though water was exported from the estuary during all sampling periods (Chrzanowski et al. in press a, b).

Only crab zoeae showed consistent export from North Inlet during times of maximum larval production (Table 1). Exports of crab zoeae were significant during May and July spring tides, and were 6 to 57 times greater than corresponding neap tide exports. Spring tide export of crab zoeae was 2.4 times greater than neap export in October/November as well, but was not significant. During times of significant export, densities of crab zoeae ranged as high as 28,766 m⁻³, while mean densities ranged from 462 to 9423 m⁻³, depending upon the creek sampled (Table 2). There was considerable fluctuation in numbers of crab zoeae with time of day, tidal height and velocity, but patterns are difficult to interpret due to the lack of replication and large between-sample variation.

The proportion of the larval population that is entrained in the flow of water through the transects and exported over a tidal cycle can be approximated by comparing the absolute flux (direction ignored) with the net flux. Most of the categories had net fluxes which were 0.3-5.0% of the absolute flux. When crab zoeae were significantly exported, however, they had net fluxes that were 8.3% (May spring tide) and 7% (July spring tide) of the absolute flux. Net flux of crab zoeae on the corresponding neap tides was 2.3 and 3.0%. Absolute flux is equal to two times the population crossing the boundaries (all organisms out plus all organisms in) minus the organisms which do not return (net export). This indicates that about 13-15% of the crab zoeal population was exported during each tidal cycle. Thus, in five to seven tidal cycles, nearly all of the crab zoeae in the water flowing across the boundaries of the estuary could be lost through export.

Brachyuran Larval Production

Stage I zoeae of 14 taxa (16 species) were identified and enumerated in the samples taken each night near the time of high tide in the upper marsh (Table 3). *Uca* spp. clearly dominated all samples, accounting for about 94% of all zoeae counted. Zoeae of the grapsids, *Sesarma cinereum* and *S. reticulatum*, the xanthid, *Panopeus herbstii*, and the pinnotherid, *Pinnixa*

Table 1. Net flux (numbers per tidal cycle $\times 10^6$) of larval forms through the North Inlet estuary, SC, for different tidal periods and different seasons. Negative values are imports; positive values are exports. * $P \leq 0.05$

Larval Category	Feb 1979		May 1979		July 1979		Oct/Nov 1979	
	Mid	Spring	Neap	Spring	Neap	Spring	Neap	Spring
Acartia copepodids	0.0	0.0	106.90	0.0	-3953.00	129.80	-657.10*	-608.00
Other copepodids	63.30	-25.10	-20.60	-19.00	94.60	24.10	-329.10*	-18.25
Copepod nauplii	-89.50	-13.80	29.50	10.10	-2604.00*	11.52	-0.83	-33.90
Hydrozoan larvae	0.0	0.13	-82.60	4.54	36.90	-8.42	-1.16	-22.70*
Muller's larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.34
Plidium larvae	0.19	0.0	-0.17	-1.80*	7.64	-3.54*	-0.12	2.47
Trochophore larvae	-54.67	-27.50	10.83	-0.23	9.83	2.83	0.16	5.00
Polychaete larvae	138.00	14.56	-37.65	13.40	13.20	-119.60	-11.47	-11.03
Bivalve larvae	3.40	1.16	11.68	47.10	-137.50	-106.70	20.50	0.40
Gastropod veligers	-3.93	-0.008	0.36	-6.07	28.93	-3.93	3.84	-5.71
Cyphonautes larvae	0.02	0.05	-24.21	2.31	-173.30	-20.45	-3.14	-42.21
Actinotroch larvae	0.0	0.0	-0.15	0.0	0.0	-0.07	0.03	0.37
Crab zoeae	0.0	-0.05	150.80	919.10*	15.40	876.90*	0.90	2.20
Crab megalopae	0.0	0.0	-0.008	2.62	0.57	-0.85	0.45	0.28
Shrimp zoeae	0.0	0.06	8.62	16.69	-15.91	9.0	0.10	-0.59
Barnacle nauplii	1.29	0.98	-4.25	9.94	-13.78	-38.25	6.50	-24.25
Barnacle cyprids	5.92	-31.60*	-16.20	-443.60*	-206.70	171.10	-0.098	2.68
Pluteus larvae	0.0	0.0	-25.00	2.10	417.00	-25.00*	-1.05	-1.80
Tornaria larvae	0.0	0.0	-0.08	0.0	0.0	0.0	-0.06	7.00
Ascidian larvae	0.0	0.0	0.0	0.0	0.0	0.42	-0.10	1.97

Table 2. Average densities (± 1 standard error of the mean) of crab zoeae over two tidal cycles in the creeks near the boundaries of the North Inlet estuary.

Month, 1979	Tidal Period	Creek	Number of Zoeae m^{-3}
February	Mid	Town	0
		North Jones	0
		South Jones	0
	Spring	Town	0
		North Jones	0.5 ± 0.50
		South Jones	0
May	Neap	Town	973.0 ± 103.58
		North Jones	1133.6 ± 172.46
		South Jones	2939.8 ± 807.40
	Spring	Town	2463.0 ± 551.69
		North Jones	2397.5 ± 473.10
		South Jones	9423.5 ± 1762.36
July	Neap	Town	306.7 ± 38.95
		North Jones	362.8 ± 45.10
		South Jones	1610.8 ± 307.52
	Spring	Town	916.5 ± 150.80
		North Jones	462.1 ± 116.01
		South Jones	1927.7 ± 468.22
October	Neap	Town	4.9 ± 1.86
		North Jones	5.1 ± 1.88
		South Jones	0.7 ± 0.40
November	Spring	Town	5.8 ± 2.18
		North Jones	11.6 ± 4.75
		South Jones	0.3 ± 0.27

chaetoptera, also were frequently observed at lower densities. Together, these seven species comprised 99.5% of all zoeae. Their relative abundance was unaffected by variation in zoeal densities, and did not change significantly between semilunar maxima and minima. Later zoeal stages made up only 0.019% of all zoeae counted (16 stage II and 5 stage V *Uca* spp.; 3 stage II *Eurypanopeus depressus*). Species composition and relative abundance of zoeae in flux samples compared favorably with samples from the upper marsh. The seven species that were dominant in the upper marsh comprised 98% of the zoeae present in eight representative flux samples taken during May and July spring tidal periods, and 83% of the zoeae in six samples collected during the respective neap tidal periods. Later zoeal stages also were rare in flux samples, accounting for only 0.1% of 5066 zoeae identified to species in 14 representative samples from all transects.

The density of *Uca* spp. zoeae varied significantly among the three samples taken each night from 18 May to 23 July (Freidman's two-way

Table 3. Zoal species composition and abundance in samples taken at night near the time of high tide at a station in the upper reaches of the North Inlet estuary.

Taxon	Number of zoeae counted	% of total	Cumulative % of total
<i>Uca</i> spp.	115090	93.80	93.80
<i>Sesarma cinereum</i>	2749	2.24	96.05
<i>Sesarma reticulatum</i>	1842	1.50	97.55
<i>Panopeus herbstii</i>	1411	1.15	98.69
<i>Pinnixa chaetoptera</i>	978	0.79	99.49
<i>Pinnotheres ostreum</i>	299	0.24	99.74
<i>Eurypanopeus depressus</i>	250	0.20	99.94
<i>Pinnotheres maculatus</i>	31	0.03	99.97
<i>Pinnixa sayana</i>	25	0.02	99.98
Porcellanid	8	0.01	99.99
<i>Neopanope texana</i>	5	} <0.01	100.00
<i>Emerita talpoida</i>	2		
<i>Menippe mercenaria</i>	1		
<i>Rhithropanopeus harrisi</i>	1		
Total	122692		

ANOVA; $\chi^2 = 10.897$; 2 df; $P < 0.005$). Densities in the third sample were consistently lower than in the first two samples. This suggests that the time of sampling could have affected the daily estimates of zoeal densities significantly. However, there was no correlation between the time a set of three samples was begun and the density estimate (*Uca* spp.) for that night ($r = -0.149$; $N = 57$; $P > 0.10$). Errors introduced by variation in sampling time were sufficiently small to be masked by true daily variation in density. Sampling time varied little from 24 July to 10 October.

Densities of stage I zoeae of each of the seven most abundant species varied markedly (Fig. 2). *Uca* spp. were 1000 to 10,000 times more dense when abundant than when rare. Densities of the other species varied over two to three orders of magnitude. All species displayed the same temporal variation; maximum densities occurred during the spring tides near the time of the full and new moons and minimum densities occurred during neap tides near the first and last quarter moons. Semilunar variation in zoeal densities was most pronounced from June through September.

Uca spp., and, to a lesser extent, *Sesarma reticulatum* and *Panopeus herbstii*, displayed a lunar cycle in maximum zoeal densities from June through August. Zoeae were 3 to 5 times more abundant during the new moon spring tides than during full moon spring tides (Fig. 2).

Although all seven dominant species displayed strong semilunar periodicities in zoeal densities, each also exhibited unique short term variation. An exception appears to be the marked and unexpected decline in densities

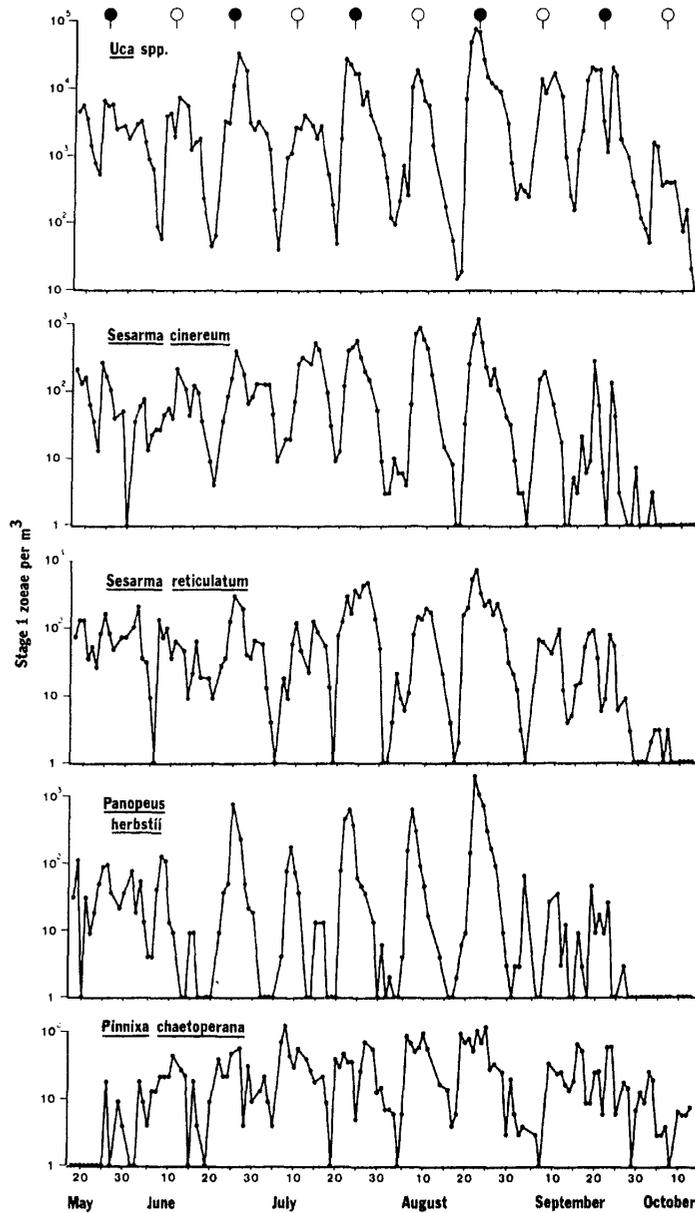


Figure 2. Densities of common stage I brachyuran zoeae in the samples taken in the upper reaches of the North Inlet estuary. Densities of 0 m^{-3} or 1 m^{-3} are plotted as 1 m^{-3} . The dates of new moons are indicated by closed circles and the dates of full moons are indicated by open circles.

for a 2-3 d period during the new moon spring tides on 21-23 September, which occurred about 15 d after Hurricane David affected the marsh.

Discussion

Few larval forms showed significant imports or exports from North Inlet estuary. Retention of larvae in this system may have been affected by aggregation of larvae in water masses which maintain their integrity over several

tidal cycles (Dyer 1982). Coefficients of variation between sequential samples ranged from 85-200%, whereas simultaneous oblique plankton tows in North Inlet have coefficients of variation of 15% or less (S. E. Stancyk and L. Barker, unpublished). Large variation between sequential samples probably reflects true patchiness in the plankton as has been described in numerous other planktonic environments (Steele 1980). Dye patches placed in tidal creeks adjacent to the transects used during this study remained visible for 3-4 tidal cycles and longer under certain conditions (B. Kjerfve, pers. comm.). Patches of larvae may have been passing back and forth across the inlet boundaries with little net loss or gain.

Alternatively, vertical migration by larvae may have minimized export from the estuary. Trinast (1975) showed that *Acartia (Acanthacartia)* n. sp. tended to congregate at depth during ebb tide, becoming entrained in a gyre system which enhanced retention. Similarly, some copepods (*Pseudodiaptomus hessei*, *Acartia longipatella*, *A. natalensis*) and mysids (*Rhopalophthalmus terranatalis*, *Mesopodopsis slabberi*) aggregate with respect to tidal currents, thereby maintaining position in the estuary (Wooldridge and Erasmus 1980). Whether larvae with clumped distributions in North Inlet behave similarly requires further study.

Although water was exported from the North Inlet estuary during all sampling periods (Chrzanowski et al. in press a, b), some larval forms showed significant imports. High rates of consumption or settlement within the estuary may explain net imports of larvae that may have originated and occurred at high densities in the ocean (e.g. pilidium larvae, plutei). Other larval forms, such as barnacle cyprids (Bousfield 1955) and crab megalopae (Sandifer 1975; Sulkin et al. 1980), may exhibit behavior that enhances import into the estuary.

Only crab zoeae were significantly exported from the North Inlet estuary. Exports were greatest during spring tidal periods in the summer when densities of stage I zoeae of the seven dominant brachyuran crabs reached semilunar maxima in both the upper and the lower estuary. Plankton samples were taken in the upper estuary near the time of high tide at night, the time when *Uca* spp. release larvae (DeCoursey 1979; Bergin 1981), suggesting that semilunar variation in the abundance of stage I zoeae of *Uca* spp. resulted directly from cycles of larval release. This suggestion is supported by the observation that *U. pugilator*, *U. pugnax*, and *U. minax* all exhibited peaks of larval release in the laboratory near the time of the full and new moons throughout most of the 1979 breeding season (J. Christy, unpublished). Independent evidence of semilunar timing of larval production among the other dominant brachyurans is available only for *Sesarma cinereum* (Dollard 1980); this species also released larvae near the time of the syzygies during the summer of 1979 at North Inlet. If there is a constant proportional relationship between the magnitude of larval release at high tide at night and at other times of the day and phases of the tide, then semilunar

variation in the abundance of stage I zoeae of the other species may result from semilunar timing of larval production by these crabs as well. Since stage I zoeae of *Uca* spp. (Christiansen and Yang 1976; Wheeler 1978), *Sesarma cinereum* (Costlow et al. 1960) and *Panopeus herbstii* (Costlow et al. 1962) take 2-4 d to reach stage II at summer temperatures (25-30°C), some stage I zoeae in the upper marsh samples may not have been released the night they were collected. However, larval mortality and seaward transport, which may be rapid in this estuary, will remove older stage I zoeae from the upper estuary, increasing the correlation between nightly densities of stage I zoeae and the magnitude of larval release.

The lunar cycle of variation in the density of stage I zoeae, most evident for *Uca* spp., may result from lunar variation in the tidal prism, not from lunar periodicity in the intensity of larval release. During July and August, 1979, the lunar perigee (when the moon is closest in its orbit to the earth) and the full moon were nearly coincident. Tides were about 0.5 m higher and the volume of water on the marsh correspondingly greater during the full moon spring tides than during the new moon spring tides, which may have produced a relative dilution and concentration of zoeae, respectively.

The unexpected reduction in zoeal densities for all species during the spring tides in late September occurred one semilunar cycle after the unusually severe weather associated with Hurricane David. Males of several species of *Uca* exhibit semilunar cycles of courtship (von Hagen 1970; Zucker 1976, 1978; Christy 1978) which coincide with cycles of female sexual receptivity, mating, and oviposition (Christy 1978). The incubation period for several species of *Uca* is 12-15 d at summer temperatures (Feest 1969; von Hagen 1970; Greenspan 1975; Christy 1978). The Hurricane may have disrupted breeding behavior sufficiently to reduce sharply the number of matings on 4-6 September, resulting in the observed decline in zoeal densities 15 d later.

Peaks of larval production by the seven dominant brachyuran crabs in the upper reaches of the North Inlet estuary occurred near the time of the full and new moons when nocturnal ebb tides were greatest in amplitude. Semilunar cycles of larval production have been described for several species of *Uca* (Christy 1978, and references therein; Wheeler 1978), four grapsid crabs (Warner 1967; Saigusa and Hadaka 1978; Dollard 1980), and two gecarcinids (Gifford 1962; Henning 1975; Klaasen 1975) at sites ranging from the east coast of India to the mid-Atlantic coast of the United States. With one exception, peaks of larval release by these crabs and nocturnal ebb tides of maximum amplitude occur near the time of the full and new moons. At a site in Charlotte Harbor on the west coast of Florida, larval release by *Uca pugilator* and nocturnal ebb tides of maximum amplitude usually occur during the quarter moons (Christy 1978; NOAA Tide Tables). This strongly suggests that larval release is timed to occur during large amplitude nocturnal ebb tides, not during a particular phase of the moon.

The immediate consequence of the timing of larval production seen in

the brachyurans will be rapid seaward transport of newly hatched zoeae. Few later stage zoeae were collected in either the upper or lower estuary and up to 15% of the zoeal population passing across the boundaries of the North Inlet estuary was exported each tidal cycle. Rapid export of stage I zoeae into coastal or oceanic waters appears to be an important aspect of the dynamics of the dispersal of brachyuran larvae in this well-mixed estuary. Export of other larvae from the North Inlet estuary was rare and non-significant when it occurred. Large exports of water were not necessary to effect transport of larvae, and imports or zero fluxes occurred despite water exports. Further study may reveal that some larval forms possess behavioral adaptations that aid retention. Models dealing with transport of crab zoeae should be extended to include larvae of other groups only with extreme caution.

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