

Abundance of post-larval *Callinectes sapidus*, *Penaeus* spp., *Uca* spp., and *Libinia* spp. collected at an outer coastal site and their cross-shelf transport

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ABSTRACT: The abundance of the megalopae of *Callinectes sapidus*, *Uca* spp., and *Libinia* spp. and the post-larvae of *Penaeus* spp. settling on collectors hung from the end of the Army Corps of Engineers' Field Research Facility (FRF) pier in Duck, North Carolina, USA, was measured daily during the period 2 August through 3 November 1994. During this period the coastal oceanography was dominated by the effects of the winds; winds from the NE tended to generate surface onshore flow and downwelling while those from the SW tended to generate surface offshore flow and upwelling. If the post-larvae were transported shoreward by coastal currents then variations in their abundance should relate to the physical parameters which generate the transporting currents. Using time-series analysis the daily abundance of post-larvae was statistically analyzed and compared to along- and cross-shore wind stress, along- and cross-shore current speed near the bottom (23 m) and near the surface (4 m), and temperature, salinity, and current speed measured at the end of the FRF pier. Fourier analysis suggested that the abundance of post-larval *C. sapidus* and *Penaeus* spp. varied on a semi-lunar cycle, e.g. 15 d. No cycles were apparent in the Fourier analysis of the abundance of *Uca* spp. megalopae and the megalopae of *Libinia* spp. varied on an 18 d cycle. Significant cross-correlations were found between the log-transformed daily abundance of post-larval *C. sapidus* and *Penaeus* spp. and the maximum daily tidal range, which, coupled with the Fourier analysis, suggests that peak catches of these post-larvae tended to occur at and just after the spring tides. The cross-correlation analysis suggests that abundance of *Uca* spp. megalopae was weakly related to the tides, with peak catches tending to occur around the spring tides. No significant cross-correlations were found between the abundance of *Libinia* spp. megalopae and the maximum daily tidal range. To test for the effects of the other physical variables on post-larval abundance Autoregressive Integrated Moving Average (ARIMA) models were fitted to the biological and physical data, and cross-correlations were run between the residuals from these models. The analysis suggests that the abundance of *C. sapidus* megalopae did not vary with any of the measured physical variables, *Penaeus* spp. and *Uca* spp. tended to be more abundant during periods of onshore surface flow and downwelling, while *Libinia* spp. megalopae tended to be more abundant during periods of offshore surface flow and upwelling. The results of this study suggest that post-larval *C. sapidus* and *Penaeus* spp. were transported shoreward by tidally driven processes, both *Penaeus* spp. and *Uca* spp. were transported shoreward by wind-driven surface currents, and *Libinia* spp. megalopae were transported shoreward in near-bottom waters during upwelling events.

KEY WORDS: Megalopae · Post-larvae · Dispersal · Transport · *Callinectes* · *Uca* · *Libinia* · *Penaeus* · Recruitment · Settlement

INTRODUCTION

Many intertidal and estuarine invertebrates and fish produce planktonic larvae which go through their larval development in the waters over the continental shelf. Larval development times can be as short as days, but are more typically on the order of several

weeks to months. During their residence in the plankton, larvae can be transported tens to hundreds of kilometers offshore. At the end of this planktonic period the larvae must migrate (sensu Kennedy 1961) from their location in the plankton back to the habitat into which they will settle.

The return migration of most intertidal or estuarine invertebrates to the coastline is probably due to transport in shoreward directed currents. A variety of shore-

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ward transport mechanisms have been suggested (reviewed in Shanks 1995), including wind-driven currents, shoreward propagating convergences associated with tidally driven internal waves or the relaxation of a wind- or tidally generated upwelling front, transport within shoreward propagating tidally generated internal bores, and currents generated by the density structure over the continental shelf. The dominant shoreward transport mechanism for a species will be dependent on the behavior of the larvae and the local oceanography. Variations in a time-series of settlement or abundance of the migrating larval stage should be significantly related to the physical variables which are causing their shoreward transport.

Using this time-series approach the return migration of megalopae of the blue crab *Callinectes sapidus* has been extensively studied along the Atlantic and Gulf of Mexico coasts of North America (Rabalais et al. 1995, van Montfrans et al. 1995, Morgan et al. 1996). Time-series of the daily abundance of megalopae have been made by deploying collectors which exploit the high thigmokinesis of the megalopae (Metcalf et al. 1995). The collectors, which generally consist of a mesh cylinder, are hung in the water; megalopae encountering the trap cling to it, and, when the trap is retrieved, the megalopae are washed off into a bucket. This technique provides a simple, inexpensive and reliable (Metcalf et al. 1995) means of estimating the relative abundance of megalopae.

All of these time-series of blue crab megalopal abundance have been made within estuaries (Rabalais et al. 1995, van Montfrans et al. 1995, Morgan et al. 1996). These studies have found that the abundance of blue crab megalopae varies greatly from day to day, with a tendency for peak catches to occur on a fortnightly lunar cycle and/or when the winds generate shoreward surface flow. Megalopae caught within an estuary have been transported across the continental shelf and then have entered and migrated up an estuary (Boehlert & Mundy 1988). Hence, the fluctuations in their abundance may be due to at least 2 processes — transport to the coast and ingress into the estuary. These time-series cannot be used to unambiguously investigate the mechanism(s) of cross-shelf migration of blue crab megalopae.

The mechanism(s) of onshore transport for a species is dependent on the depth at which they reside. *Callinectes sapidus* megalopae inhabit the neuston (Smyth 1980, Johnson 1985); hence, their transport mechanisms must be ocean surface phenomena. In contrast, post-larval *Penaeus* spp. vertically migrate between the near surface waters and depths (e.g. >10 m) within the water column (Temple & Fischer 1965), and *Uca* spp. megalopae have been collected in deeper plankton tows (Johnson 1985) as well as near the surface

(Dudley & Judy 1971). Phenomena responsible for the onshore transport of the post-larvae of *Penaeus* spp. and *Uca* spp. may not be the same as those responsible for the shoreward transport of *C. sapidus* megalopae.

In this paper I present the results of a study of the abundance of 4 species (*Callinectes sapidus*, *Penaeus* spp., *Uca* spp., and *Libinia* spp.) caught on collectors deployed outside of an estuary. Using time-series analysis, the daily abundance of post-larvae was statistically compared to physical variables which might generate onshore transport.

METHODS

Samples were collected between 2 August and 3 November 1994 from the pier at the Army Corps of Engineers' Field Research Facility (FRF), Duck, North Carolina, USA (36° 10' 54.6" N, 75° 45' 5.2" W) and from the Atlantic Ocean adjacent to the FRF pier (Fig. 1). The pier at FRF is located along the Outer Banks approximately 40 km north of Oregon Inlet which is connected to Currituck Sound and approximately 100 km south of the mouth of the Chesapeake Bay. The shoreline around the pier is sandy beach which extends for tens of km up and down the coast. The maximum tide range is around 1 m.

The FRF pier extends 403 m out to sea (Birkemeier et al. 1981). The pier pilings are 12.2 m apart. Cylindrical mesh collectors similar to those used to sample megalopae in a number of previous studies (e.g. Metcalf et al. 1995) were hung at a distance of 385 m from shore. The collectors were cylinders 10 cm in diameter and 41 cm long composed of 2 cm thick Enkamat®. Enkamat® is a matrix of semi-rigid nylon monofilaments fused at their intersections which is used in aquaculture as an egg-laying mat for fish. Two collectors were fished. One was buoyant and rose and fell with the tide. The second was positioned approximately 1 m off the bottom at a depth of 5.6 m below mean low water. The collectors were hung midway between the second and third pair of pier pilings from the seaward end of the pier. In this position the collectors were 6.4 m from any pilings.

The collectors were removed once a day and vigorously shaken in separate buckets of seawater. Repeated washing of collectors demonstrated that nearly all of the attached organisms were removed by one washing. The contents of the buckets were poured through 53 µm mesh screens and the retained material taken to the laboratory for counting. The entire contents of each collector was enumerated under a dissecting microscope and megalopae were identified using standard sources (Hyman 1920, Costlow & Bookhout 1959, Cook 1966, Sandifer & Van Engel

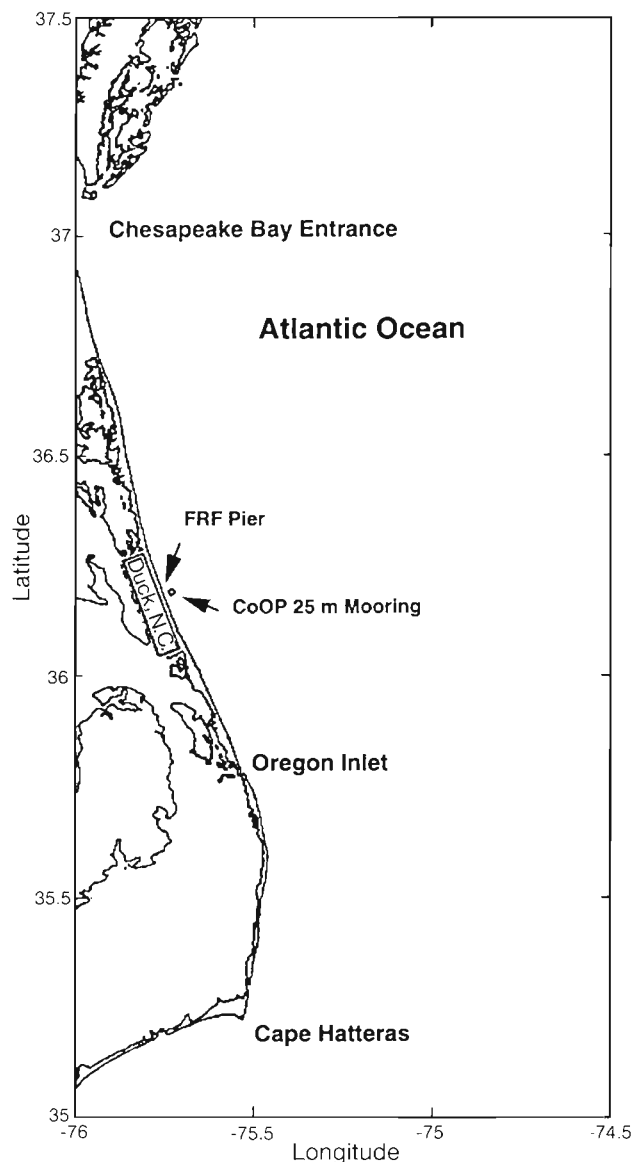


Fig. 1. Location of the Army Corps of Engineers' Field Research Facility (FRF) pier, Duck, NC, USA, where the time-series of daily abundance of post-larval crabs and shrimp was measured. Temperature, salinity, wind speed and direction, and current speed were also measured at the pier by the Army Corps of Engineers. The locations of the CoOP oceanographic mooring and the FRF pier are indicated

1971, Johns & Lang 1977). Samples were preserved in 5% buffered formalin.

Physical data were collected at FRF and at instrumented moorings deployed by CoOP (Coastal Ocean Processes) study participants. Wind speed and direction were measured at a weather station located at FRF. FRF also provided predicted tidal range and current speed data from the end of the FRF pier. Temperature and salinity measurements were made with Seabird Seacat[®] CTDs (conductivity-temperature-

depth profilers) mounted on the pier pilings of the FRF pier. Measurements were made every 4 min throughout the sample period. Measurements of temperature, salinity, and current speed and direction were also collected by instruments on a mooring which was set at approximately 16 km offshore at a depth of 25 m. Temperature and salinity were measured by CTDs while current speed and direction were measured with vector-measuring current meters (VMCM). Measurements began on 7 August and were made every 4 min throughout the sample period. More detailed descriptions of the sampling at FRF and the offshore moorings can be found in Birkemeier et al. (1981) and Alessi et al. (1996), respectively.

The wind data were used to compute along- and cross-shore wind stress using standard equations (Pedlosky 1987). Currents were also broken into their along- and cross-shore components. Data were averaged over each day. The maximum daily tidal range was defined as the maximum change in tidal elevation between a high and adjacent low tide during a 24 h period.

In most of the following analysis of megalopal abundance the number caught on the surface and bottom collectors were combined. Large day to day fluctuations in number were observed (see 'Results', Fig. 4). To reduce the influence of occasional large peaks in the data sets the series were $\log_{10}(x+1)$ transformed (Thorrold et al. 1994). To search for periodicity in the megalopal abundance time-series, the data were analyzed with a Fourier transfer function. In 2 of the time-series (see 'Results') the Fourier analysis suggested that the abundances of the megalopae varied with a 15 d period, approximately that of the fortnightly tidal cycle. Cross-correlations were run between the maximum daily tidal range and daily abundances. Both the time-series of maximum daily tidal range and megalopal abundances displayed significant autocorrelations. The presence of these significant autocorrelations could artificially inflate the r values in a cross-correlation. To account for the effects of the significant autocorrelations the corrected standard error of the cross-correlation r was computed following Wing et al. (1995). This corrected standard error was used whenever it was more conservative than the white noise standard error calculated with the cross-correlation analysis.

The cross-correlations suggested that the daily abundance of some types of megalopae fluctuated with the tides. This signal was strong enough to obscure the potential effects of winds or currents on the daily abundance of megalopae. To control for the effect of tides on megalopa abundance ARIMA (autoregressive integrated moving average) models were fitted to the log-transformed megalopal abundance data. Where

appropriate (e.g. as indicated by autocorrelations) the seasonal component of the ARIMA model was set to the time between spring tides. Models were selected following standard criteria (Jassby & Powell 1990, Dunstan 1993). The residuals between the ARIMA model and the log-transformed megalopal abundance data were cross-correlated with residuals between ARIMAs fitted to the physical data and the values of the physical parameter.

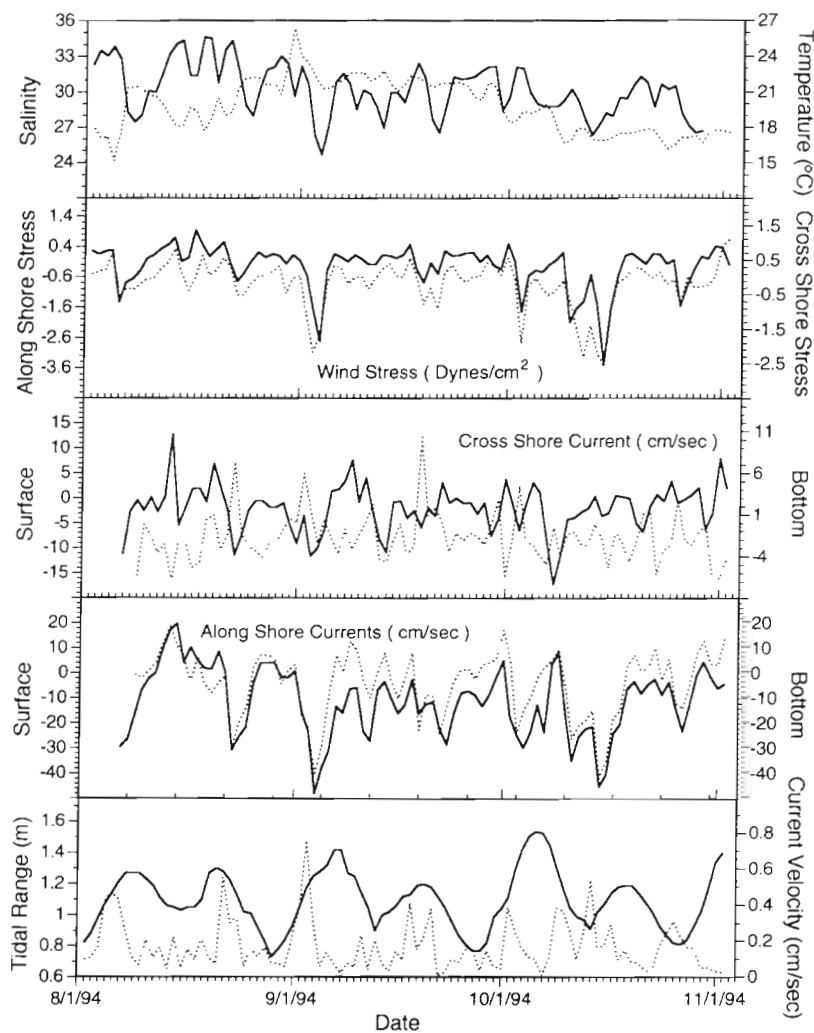
RESULTS

Physical measurements

During the approximately 3 mo of the study, due to the influence of passing weather fronts, the winds tended to blow

Table 1. Cross-correlations between bottom and surface coastal currents and wind stress. Wind data were collected near the end of the FRF pier. Current data were collected at the 25 m mooring, which was 6 km offshore. Values are days lag followed by the cross-correlation coefficients at which significant ($p < 0.05$) cross-correlations were found

	Currents			Wind stress	
	Cross-shore, surface	Cross-shore, bottom	Along-shore, surface	Along-shore	Cross-shore
Cross-shore currents					
Surface				0: 0.343	0: 0.349
Bottom	0: -0.336		0: -0.243	0: -0.316	0: -0.386
Alongshore currents					
Surface	-1: 0.242			0: 0.689	0: 0.576
	-3: 0.234			-1: 0.706	-1: 0.624
				-2: 0.426	-2: 0.475
					-3: 0.369
Bottom	0: 0.250	0: -0.420	0: 0.837	0: 0.721	0: 0.707
			-1: 0.508	-1: 0.714	-1: 0.691
				-2: 0.337	-2: 0.439
					-3: 0.302



from either the northeast or the southwest (Fig. 2). These winds strongly affected the coastal currents.

The cross-shore components of the surface and bottom currents measured at the 25 m mooring (approximately 16 km offshore) were significantly positively and negatively cross-correlated, respectively, with 0 d lag with both the cross-shore and along-shore components of the wind (Table 1). Further, the cross-shore surface and bottom currents were significantly and negatively cross-correlated with each other at 0 d lag (Table 1). In other words, surface currents tended to be in the direction of the wind. Bottom currents tended to flow in the opposite direction to the surface currents and the winds.

Fig. 2. Variation in the physical parameters during the period of the study (2 August through 3 November 1994). In each frame the values for the left hand axis are plotted as solid lines and those for the right hand axis as dashed lines. Positive and negative values of along-shore wind stress and currents represent winds or currents to the north and south, respectively. Positive and negative values of cross-shore wind stress and currents represent winds or currents flowing to the east and west, respectively. Note that current meters on the mooring were not turned on until 7 August

Table 2. Cross-correlations between along- and cross-shore wind stress and physical variables measured at the end of the Army Corps of Engineers' Field Research Facility pier. Values are days lag followed by cross-correlation coefficients at which significant ($p < 0.05$) cross-correlations were found. ns: not significant

Wind stress	Salinity	Temperature	Nearshore flow	Maximum daily tidal range
Along-shore	0: 0.454	ns	0: -0.869	ns
	-1: 0.666		-1: -0.371	
	-2: 0.495			
Cross-shore	0: 0.521	0: -0.229	0: -0.770	ns
	-1: 0.651		-1: -0.415	
	-2: 0.396			

The alongshore components of the surface and bottom currents were both positively and significantly cross-correlated with 0 to -2 or -3 d lag, respectively, with the along- and cross-shore component of the wind stress (Table 1). The alongshore components of the surface and bottom currents were strongly and negatively cross-correlated with each other at 0 and -1 d lag (Table 1) and they were significantly positively cross-correlated with the cross-shore components of the currents at the surface and bottom with -1 and -3 d lag and 0 d lag, respectively (Table 1). In other words, the alongshore components of the surface and bottom currents were in phase and in the direction in which the wind was blowing.

Salinity, temperature, water velocity, and tidal range measured at the end of the FRF pier were cross-correlated with the along- and cross-shore wind stress (Table 2). Surface salinity was significantly and positively cross-correlated with lags of 0 to -2 d with both the along- and cross-shore wind stress (Table 2). Surface temperature was not significantly cross-correlated at any lag with the alongshore wind stress, but it was significantly and negatively cross-correlated at 0 d lag with the cross-shore wind stress (Table 2). Due to the proximity of the shore, flow at the end of the FRF pier was almost entirely alongshore. This flow was significantly and negatively cross-correlated with both the along- and cross-shore wind stress at lags of 0 and -1 d (Table 2). There were no significant cross-correlations between the maximum daily tidal range and either component of the wind stress. Further, the maximum daily tidal range was not significantly cross-correlated with salinity, temperature, or current velocity at the end of the pier, suggesting that tidal range had little effect on these parameters. Along- and cross-shore wind stress to

the south and onshore, respectively, lead to low salinity surface water and high velocity currents at the end of the FRF pier. Offshore wind stress tended to be associated with low surface water temperatures at the pier.

Through August the water column was strongly stratified with the average difference in temperature and density between 4 and 23 m depth at the 25 m mooring equal to 6.3°C (SD = 0.7) and 3.2 sigma-t (SD = 0.8), respectively (Fig. 3). On 3 September a strong wind event from the NE mixed the water column so that the differences in water temperature and density across the water column dropped sharply (Figs. 2 & 3). Following this storm the average differences in temperature and density across the water column dropped to 0.5°C (SD = 0.8) and 1.1 sigma-t (SD = 1.1), respectively.

The period of tidally driven internal waves is on the order of minutes. The interval between measurements of the physical variables (4 min) was too long to allow tidally driven internal waves to be resolved. Tidally generated internal bores would be apparent in the physical data as rapid increases in density which last for several hours (Cairns 1967, Winant 1974, Pineda 1994). The density data collected every 4 min from the 23 m deep CTD on the 25 m mooring were plotted and the plots were inspected for rapid increases in density which might indicate the passage of internal bores. The number of rapid density increases per day (bore index) was cross-correlated with the other physical parameters.

The bore index was only significantly cross-correlated with the alongshore surface currents (at lags of 0 and -1 d; $r = -0.220$ and -0.256 , respectively) and the cross-shore surface currents (at lags of -3 and -4 d; $r = -0.257$ and -0.302 , respectively). Because for much of the study the density difference across the water column was < 1 sigma-t, this index is probably not a sensitive indicator of the presence of internal bores.

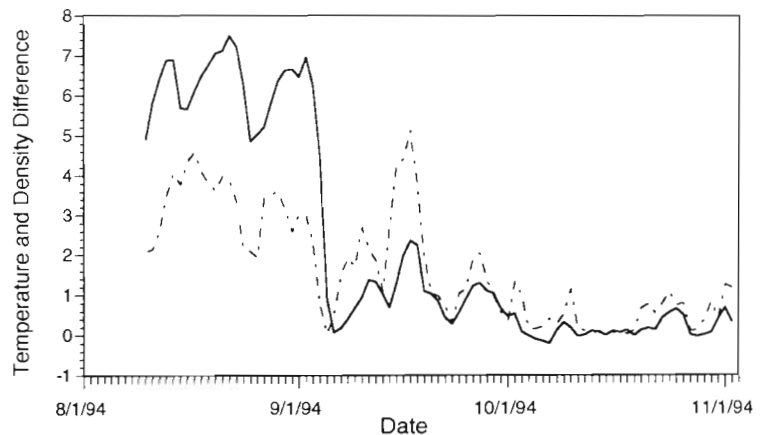


Fig. 3. Temperature (solid line) and density (sigma-t; dashed line) differences at the 25 m mooring between the surface (4 m depth) and near the bottom (23 m depth) during the study period

Table 3. *Callinectes sapidus*, *Penaeus* spp., *Uca* spp. and *Libinia* spp. Summary of post-larval sampling. Samplers were set at the surface and near the bottom at the end of the Army Corps of Engineers' Field Research Facility pier at Duck, NC, and were deployed from 2 August to 3 November 1994

Species	Dates present (no. of days)	Sampler location				Percent at surface Average (SD)
		Surface		Bottom		
		Avg. no. d ⁻¹ (SD)	Total	Avg. no. d ⁻¹ (SD)	Total	
<i>Callinectes sapidus</i>	2 Aug – 2 Nov (93)	94 (427)	8658	22 (52)	2063	60 (32)
<i>Penaeus</i> spp.	3 Sep – 2 Nov (64)	0 (0)	0	10 (30)	582	0 (0)
<i>Uca</i> spp.	2 Aug – 14 Oct (77)	3 (10)	229	2 (5)	168	35 (40)
<i>Libinia</i> spp.	20 Aug – 2 Nov (73)	2 (4)	124	25 (52)	1851	11 (23)

Biological measurements

A variety of post-larval crustaceans clung to and were caught on the collectors deployed from the FRF pier. The 4 most abundant post-larvae caught in order of abundance were *Callinectes sapidus*, *Libinia* spp., *Penaeus* spp., and *Uca* spp. (Table 3). This paper focuses on these organisms.

Callinectes sapidus megalopae were present in the samples throughout the study. Over 10000 individuals

were sampled, most of which were caught on the surface trap (Table 3). *Uca* spp. megalopae were also present in the samples from the start of the study, but they dropped out of the samples after 14 October. A total of 397 individuals were caught, mostly on the bottom trap (Table 3). *Libinia* spp. megalopae first appeared in the samples on 20 August and continued to be caught to the end of the study. Most of the 1975 individuals were caught on the bottom trap (Table 3). *Penaeus* spp. post-larvae were the last to appear in the samples. They were first collected on 3 September and continued through the remainder of the study. A total of 582 individuals were caught all on the bottom trap (Table 3). The daily catch of *C. sapidus* varied over 3 orders of magnitude while the daily abundance of *Uca* spp., *Penaeus* spp., and *Libinia* spp. varied over 2 orders of magnitude (Fig. 4).

In the following data presentation and analysis the number of individuals caught on the surface and bottom collectors have been combined.

The number of megalopae which were caught on the collectors could simply be a reflection of the amount of water which flowed past the end of the pier. The abundances of *Uca* spp. and *Penaeus* spp. were not significantly cross-correlated with the water velocity at any of the lags. The abundances of *Callinectes sapidus* and *Libinia* spp. megalopae were significantly but negatively correlated (r equal to -0.279

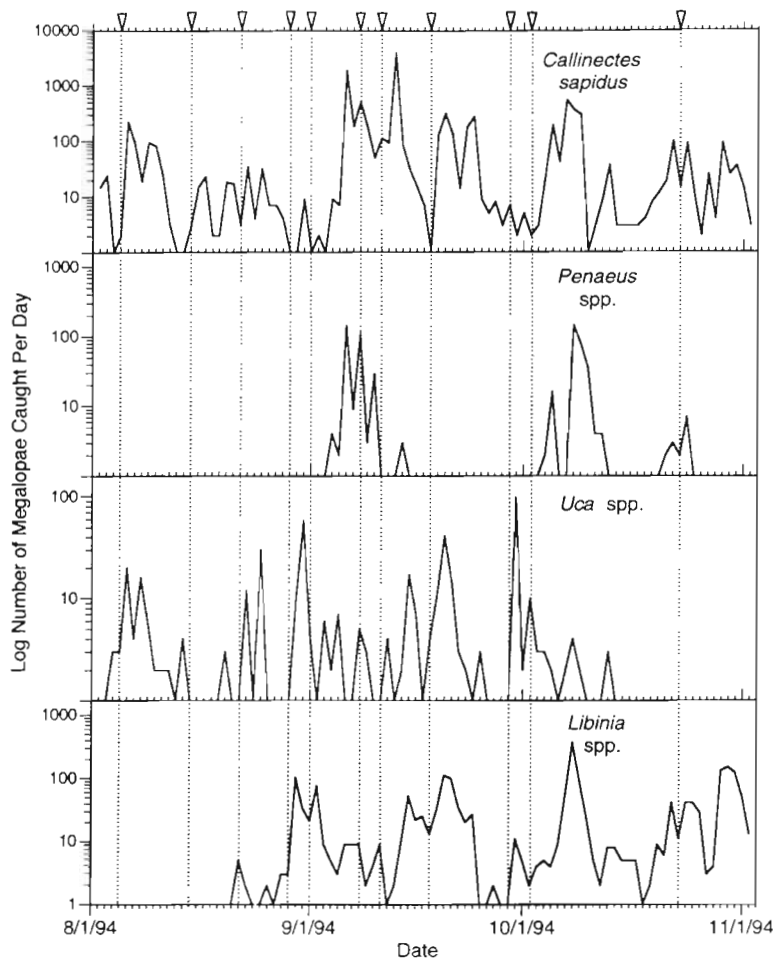


Fig. 4. *Callinectes sapidus*, *Penaeus* spp., *Uca* spp. and *Libinia* spp. Time-series of the daily abundance (log scale) of post-larval crabs and shrimp sampled at the Army Corps of Engineers' Field Research Facility. Arrowheads at the top of the figure and vertical dotted lines indicate days when wind reversals suggest that upwelling fronts may have been relaxing toward shore

Table 4. *Callinectes sapidus*, *Penaeus* spp., *Uca* spp. and *Libinia* spp. Post-larval abundances in relation to the lunar month and the fortnightly tidal cycle. Values are averages of the log-transformed abundance data (standard deviation and n are given in parentheses). χ^2 and p values are the results of a Kruskal-Wallis non-parametric analysis of variance applied to the log-transformed abundance data. The lunar month started on the day of the new moon while the tidal cycle started on the day of maximum tidal range during the new moon spring tides. The day of maximum tidal range during spring tides tended to occur about 2 d after the new or full moon. ns: not significant

Species	Phase of lunar month				Result of K-W test	
	First (>26 and <4 d)	Second (Days 4–11)	Third (Days 12–19)	Fourth (Days 20–26)	χ^2	p
<i>Callinectes sapidus</i>	1.77 (0.78, 23)	1.00 (0.91, 24)	1.33 (0.64, 24)	0.69 (0.57, 22)	4.88	ns
<i>Penaeus</i> spp.	0.83 (0.83, 16)	0.32 (0.59, 16)	0.12 (0.24, 16)	0.00 (0.00, 16)	12.80	0.005
<i>Uca</i> spp.	0.47 (0.38, 20)	0.22 (0.34, 24)	0.48 (0.58, 18)	0.49 (0.63, 15)	6.46	ns
<i>Libinia</i> spp.	1.02 (0.61, 16)	0.96 (0.52, 16)	0.83 (0.72, 20)	1.06 (0.73, 21)	5.15	ns
Species	Phase of tidal cycle				Result of K-W test	
	First (>26 and <4 d)	Second (Days 4–11)	Third (Days 12–19)	Fourth (Days 20–26)	χ^2	p
<i>Callinectes sapidus</i>	1.54 (0.78, 21)	1.36 (0.89, 24)	0.80 (0.77, 24)	1.07 (0.73, 24)	12.51	0.006
<i>Penaeus</i> spp.	0.12 (0.22, 14)	0.73 (0.74, 16)	0.17 (0.60, 16)	0.00 (0.00, 18)	19.47	0.0002
<i>Uca</i> spp.	0.51 (0.47, 19)	0.23 (0.29, 24)	0.41 (0.53, 17)	0.47 (0.60, 17)	4.09	ns
<i>Libinia</i> spp.	0.87 (0.68, 14)	1.03 (0.56, 16)	1.00 (0.75, 22)	0.92 (0.68, 21)	1.32	ns

and -0.290 , respectively) with water velocity at 0 and -1 d lag, respectively. Flow past the end of the pier either had no effect on catch or as flow increased catch decreased.

To investigate the possibility that the abundance of post-larvae varied with the lunar month or the fortnightly tidal cycle the log-transformed abundance data were sorted by lunar or tidal phase and averaged; these average values were tested with a Kruskal-Wallis non-parametric analysis of variance (Table 4). For the phases of the tidal cycle the spring and neap tides were defined as the days on which the tidal range was maximal and minimal, respectively. Maximum spring tides tended to occur about 2 d after the new or full moon.

In the 4 quarters of the lunar month there were no significant differences in the abundance of the megalopae of *C. sapidus*, *Uca* spp., or *Libinia* spp. The abundance of post-larval *Penaeus* spp. was significantly different from random. They tended to be most abundant in the period around the first quarter moon (Table 4). When the month was divided by the phases of the fortnightly tidal cycle, no significant differences were found in the abundances of *Uca* spp. or *Libinia* spp. In contrast, the abundances of post-larval *Penaeus* spp. and the megalopae of *C. sapidus* were significantly different from random (Table 4). Post-larval *Penaeus* spp. tended to be most abundant during the second quarter of the tidal cycle. The results do not clearly indicate in which quarter blue crab megalopae were most abundant (Table 4).

To further investigate the potential fortnightly periodicity in the time-series of post-larval abundance, Fourier analyses were performed on each of the log-

transformed post-larval abundance time-series. Strong peaks were found in the periodograms of both *Callinectes sapidus* and *Penaeus* spp. at a period of 15 d (Fig. 5). During the study, the average number of days between spring tides was 14.7 d. No strong peaks were apparent in the Fourier analysis of the *Uca* spp. time-series and in the *Libinia* spp. time-series, a strong peak was found at a period of about 18 d (Fig. 5).

These results suggest that the abundance of *Callinectes sapidus* megalopae and *Penaeus* spp. post-larvae may vary with the fortnightly tidal cycle. However, the lack of any evidence for a roughly 14.7 d cycle in the abundance of *Uca* spp. or *Libinia* spp. suggests that their abundance did not vary with the fortnightly tidal cycle. To investigate this hypothesis cross-correlations were run between the maximum daily tidal range and the log-transformed daily abundance of megalopae and post-larvae (Fig. 5). This analysis found significant positive cross-correlations between the abundance of *C. sapidus* and *Penaeus* spp. and the maximum daily tidal range at lags of $+2$ to -4 or -5 d lag (Fig. 5). In contrast, no significant cross-correlations were found between the abundance of *Libinia* spp. and the maximum daily tidal range. Weak, but still significant, negative cross-correlations were found at -4 to -6 d lag between the tidal range and the abundance of *Uca* spp. Peaks in the catch of *C. sapidus* and *Penaeus* spp. tended to occur at or several days after the spring tides and there was a tendency for *Uca* spp. to be least abundant during the neap tides.

The abundance of megalopae was tested against the internal bore index. The bore index was not significantly cross-correlated with the abundance of *C. sapidus*, *Penaeus* spp., or *Uca* spp. at any of the lags.

Table 5. *Callinectes sapidus*, *Penaeus* spp., *Uca* spp. and *Libinia* spp. Cross-correlations between the daily abundance of post-larvae and the physical variables. The wind, nearshore current, temperature, and salinity data were collected near the end of the FRF pier. Cross-shore and alongshore current data were collected at the 25 m mooring located 6 km offshore. Autoregressive integrated moving average models (ARIMA) were fitted to the time-series of physical data and to the log-transformed post-larval abundance data. The residuals between the ARIMA models and the raw data were calculated, and these residuals were used in the cross-correlation analysis. Values are days lag and cross-correlation coefficients at which significant ($p < 0.05$) cross-correlations were found. ns: not significant

Species	Wind stress		Cross-shore currents		Alongshore currents		Nearshore current	Temperature	Salinity
	Along-shore	Cross-shore	Surface, 4 m	Bottom, 18 m	Surface, 4 m	Bottom, 18 m			
<i>Callinectes sapidus</i>	ns	ns	ns	ns	ns	ns	ns	ns	ns
<i>Penaeus</i> spp.	ns	-2: -0.290	0: -0.366 -1: -0.309	ns	ns	ns	ns	ns	ns
<i>Uca</i> spp.	ns	ns	-1: -0.239	0: 0.373	ns	ns	ns	ns	0: -0.255
<i>Libinia</i> spp.	ns	ns	ns	ns	0: 0.310	ns	ns	ns	ns

The index was significantly negatively cross-correlated with the abundance of *Libinia* spp. at lags of -1, -2, and -4 d ($r = -0.261, -0.254, \text{ and } -0.295$, respectively).

The residuals from the *Callinectes sapidus* ARIMA were not significantly cross-correlated with any of the physical variables at any of the lags (Table 5). The strong tidal signal in the *C. sapidus* time-series and the lack of any significant cross-correlations with the other physical variable suggest that onshore transport of *C. sapidus* megalopae was dominated by some tidally driven mechanism.

In contrast, the residuals from the *Penaeus* spp. ARIMA were significantly and negatively cross-correlated at -2 d lag with the cross-shore wind stress and at 0 and -1 d lag with the cross-shore surface current (Table 5). These significant cross-correlations suggest that, in addition to some factor related to the fortnightly tidal cycle, the abundance of *Penaeus* spp. on the collectors was also higher during periods of onshore movement of the surface waters.

Similar results to those found for *Penaeus* spp. were found for *Uca* spp., i.e.

significant negative cross-correlations were found at -1 d lag between the residual and the cross-shore surface current and a significant positive cross-correlation

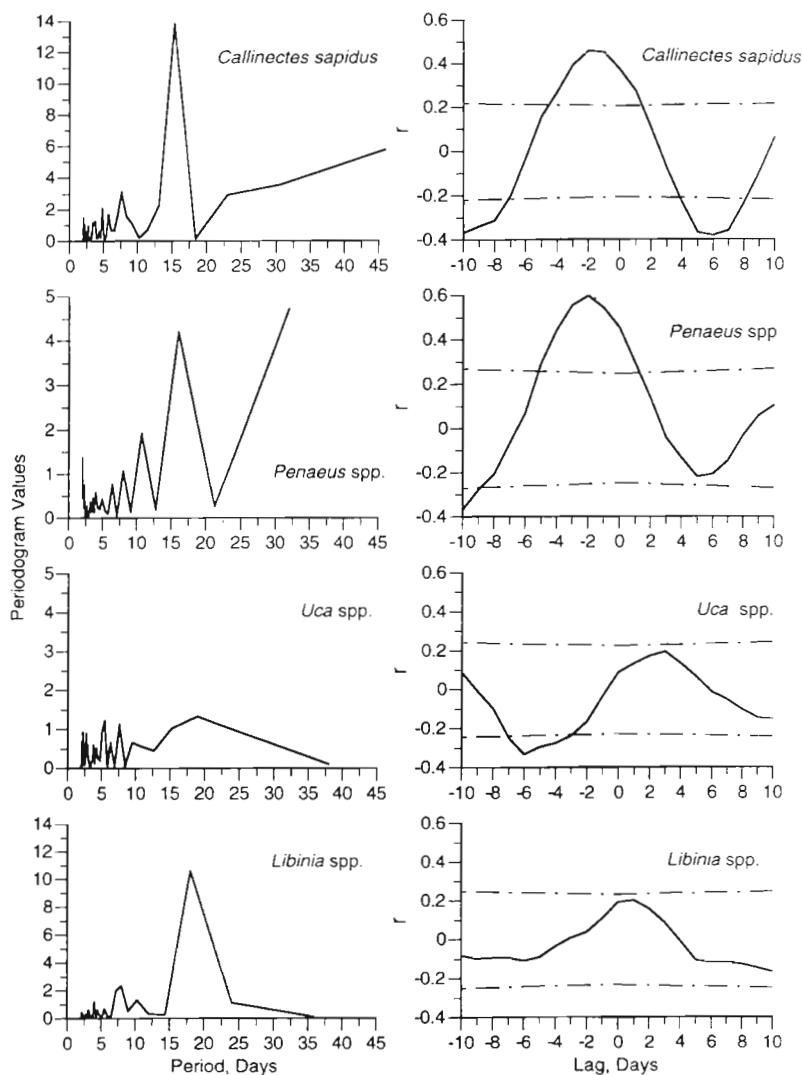


Fig. 5. *Callinectes sapidus*, *Penaeus* spp., *Uca* spp. and *Libinia* spp. Time-series analysis of the abundance of post-larval crabs and shrimp. On the left are the results of Fourier analysis of the log-transformed daily abundance of post-larvae. On the right are the results of cross-correlations between the maximum daily tidal range and the log-transformed daily abundance of post-larvae. The dashed lines indicate the r values needed to obtain a $p < 0.05$

was found at 0 d lag with the cross-shore bottom current (Table 5). In addition, a significant negative cross-correlation was found at 0 d lag with salinity at the end of the FRF pier (Table 5). This combination of significant cross-correlations suggests that, in addition to the effect of the tides, larger catches of *Uca* spp. were associated with onshore movement of surface waters.

The residuals from the *Libinia* spp. ARIMA were also significantly cross-correlated with some of the physical variables. A significant positive cross-correlation at 0 d lag was found between the residuals from the ARIMA of megalopal abundance and the alongshore surface currents (Table 5). Additionally, a significant negative cross-correlation was found at -1 d lag with the nearshore current flow at the end of the FRF pier (Table 5). These significant cross-correlations are consistent with higher catches of *Libinia* spp. occurring during periods of northward flowing currents and upwelling.

Recent evidence suggests that larval invertebrates can be transported shoreward at the end of an upwelling event as the upwelling front relaxes toward shore (Shanks 1998). At the Duck sample site upwelling fronts have been observed to propagate past the end of the FRF pier and into the surf zone (Porter et al. 1998). To identify days when an upwelling front might have been propagating shoreward, the wind record was inspected for periods when the winds reversed from upwelling favorable (e.g. from the west through to the south) to downwelling favorable (e.g. from the north through to the east). The arrows at the top of Fig. 4 indicate the days when upwelling fronts may have been propagating onshore. We expect the catch to be significantly higher on days when upwelling fronts came ashore than on days when they did not. To test this hypothesis a *t*-test was run comparing megalopal abundances on days when an upwelling front was predicted to have been propagating ashore to the abundances on all other days. No significant *t* values (1-tailed test, $p > 0.05$) were found for any of the organisms investigated. This was true whether the *t*-test was run on the log-transformed abundances or on the ARIMA residuals.

DISCUSSION

Currents over the Mid-Atlantic Bight are dominated by the winds (Wright 1995). The dominant winds during the study were from the NE and SW (Fig. 2). Winds from the NE caused downwelling events with southward-flowing alongshore currents, shoreward-flowing surface currents, and bottom currents flowing offshore. During downwelling the coastal waters tended to be warmer and have lower salinity. Winds from the SW

caused upwelling with northward-flowing alongshore currents, seaward-flowing surface currents, and bottom currents flowing onshore. At these times, the coastal waters tended to be cooler and have higher salinity. The winds caused the coastal currents to cycle between downwelling and upwelling.

The Chesapeake Bay injects a tremendous amount of low salinity water into the Mid-Atlantic Bight (Boicourt 1973). During NE winds the onshore surface flow pushed this plume of low salinity water against the shore and directed the plume southward along the coast (S. E. Rennie, J. L. Largier & S. J. Lentz unpubl. data). In this study, the velocity of the plume ranged from 30 to 70 cm s⁻¹ and was driven by buoyancy and the winds. The presence of the plume is apparent in the physical data as periods of very low salinity (<30) and high alongshore flows at the FRF pier. During upwelling, the offshore movement of the surface waters caused the plume to thin, spread seaward, and detach from the coast.

The collectors at the FRF pier on average caught >90 blue crab megalopae d⁻¹ with peak catches in the thousands (Table 3, Fig. 4). The results of the Fourier analysis and cross-correlations suggest that the abundance of blue crab megalopae at this site outside of an estuary tended to peak around the spring tides. Using similar sampling techniques for post-larvae a number of investigators (van Montfrans et al. 1990, 1995, Olmi 1991, Rabalais et al. 1995, van Montfrans et al. 1995) have looked at variations in the daily abundance of *Callinectes sapidus* megalopae within estuaries. In most of these previous studies researchers also found that the daily abundance of blue crab megalopae varied with the phase of the moon, and, hence, the tides (Goodrich et al. 1989, van Montfrans et al. 1990, Boyland & Wenner 1993, Jones & Epifanio 1995, Mense et al. 1995, Metcalf et al. 1995, Olmi 1995, Wrona et al. 1995). Over all, these previous studies and the results from this study are in agreement.

A number of studies along the Atlantic coast of North America have attempted to relate the daily abundance of blue crab megalopae to the coastal winds (Goodrich et al. 1989, Boyland and Wenner 1993, Blanton et al. 1995, Mense et al. 1995, Olmi 1995). In general, these studies suggest that samples collected within an estuary tend to vary with wind direction, with peak catches tending to occur when the winds are from the northeast. In the work reported here, no significant relationships were found between wind direction and the abundance of blue crab megalopae.

What might account for the similarities and differences between the previous studies which sampled within estuaries and the study reported here which took place on the open coast? The abundance of megalopae at a site within an estuary will be depend on at

least 2 factors, which are: (1) the transport of larvae to the coast and (2) the ingress of the larvae into the estuary. The abundance of megalopae at a coastal site is only dependent on the shoreward transport of larvae. Perhaps the consistent similar features of the time-series collected within estuaries and the one collected on the open coast are due to the transport mechanism across the shelf. Consistent amongst all of the data sets is a variation in blue crab megalopal abundance with either the phase of the moon or tides. These results suggest that onshore transport is due to a tidally driven phenomena. What is apparent in most of the estuarine time-series, but not in the coastal samples, is a wind-related variation in the megalopal abundance. The work of Goodrich et al. (1989) suggests that ingress into the Chesapeake Bay is, at least in part, dependent on wind-driven coastal set up forcing coastal waters into the estuary. Perhaps the significant effect of the winds seen in the time-series collected within estuaries is an indication of the importance of wind-driven flow on the ingress of megalopae into an estuary.

The shoreward migration of blue crab megalopae appears to be driven by tides and we know that the blue crab megalopae inhabit the neuston (Smyth 1980, Johnson 1985). Given this combination of facts, there are 2 possible mechanisms which might explain their onshore migration; they may be transported shoreward (1) in convergences over tidally generated internal waves (Shanks 1988), or (2) in convergences generated during the relaxation from an upwelling event generated by an internal tidal bore (Pineda 1994).

Tidally driven internal waves are a characteristic feature of many continental shelves (Arthur 1954, Curtin & Mooers 1975, Gargett 1976, Chereskin 1983, Sawyer 1983, Kingsford & Choat 1986). Using satellite images researchers have observed the surface manifestations of internal waves in the Mid-Atlantic Bight. Sawyer (1983) studied 3 yr of Landsat images (1972–1974) of the Mid-Atlantic Bight collected during the months of May through September. In the Landsat images internal waves were apparent throughout the Mid-Atlantic Bight, including directly offshore of the Duck sample site. From the satellite images Sawyer (1983) and Apel et al. (1975) determined that internal wave packets can last for several days, during which time they were found to traverse even the broad continental shelf of the Mid-Atlantic Bight. During the CoOP study, sets of surface slicks characteristic of internal wave convergences were observed in the coastal waters adjacent to the FRF pier (pers. obs.). In the Mid-Atlantic Bight between Cape Hatteras and the Delaware Bay, tidally generated internal waves are present and common.

In the waters off Beaufort, North Carolina, Shanks (1988) tested the hypothesis that internal waves could

cause the shoreward transport of larval invertebrates and fish. This study demonstrated that internal waves transport a variety of larvae, including blue crab megalopae and post-larval *Penaeus* spp., shoreward. The magnitudes of the internal tides, internal tidal bores, and tidally generated internal waves all vary with the fortnightly tidal cycle (Cairns 1967, 1968, Pineda 1991); the larger the tidal range, the larger the internal waves generated. This fortnightly variations in the size of the internal waves may lead to a fortnightly variation in settlement. For example, Shanks & Wright (1987) demonstrated that the cyprids of some types of intertidal barnacles are transported shoreward in the convergence over internal waves. Pineda (1991) and Shanks (1986) found that peaks in barnacle settlement tended to occur between the neap and spring tides when large internal bores and the accompanying internal waves (Winant 1974) impinged on the coast. These studies suggest that variation in barnacle settlement was driven by variations in the strength of an onshore transport mechanism: tidally driven internal waves or internal bores. The often observed fortnightly variations in blue crab abundance may be due to the fact that they can be transported shoreward in the convergences over tidally driven internal waves (Shanks 1988) and the transporting capacity of internal waves may vary over the spring to neap tidal cycle.

Peak catches of *Penaeus* spp. post-larvae tended to occur at or slightly after the new moon (Table 4). No or few post-larvae were caught around the time of the full moon (Table 4). A number of studies have arrived at a similar conclusion (Williams & Deubler 1968, Allen et al. 1980, Olmi 1986, Brady 1994, DeLancey et al. 1994). The cross-correlation analysis also suggested that the abundance of *Penaeus* spp. tended to be larger 1 to 2 d after periods of onshore winds and currents. Williams & Deubler (1968) did not find a statistically significant relationship between catch of *Penaeus* spp. larvae and wind direction at 0 d lag, but they did not test longer lags.

Penaeus spp. post-larvae make a diel vertical migration from within the water column during the daylight hours to the surface waters at night (Temple & Fischer 1965, Jones et al. 1970). Like the larvae of the western Australian rock lobster (Phillips et al. 1978), *Penaeus* spp. post-larvae may migrate into the surface waters and neuston during dark moonless nights. When in the neuston, the post-larvae should be transported downwind by wind-driven surface currents such as Langmuir circulation (Leibovich 1983). Like blue crab megalopae, *Penaeus* spp. post-larvae, when in the neuston, should become concentrated in convergence zones and if the convergence zone moves shoreward then so should the post-larvae within the convergence zone. Shanks (1988) found that *Penaeus* spp. post-lar-

vae were concentrated in the convergence zone over tidally forced internal waves, and as these internal waves propagated shoreward the post-larvae were transported shoreward in the internal wave convergences. Further, *Penaeus* spp. post-larvae may be transported shoreward in the moving convergence zone associated with the relaxation events following wind-driven or tidally driven upwelling events (Roughgarden et al. 1991, Pineda 1994, Shanks 1998).

The observed pattern of abundance of shrimp post-larvae at the FRF pier may be due to a combination of onshore transport mechanisms modified by vertical migration. If the shoreward transport of post-larvae occurs via shoreward propagating surface convergences, then transport will only occur when the larvae are at the surface. Around the time of the dark of the new moon, larvae which migrate to the ocean's surface may be transported shoreward in convergences. In contrast, around the time of the full moon shrimp post-larvae may avoid the more illuminated surface waters, in which case they would not be transported shoreward.

Uca spp. post-larvae must settle in an estuarine environment. Their larvae are dispersed over the continental shelf out to about 60 km from shore (Smyth 1980) and they tend to be found during the day below the pycnocline or at least deep in the water column (Johnson 1985). Within Chesapeake Bay, fiddler crab megalopae make a diel vertical migration (Maris 1986). There are, however, apparently no observations of the vertical migratory behavior of *Uca* spp. larvae over the shelf.

The daily abundance of *Uca* spp. has been measured in several estuaries along the east coast of North America. Boylan & Wenner (1993) found that abundance peaks occurred around neap tides, while Mense et al. (1995) and Wrona et al. (1995) found peaks occurring around the times of the new and full moons. Jones & Epifanio (1995) found no relationship between catch and phase of the moon. None of these studies found relationships between the abundance of *Uca* spp. megalopae and the wind. The differences between these studies may be due to real differences between locations or may simply be due to the variety of statistics applied to the data sets.

The small correlation coefficient between the abundance of *Uca* spp. and the tidal range suggests a weak tidal effect, with peak catches occurring around the spring tides. The effect of the wind appears to be stronger, with peak catches tending to occur during periods of wind-driven onshore surface flow (Fig. 4, Table 5).

Libinia spp. megalopae tend to be found below the pycnocline or in the lower half of the water column (Williams 1984, Johnson 1985). The Fourier analysis

suggested there was an 18 d cycle to settlement, there were no significant cross-correlation with the tides, and peak catches tended to occur when surface currents were flowing to the north. Comparing the wind stress (Fig. 2) with settlement (Fig. 4) one can see that peaks in settlement of *Libinia* spp. tended to occur during periods when the wind stress was to the north and, to a lesser extent, offshore, e.g. upwelling winds. Peaks in settlement and wind events were on average 19 d apart, close to the 18 d cycle found in the Fourier analysis. The shoreward transport of *Libinia* spp. megalopae appears to have been primarily due to upwelling.

Callinectes sapidus, *Uca* spp., and *Penaeus* spp. all recruit into estuaries. The pattern of abundance of these organisms suggests that their onshore transport was due to a tidally driven mechanism and/or onshore wind-driven surface flow. The available data on the pattern of settlement of intertidal crabs (Shanks 1983, 1985, 1988) and barnacles (Hawkins & Hartnoll 1982, Shanks 1986, Shanks & Wright 1987, Pineda 1991) suggest that these organisms are also transported shoreward by the tides or winds. In contrast, post-larvae of *Libinia* spp., which inhabits the shallow subtidal benthos over the continental shelf or the higher salinity outer reaches of estuaries (Williams 1984), were apparently transported shoreward in near-bottom waters during upwelling conditions. Perhaps organisms which must settle in the intertidal or are estuarine dependent have evolved behaviors which exploit onshore transport which occurs at the surface, while organisms which settle more broadly over the shelf have evolved behaviors which exploit transport by bottom currents.

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