

Mechanism for the re-invasion of an estuary by two species of brachyuran megalopae

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ABSTRACT: *Callinectes sapidus* and *Uca* spp. megalopae were sampled extensively during September 1985 and August to October 1986 in a secondary estuary near the mouth of Delaware Bay, USA. Collections taken every 2 h over as many as 12 consecutive tidal cycles indicate that megalopae of both species were significantly more abundant in the water column during flood than ebb tides, and that maximum abundance occurred during nocturnal flood tides. This pattern of abundance provides a mechanism for upstream transport of megalopae by flooding tidal currents. Seasonal peaks in abundance of megalopae corresponded to periods in coastal set-up; this suggests that megalopae are dependant on wind-driven exchange for transport into the estuary from the adjacent continental shelf. The coincidence of wind events resulting in coastal set-up with the occurrence of patches of megalopae near the mouths of estuaries may be responsible for much of the inter- and intra-annual variation in recruitment in these taxa.

INTRODUCTION

The Atlantic blue crab *Callinectes sapidus* is by far the most abundant species of *Callinectes* found in Delaware Bay, USA (Williams 1974, Leathem & Maurer 1980). Gravid females migrate to the mouth of the bay to spawn from late spring through early autumn. Peak spawning for the species occurs in July and August (Dittel & Epifanio 1982, Epifanio et al. 1984). After hatching, the larvae undergo 7, and sometimes 8, zoeal stages and 1 megalopal stage (Costlow & Bookout 1959). Stage I zoeae are most abundant in surface waters, which facilitates their seaward transport (Provenzano et al. 1983, Epifanio et al. 1984, Epifanio 1988). As these zoeae undergo development on the continental shelf, they remain in the surface water (Smyth 1980, McConaughy et al. 1983, Epifanio et al. 1988, Epifanio et al. 1989). Unlike the zoeae, megalopae are found throughout the water column (Smyth 1980, Johnson 1985). Previous investigations indicate that megalopae are the primary agents of estuarine re-invasion by *C. sapidus* (Epifanio et al. 1984, Johnson 1985), but the mechanism of transport into estuaries is controversial. Various authors have suggested passive transport in bottom waters (Sulkin & Epifanio 1987), vertical migration utilizing flood tides for enhanced shoreward transport (Meredith 1982,

Epifanio et al. 1984, Brookins & Epifanio 1985), or wind-driven exchange (Goodrich et al. 1989).

The fiddler crab *Uca* spp. is represented chiefly by *Uca minax* and *U. pugnax* in the Delaware River Estuary (Miller & Maurer 1973). A third species, *Uca pugilator*, occurs only rarely. In spite of a semi-terrestrial adult existence, *Uca* spp. zoeae are rapidly flushed from tidal creeks and out onto the continental shelf (Sandifer 1973, Christy & Stancyk 1982, Lambert & Epifanio 1982). *Uca* spp. megalopae are most abundant in bottom waters on the continental shelf and are thus transported onshore in residual estuarine flow (Johnson 1985). However, it has been suggested that *Uca* spp. megalopae may augment passive transport in bottom water through the use of upward vertical migration during flood tides (DeCoursey 1976, Meredith 1982, Epifanio et al. 1988). During the re-invasion of the estuary by *Uca* spp. megalopae, further separation of species into their respective adult habitats is at least partially dependent upon salinity gradients within the estuary (O'Connor & Epifanio 1985, Rowe 1987).

This paper presents the results of extensive collections during 2 consecutive years in a secondary estuary adjacent to the mouth of Delaware Bay. These results are combined with local subtidal sea level data, as an indicator of coastal forcing, to describe the mechanism by which the megalopae of *Callinectes sapidus* and

Uca spp. are recruited back to the parental estuary after development on the continental shelf.

MATERIALS AND METHODS

Megalopal collection. Megalopae were collected from one station in the mouth of the Broadkill River, a secondary estuary located ca 5 km from the mouth of Delaware Bay (Fig. 1). In 1985, sampling was con-

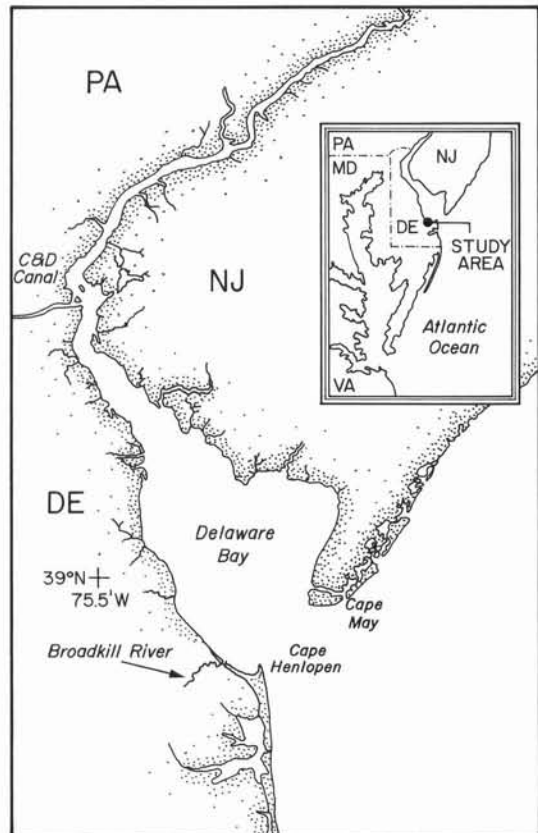


Fig. 1. Location of study site in the Broadkill River near the mouth of Delaware Bay, USA

ducted during 10 consecutive tidal cycles from September 6 to 12. Samples were taken every 2 h with an automated submersible pump positioned 1 m beneath the surface of the water column. Each sample was the result of continuous pumping for 20 min resulting in a volume of 4.1 m³ per sample. The output was passed through a 0.5 m plankton net (571 μ m mesh) connected to the pump output hose. Samples were preserved in 4% formaldehyde and brought to the laboratory for analysis.

In 1986, 2 submersible pumps were deployed at 1 and 2 m below the surface of the water column (total depth = 3 m at mean low water). Samples were collected every 2 h at both depths over two 7 d periods: September 24 to 30 and October 7 to 14, 1986. Each

sample was the result of continuous pumping for 40 min resulting in a volume of 8.2 m³ per sample.

In 1986, weekly plankton samples were also collected from August 5 to October 28. Sampling each week consisted of collections at 2 depths (1 and 2 m from the surface) over each of 2 consecutive tidal phases (one flood and one ebb) during daylight. Each flood or ebb sample was the accumulated outflow of continuous pumping during that tidal phase, yielding a volume of ca 70 m³ per flood or ebb sample.

General analysis of field samples. In the laboratory, all plankton samples were transferred to 70% ethanol. For ease in counting, samples were subdivided using a Folsom plankton splitter (Dittel & Epifanio 1982). A table of random numbers was used to determine which subsample was to be analyzed. Megalopae were identified by using a key for decapod larvae (Sandifer 1972) in combination with the original description of the larvae (Hyman 1920, Costlow & Bookout 1959).

Data analysis. Data were converted to megalopal abundance per m³ and then compared for differences in diel phase, tidal phase, and depth through the use of nonparametric Friedman Random Block Tests (Sokal & Rohlf 1981). The data were blocked by date in order to eliminate any dependence in larval abundance among samples collected close together in time. Inference was made at $\alpha = 0.05$.

Wind correlation. Effects of wind on megalopal abundance for each species were assessed in 2 ways. For each of the 6 d sampling periods in 1985 and 1986, morning and afternoon wind speeds and directions were obtained from the US Weather Service Station at the University of Delaware in Lewes, Delaware (< 1 km from study site). These velocities were then plotted as a time series of vectors for each 6 d period. These time series were compared qualitatively with the time series of megalopal abundance for each respective sampling period.

In addition, the occurrence of peaks in megalopal abundance for each species was compared to the occurrence of coastal set-ups of water along the adjacent continental shelf for all sampling periods during 1985 and 1986. In the Delaware Bay region, coastal set-ups occur when Ekman flow associated with strong southward winds causes water to accumulate at the coast. This results in a rise in subtidal sea level (SSL) with a consequent subtidal flow of water into Delaware Bay (Wong & Garvine 1984). The existence of a coastal set-up was determined from hourly sea-level data measured at a NOAA tide gauge in Breakwater Harbor in the mouth of Delaware Bay (ca 5 km from the study site). A coastal set-up occurred whenever the SSL for a given hour was greater than the mean SSL for the entire sampling period; this was termed a positive anomaly.

In order to determine the occurrence of a positive anomaly, running averages with 13 h intervals (Chatfield 1975) were calculated from each sampling period in 1985 and 1986 to remove sea-level oscillations at tidal frequencies. This provided an hourly series of SSL. Next, the mean SSL of each series was calculated by summing values for SSL at each hour over the series and dividing by the number of hours in that series. Finally, the mean SSL for each series was subtracted from the SSL at each hour. So, for 1985, the mean SSL for the month of September was subtracted from each hourly value for the subtidal series comprising September. For the 1986 data, the mean SSL for the period of August 1 through October 31 was subtracted from each of the respective hourly values.

Correlative analysis consisted of the determination of the number of peaks (≥ 3 megalopae m^{-3}) in megalopal abundance that were concurrent with coastal set-ups (= positive anomalies). The probability that a given number of peaks in megalopal abundance were coincident with positive anomalies was determined from an equation derived from the binomial distribution (Zar 1984):

$$P = K! [X! (K-X)!]^{-1} p^X q^{K-X}$$

where P = probability of coincident occurrence; K = total number of peaks in abundance; X = number of peaks coincident with positive anomalies; p = probability of a coastal set-up; and q = probability of a coastal set-down. The probability of a coastal set-up (or set-down) was determined by dividing the number of hours when subtidal height was positive (or negative) by the total number of hours in the sampling period. Inference was made at $\alpha = 0.05$.

RESULTS

Larval collection: *Callinectes sapidus*

Megalopae were rare in September 1985 until the last 36 h of sampling (Fig. 2). This increase in abundance appears related to wind speed and direction. From September 6 to 10, winds were eastward and weak (2 to 7 $m s^{-1}$), while from September 11 to 12, the winds were southward and stronger (6 to 10 $m s^{-1}$). Statistical tests were run using only data from September 11 to 12. During this period, megalopae tended to be more abundant during flooding periods than ebbing periods with mean densities of 14.9 ± 16.4 and 1.6 ± 1.4 megalopae m^{-3} , respectively. Megalopae were significantly more abundant during the night diel phase ($p < 0.05$) with a mean density of 1.2 ± 2.1 megalopae m^{-3} during the day versus 8.3 ± 14.3 megalopae m^{-3} at night.

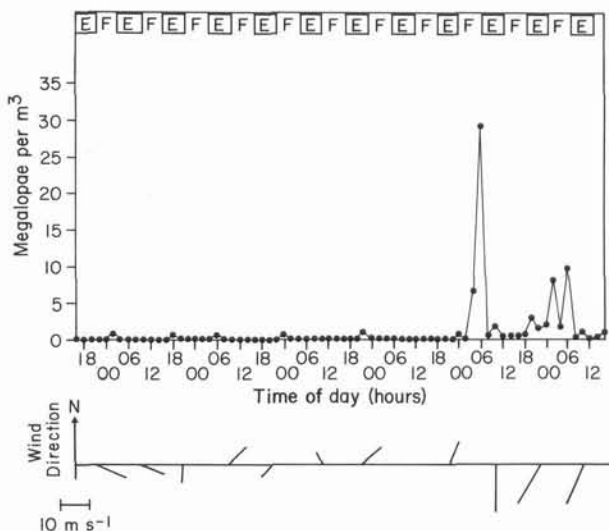


Fig. 2. *Callinectes sapidus*. Abundance of megalopae collected at 1 m from 6 to 12 September, 1985. E: ebb tide; F: flood tide. Simultaneous measurements of wind are represented as a vector time series

Megalopal abundances from September 24 to 30, 1986, never exceeded 0.6 megalopae m^{-3} (Fig. 3). There were no major influxes of megalopae during this

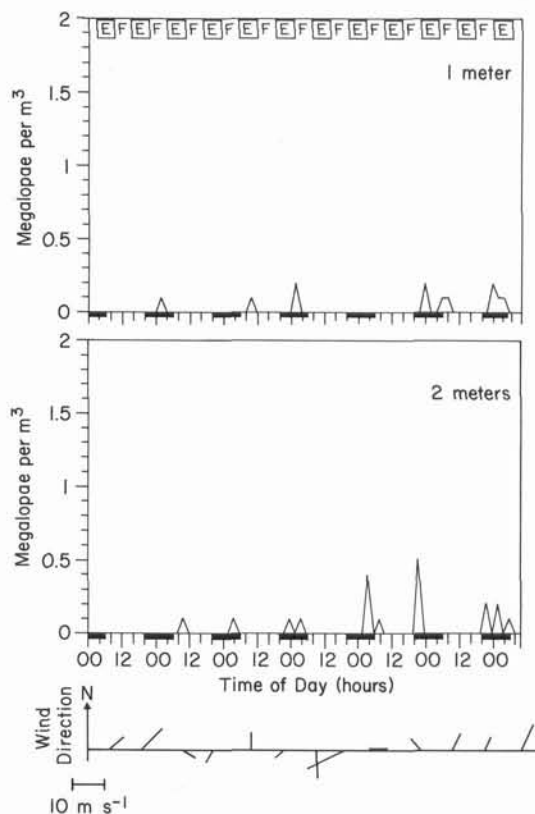


Fig. 3. *Callinectes sapidus*. Abundance of megalopae collected at 1 and 2 m, September 24 to 30, 1986. Dark bars on the horizontal axis indicate nocturnal periods

period and winds were highly variable. However, there were significantly more megalopae collected during flood than ebb tidal phases ($p < 0.01$). While megalopal abundance tended to be greater at night than during the day, there was no difference in megalopal abundance between depths.

During most of the period of October 7 to 14, 1986, megalopal abundances ranged from 0.1 to 2.0 megalopae m^{-3} (Fig. 4). However, on October 10 the

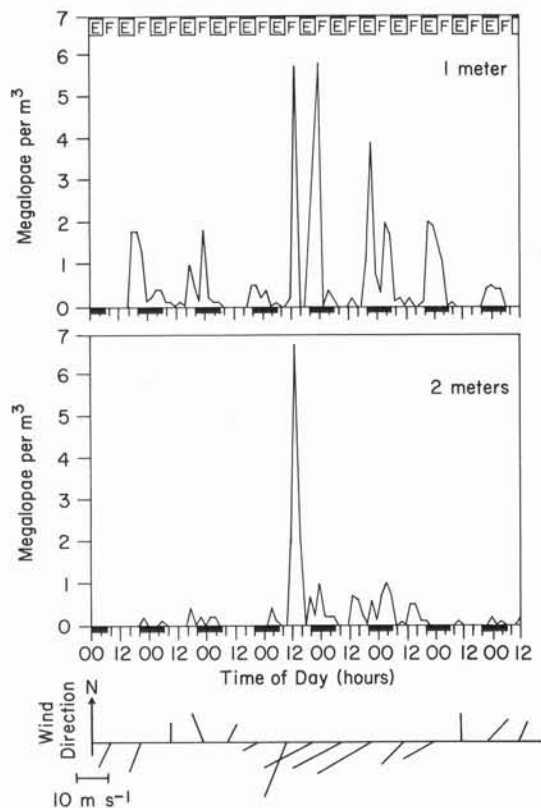


Fig. 4. *Callinectes sapidus*. Abundance of megalopae collected at 1 and 2 m, October 7 to 14, 1986. Dark bars on the horizontal axis indicate nocturnal periods

abundance peaked at 6.0 megalopae m^{-3} and then decreased by October 11 to 4.0 megalopae m^{-3} . This shift in abundance appears related to the wind variations. Prior to October 7, the wind direction was variable, while after this date the wind was persistently southwestward and relatively strong, from 4 to 11 $m s^{-1}$. Additionally there was a significantly greater abundance of megalopae during flood versus ebb tidal phases ($p < 0.01$). Abundance tended to be greater during the night, and there was a significant difference in vertical distribution of the megalopae with greater densities occurring at 1 m ($p < 0.01$).

While megalopae were present throughout most of the seasonal period of weekly sampling in 1986, 2 major influxes occurred (on August 28 and October 7), with greater than 70 % of all megalopae ($n = 428$)

collected on these 2 dates (Fig. 5). These influxes both occurred when the winds were southward at speeds up to 10 $m s^{-1}$ for ca 24 h prior to sampling.

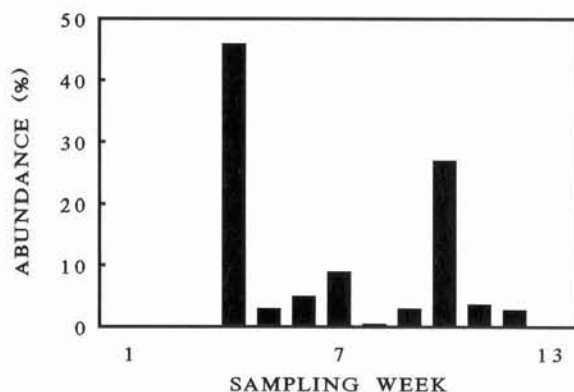


Fig. 5. *Callinectes sapidus*. Abundance of megalopae collected weekly from August 5 through October 28, 1986. Values are percentages of the total number of megalopae ($n = 428$) collected during the entire sampling period

There were also tidal differences in megalopal abundance during seasonal sampling. Average megalopal density during a given flood or ebb phase was calculated as the number of megalopae collected during that phase divided by the total volume of water sampled during the same phase. During flood phases, these values were as high as 3.2 megalopae m^{-3} , but never exceeded 0.4 megalopae m^{-3} during ebb phases (Fig. 6). Of all megalopae collected during the 13 wk sampling period, 80 % were caught during flood phases. There were no significant differences in megalopal abundance with depth.

Larval collection: *Uca* spp.

Megalopae were collected in increasing concentrations as the sampling period of September 6 to 12, 1985 progressed (Fig. 7). This may reflect increased onshore transport of water due to the wind shift from eastward to southward during the period. Megalopae were significantly more abundant in flood tidal phases versus ebb tidal phases ($p < 0.04$), with mean densities of 20.4 ± 24.5 and 4.1 ± 6.1 megalopae m^{-3} , respectively. Also, megalopae were significantly more abundant during the night ($p < 0.02$), and peak nocturnal abundances generally occurred a few hours prior to dawn.

Major pulses of *Uca* spp. megalopae did not occur during either week of intensive sampling in 1986. However, the general trends were the same as during the preceding year, with more megalopae collected during nocturnal flood tides.

While megalopae were present throughout most of

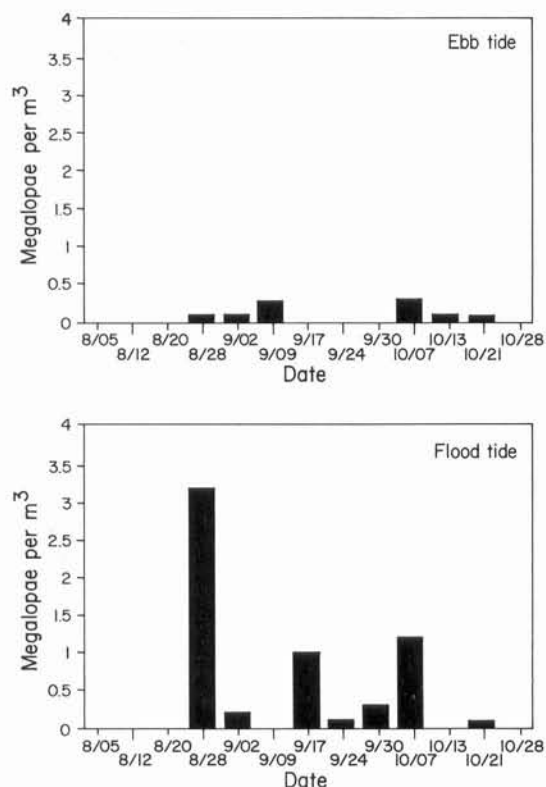


Fig. 6. *Callinectes sapidus*. Average abundance of megalopae collected weekly during consecutive ebb and flood tides from August 5 to October 28, 1986 (Dates are Month/Day)

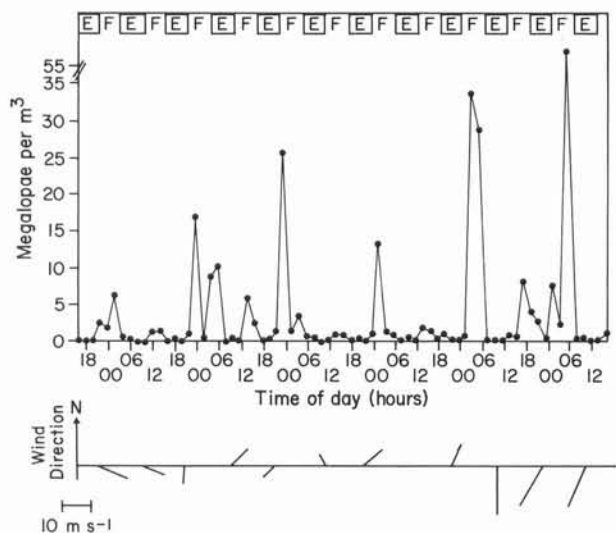


Fig. 7. *Uca* spp. Abundance of megalopae collected at 1 m from 6 to 12 September, 1985

the seasonal sampling period in 1986, 2 major influxes occurred (August 28 and September 17). Approximately 70 % of all megalopae ($n = 5628$) were collected on these 2 dates (Fig. 8). On August 28, the winds were predominately southward at 9 to 11 m s⁻¹, and on September 16 the winds were predominately south-

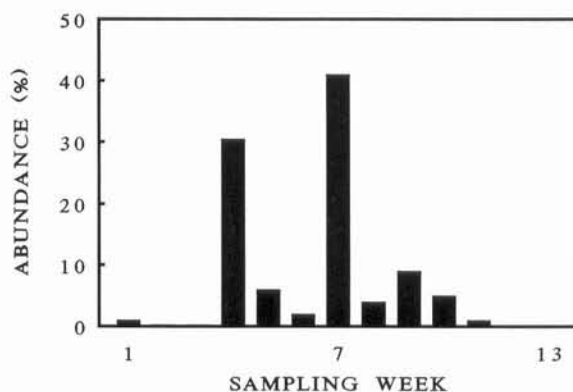


Fig. 8. *Uca* spp. Abundance of megalopae collected weekly from August 5 through October 28, 1986. Values are percentages of the total number of megalopae (n = 5628) collected during the entire sampling period

eastward at 12 m s^{-1} . The winds slackened to 2 m s^{-1} and became northward by the evening of the September 17.

There was a significant difference in megalopal abundance between tidal phases during seasonal sampling ($p < 0.05$). Values for average abundance sometimes exceeded $40.0 \text{ megalopae m}^{-3}$ during flood phases, while these values were always less than $1.0 \text{ megalopa m}^{-3}$ during ebb phases (Fig. 9). Approximate

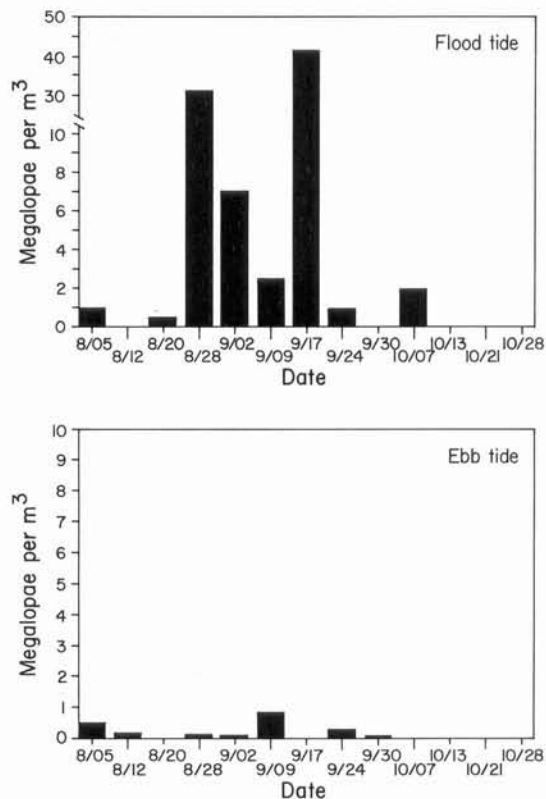


Fig. 9. *Uca* spp. Average abundance of megalopae collected weekly during consecutive ebb and flood tides from August 5 to October 28, 1986. (Dates are Month/Day)

mately 90 % of all megalopae collected during seasonal sampling were collected during the flood tide. There were no significant differences in abundance with depth.

Positive anomaly correlation

A total of 6 peaks (≥ 3 megalopae m^{-3}) in *Callinectes sapidus* abundance were identified from 1985 and 1986. All these occurred during periods of positive anomaly in SSL. The probability of a coastal set-up was 0.43 and the probability of a coastal set-down was 0.57. By the binomial distribution, the probability of all 6 peaks occurring during positive anomalies 6 times in 6 trials is 0.006 (Table 1). Therefore, there was a signifi-

Table 1. Binomial analysis of the coincident occurrence of peaks in megalopal abundance and occurrence of positive anomalies in subtidal sea level in the Broadkill River near the mouth of Delaware Bay, USA. Significance was judged at $p \leq 0.05$

Species	No. of peaks	No. Coincident	p
<i>Callinectes sapidus</i>	6	6	0.006
<i>Uca</i> spp.	11	7	0.150

cant association of peaks in megalopal abundance with positive anomalies. Approximately 55 % of all blue crab megalopae collected during this study were collected during these 6 positive anomalies.

A total of 11 peaks of *Uca* spp. occurred in 1985 and 1986, and 7 of these co-occurred with periods of coastal set-up (Table 1). The probability of 7 or more peaks out of 11 occurring during periods of positive anomaly is 0.15. Therefore, there is no significant association of peaks of fiddler crab megalopae with periods of coastal set-up. Approximately 35 % of all *Uca* spp. megalopae collected during this study were collected during these 7 peaks.

DISCUSSION

Tidally rhythmic abundance

Our seasonal data show that the total abundance of fiddler crab megalopae in the Broadkill River in 1986 was approximately an order of magnitude greater than that of blue crab megalopae. Moreover, the abundance of fiddler crab megalopae was probably underestimated as spawning in these species begins in early summer (Lambert & Epifanio 1982), and substantial recruitment of megalopae probably occurred before

our sampling period began. Regardless, the greater abundance of megalopae during flood than ebb tidal phases is suggestive of a tidally rhythmic behavior in both fiddler crabs and blue crabs. This rhythmic pattern of abundance would enable megalopae to be transported upstream in estuaries that have a net seaward flow of water. These results corroborate earlier evidence from Meredith (1982) and Epifanio et al. (1984) which suggested that megalopae may accelerate movement into estuaries by undergoing tidally rhythmic vertical migrations.

Based on these results alone, we cannot preclude an alternative hypothesis that the megalopae are simply being transported on flooding currents from Delaware Bay into the Broadkill River where they settle upstream of our sampling station before they are carried back past the sampling station on the subsequent ebb. Because the ultimate source of megalopae is downstream of our station (on the adjacent continental shelf), megalopae would be expected in the water column on flooding tidal currents, and because megalopae would be settling upstream of our station, ebb-tide abundance would always be less than flood-tide abundance. But if this were the case, approximately equal abundances of megalopae would be expected among flood tides, while our study demonstrated increased abundances during nocturnal flood tides. This suggests that megalopae are vertically migrating in the water column. Regardless, the occurrence of active vertical migration is not the important point. As long as megalopae are predominant in flood tidal currents, their net transport will be up-estuary.

Positive anomaly correlation

In Delaware Bay, Wong & Garvine (1984) have demonstrated that southward wind forcing can result in the transport of water into the Delaware Bay. Since strong, southward wind events occur ca every 10 d along the Delaware coast (Wong & Garvine 1984), these events may play an important role in the recruitment of megalopae. Our research shows the occurrence of peaks in blue crab megalopal abundance to be significantly associated with periods of coastal forcing into Delaware Bay. Wind-driven exchange has recently been indicated as an important factor in the transport of the blue crab megalopae into the Chesapeake Bay as well (Goodrich et al. 1989).

While the present study showed no significant association between peaks of fiddler crab megalopae and periods of positive anomaly, over 35 % of all fiddler crab megalopae were collected during these peaks, suggesting that wind plays a role in their transport. However, the lowered susceptibility of fiddler crab

megalopae to wind-driven transport may be due to their epibenthic distribution in the vicinity of the bay mouth (Johnson 1985). While wind-driven Ekman transport affects the entire column in depths < 40 m, transport is always greater near the surface.

Transport model

By integrating the results of our study with those of previous investigations, a conceptual model for the transport of zoeae and megalopae in the Middle Atlantic Bight can be constructed. For *Callinectes sapidus*, a large body of evidence suggests that zoea larvae are exported to the continental shelf where they are subject to surface advection by the buoyancy-driven, southward-flowing Coastal Current (Garvine 1987) and by a wind-driven, northward current farther offshore (Boicourt 1982, McConnaugha et al. 1983, Epifanio et al. 1989). During spawning seasons when persistent northward winds occur over the inner shelf, large numbers of megalopae can occur just offshore of the Coastal Current adjacent to Delaware Bay.

Uca spp. zoeae are also exported from Delaware Bay, but advanced zoeal stages are distributed deep in the water column, thus retarding transport away from the parent estuary (Epifanio et al. 1988). This may also result in the accumulation of megalopae in the near-shore region of the adjacent shelf (Johnson 1985) and in the mouth of the estuary itself (Dittel & Epifanio 1982).

Results of the present investigation and those of Goodrich et al. (1989) in Chesapeake Bay indicate that much of the seasonal recruitment of both blue crab and fiddler crab megalopae occurs in a few distinct pulses associated with southward wind events and consequent coastal forcing. But once within the estuary, the megalopae of both taxa appear to undergo tidally rhythmic vertical migration that augments their retention and contributes to continued transport up-estuary. There is no evidence that either blue crab (McConnaugha et al. 1983) or fiddler crab (Johnson 1985) megalopae undergo vertical migration on the open continental shelf, and the basis for the apparent change in behavior upon entering the estuary is unclear. Regardless, the tidally rhythmic pattern of abundance within the estuary would contribute a conservative aspect to the recruitment of megalopae of both taxa. In contrast, the necessity of patches of megalopae occurring near the mouth of the estuary during periods of positive anomaly may account for much of the inter- and intra-annual variation in recruitment.

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