# Mechanisms regulating estuarine ingress of blue crab *Callinectes sapidus* megalopae

## M. B. Ogburn[1,2,*], H. Diaz[1], R. B. Forward Jr.[1]

[1]Duke University Marine Laboratory, Nicholas School of the Environment, 135 Duke Marine Lab Road, Beaufort, North Carolina 28516, USA

[2]*Present address:* Savannah State University, PO Box 20228, Savannah, Georgia 31404, USA

ABSTRACT: Mechanisms of shoreward transport and estuarine ingress in blue crab *Callinectes sapidus* megalopae have been difficult to infer from time series of nightly settlement on passive hog's hair collectors. We attempted to investigate the hypothesis that separating mechanisms of shoreward transport and estuarine ingress might enable identification of important transport mechanisms by eliminating interactions between wind-driven, tide-driven or other mechanisms. To this end, we collected megalopae simultaneously at nearby coastal and estuarine locations. Megalopae were collected nightly on hog's hair collectors from June to November 2004 to 2006 near the entrance to the Newport River estuary, North Carolina, USA, and at a site within the estuary. Nightly relative abundance of megalopae was cross-correlated with wind stress, maximum daily tidal range and the duration of nighttime flood tides. Relative abundance at the coastal site was not consistently correlated with wind stress or tidal range, possibly due to behavioral responses to turbulence, preventing us from separating the effects of shoreward transport and estuarine ingress. Relative estuarine abundance was positively correlated with: (1) downwelling-favorable winds, (2) onshore winds, and (3) the duration of nighttime flood tides. Hurricanes were associated with the highest estuarine abundance in each year. There was an apparent relationship between the peak months of estuarine ingress and a period of downwelling-favorable winds in September and October known as mariners' fall. A conceptual model is proposed describing the environmental conditions under which estuarine ingress of *C. sapidus* megalopae occurs.

KEY WORDS: Blue crab · *Callinectes sapidus* · Megalopa · Shoreward transport · Estuarine ingress · Newport River estuary

## INTRODUCTION

Resolving the mechanisms involved in the transport of larvae or postlarvae from oceanic to estuarine habitats remains one of the major obstacles to understanding the population dynamics of many commercially important estuarine species. For the blue crab *Callinectes sapidus*, the relative nightly abundance of postlarvae (megalopae) arriving in US East and Gulf Coast estuaries, defined as the number which settle on passive hog's hair collectors, has been difficult to correlate with environmental variables associated with hypothesized transport mechanisms (e.g. Rabalais et al. 1995, van Montfrans et al. 1995). In contrast, identifying postlarval transport mechanisms that vary in strength

from year to year has improved our understanding of population dynamics and variability in the fishery landings of other crustaceans including the western rock lobster (Pearce & Phillips 1988) and Dungeness crab (Shanks & Roegner 2007). We conducted the present study to identify the primary mechanisms involved in transporting *C. sapidus* megalopae from the coastal ocean to estuaries as a step towards determining whether variability in fishery landings may result from year-to-year variability in wind-forced currents, tides or other factors affecting the supply of larvae to estuaries.

Transport of *Callinectes sapidus* postlarvae is thought to occur by a combination of physical and behavioral mechanisms. Following a 30 to 50 d larval

development period in the coastal ocean (Costlow & Bookhout 1959), megalopae initially remain near the surface (Johnson 1995) where shoreward transport is thought to occur during coastal downwelling events (Epifanio & Garvine 2001). Megalopae can also be transported in shoreward-moving frontal zones during relaxation of upwelling events (Shanks et al. 2000) and might be transported in convergence zones associated with tidally generated internal waves (Shanks 1988, 1998). Upon reaching nearshore areas, megalopae undergo a behavioral shift to nocturnal diel vertical migration (Little & Epifanio 1991, Forward & Rittschof 1994, Ogburn & Forward 2009) and are probably transported to estuarine inlets in alongshelf currents except when onshore winds blow surface waters (and associated megalopae) directly towards an inlet (Blanton et al. 1999a). Movement into estuaries (estuarine ingress) occurs by nocturnal flood tide transport (FTT) in which megalopae stay on the bottom during ebb tide and during the day, swim up into the water column in response to increasing salinity during nighttime flood tides, remain swimming in turbulent flood currents and settle to the bottom as turbulence declines at the end of flood tide (Forward et al. 2003). Barotropic inflow due to subtidal increases in coastal sea level may also result in ingress or enhance FTT (Goodrich et al. 1989, Blanton et al. 1995).

In order to effectively associate relative abundance with potential transport mechanisms, we developed testable hypotheses describing patterns in the relative abundance of *Callinectes sapidus* megalopae that would result from each mechanism of shoreward transport or estuarine ingress. Because of the different orientations of the shoreline and continental shelf in the study area (see Fig. 1), the alongshore (90° axis) and across-shore (0° axis) directions were distinguished from the alongshelf (15° to 60° axes) and across-shelf (105° to 165° axes) directions for interpretation of the effects of wind forcing on relative abundance. Hypotheses were as follows:

(1) During downwelling, relative coastal and estuarine abundance should increase within 4 d of the onset of winds from the northeast.

(2) Onshore winds should result in concurrent increases in relative coastal and estuarine abundance.

(3) Transport in shoreward-moving frontal zones due to relaxation of upwelling should result in increased relative coastal and estuarine abundance within 2 d of the dissipation of winds from the southwest.

(4) If megalopae are transported in convergence zones associated with internal waves, relative coastal and estuarine abundance should fluctuate with a semi-lunar or lunar periodicity that is not necessarily associated with a particular phase of the tide (Miller & Shanks 2004).

(5) FTT should result in a semi-lunar pattern in relative abundance with high abundances occurring during prolonged nighttime flood tides (neap tides in the study area), but this effect should only be apparent within the study estuary.

(6) Barotropic inflow should result in increased relative estuarine abundance during periods of high coastal sea level and decreasing estuarine water temperature (during summer and early fall when the temperature of estuarine water tends to be higher than the temperature of shelf water), indicating transport of coastal water to the estuary.

Each year about 30 to 70% of *Callinectes sapidus* megalopae that enter the Newport River estuary, North Carolina, USA, arrive in episodic ingress events characterized by high relative abundance, with the remainder entering on intervening days in low numbers (Forward et al. 2004). Because of the potential impact on population dynamics of the few ingress events occurring each year, we focused our analysis specifically on identifying the mechanisms resulting in these events. Our initial objectives were to: (1) separate the effects of shoreward transport and estuarine ingress by determining simultaneously the relative nightly abundances of *C. sapidus* megalopae at a coastal site and a nearby estuarine site, (2) identify the primary mechanisms of shoreward transport and estuarine ingress by evaluating the hypotheses listed above using time series analyses, and (3) construct a conceptual model describing the environmental conditions that result in high or low estuarine ingress. Problems with sampling at the coastal site (see 'Discussion') made comparing relative coastal and estuarine abundances difficult and prevented us from evaluating Hypotheses 1 to 4 above for the coastal site, but did not prevent completion of Objectives 2 and 3.

## MATERIALS AND METHODS

**Study location.** The nightly relative abundance of *Callinectes sapidus* megalopae was determined for 3 yr (2004 to 2006) at a coastal site near the inlet to the Newport River estuary, North Carolina, USA (Beaufort Inlet), and at a second site within the estuary. Beaufort Inlet is a relatively narrow (~1 km wide), south-facing inlet that connects the Atlantic Ocean with the partially-mixed Newport River estuary and a system of lagoonal back-barrier island sounds (Fig. 1). The coastal site was located approximately 3 km west of the inlet in 2004–2005 at Triple S fishing pier (34° 41.60′ N, 76° 38.62 W), but was moved approximately 1.5 km further west in 2006 to Sportsman's fishing pier (34° 41.68′ N, 76° 43.81′ W) following the demolition of Triple S fishing pier. The estuarine site
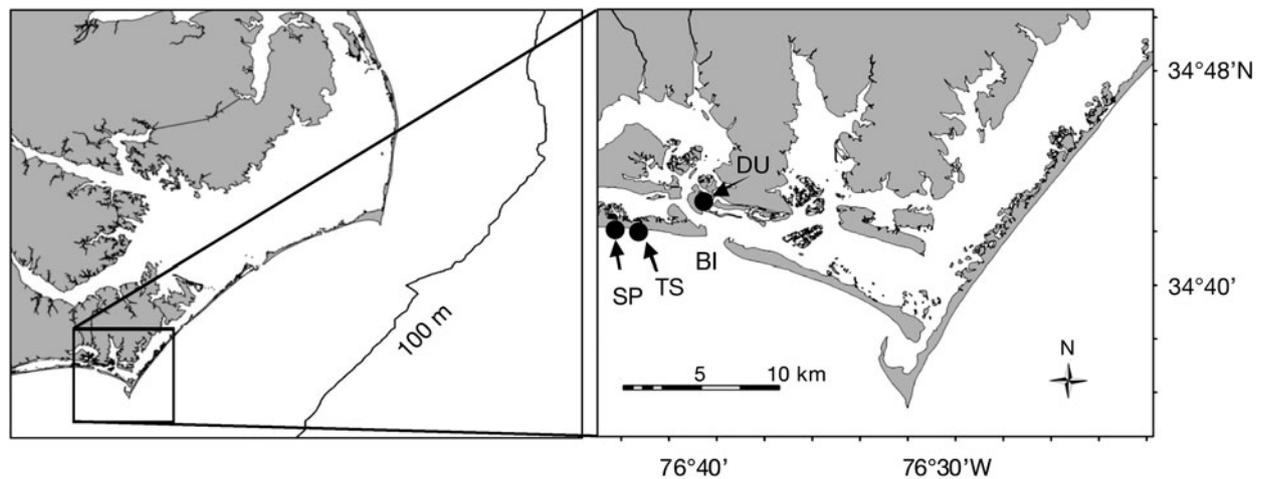
Fig. 1. Study location and surrounding area. The continental shelf margin is indicated by the 100 m depth contour. Sampling locations near Beaufort Inlet (BI) were at Triple S fishing pier (TS), Sportsman's fishing pier (SP) and the Duke University Marine Laboratory dock (DU)

was located at the Duke University Marine Laboratory dock (34° 43.01' N, 76° 40.23' W), the site of 8 previous years of *C. sapidus* megalopal collections (Forward et al. 2004).

**Biological data.** The number of *Callinectes sapidus* megalopae settling each night on passive settlement substrates was used as a relative measure of abundance. Substrates were made of a hog's hair sleeve surrounding an inner PVC cylinder (Metcalf et al. 1995). The PVC cylinder was partially filled with concrete to help maintain a vertical position in the water column. Three replicate collectors were deployed from fixed piers at each site. The collector depth was approximately 1 m below the surface at mean low water, which roughly corresponded to the middle of the water column. The relative abundance of *C. sapidus* megalopae can be higher on surface versus bottom collectors at the coast (Shanks 1998), but the location of our coastal site in a shallow water column (2 m at mean low water) probably limited this difference. There were no differences in surface and bottom numbers of *C. sapidus* megalopae at our estuarine site (De Vries et al. 1994).

Collectors were sampled at the coastal site from 16 September to 23 November 2004, 8 June to 9 November 2005 and 1 June to 5 November 2006 and at the estuarine site from 2 June to 23 November 2004, 2 June to 15 November 2005 and 1 June to 15 November 2006. Collectors were deployed on the morning prior to the first sampling date and were retrieved daily (usually in the morning). Megalopae were removed from the collectors using standard techniques (Metcalf et al. 1995), identified, counted and returned live to the field. In 2004, *Callinectes* spp. megalopae were not identified

to the species level because we expected to catch very few *C. similis*. In 2005 and 2006, *Callinectes* spp. megalopae were identified to the species level to ensure that our results were not affected by *C. similis* (Costlow & Bookhout 1959, Bookhout & Costlow 1977). All individuals were identified to species on days when the total number collected was ≤60. For days when >60 were collected, the 3 replicate samples were pooled and 60 individuals were randomly chosen for identification to species using a large mouth pipette while stirring vigorously. Choosing 60 individuals from a sample resulted in a standard error of no greater than 7% ($\sqrt{[P(1 - P)/N}$, where P equals the proportion of *C. sapidus* and N equals the number of individuals). This number was chosen because identifying larger numbers of individuals would only have resulted in small improvements in standard error.

During much of 2004 and on 6 days in 2005, large numbers of *Callinectes* spp. megalopae were collected at the coastal site (>1000 collector$^{-1}$). On these days, 3 (in 2004) or 5 (in 2005) subsamples of 10 ml were taken from each sample using a large mouth pipette from a vigorously stirred 500 ml mixture of sample and seawater. Counts were multiplied by a factor of 50 and averaged to determine the daily number for each collector. First instar juvenile (J1) *C. sapidus* were also collected regularly. We assumed that these individuals had settled on the collectors at night as megalopae and had undergone metamorphosis prior to removal from the collectors.

Prior to analysis, gaps in time series data of 5 d or less were filled using linear interpolation. Longer gaps (one 6 d gap at the coast in 2005, one 10 d gap in the estuary in 2006 and two 10 d gaps at the coast in 2006)

were excluded from analyses except where indicated. Comparisons among sites and among megalopae and juveniles were conducted using cross-correlation analysis.

**Physical data**. Wind data were obtained from NOAA's National Data Buoy Center (NDBC) Stn CLKNY at Cape Lookout, North Carolina, for 2004 to 2005. Instrument outages in 2006 made it necessary to use data from Stn 41035 located near New River Inlet, North Carolina. This station was chosen because the data were the most closely correlated with the available 55 d of Cape Lookout data for that year ($r^2 = 0.63$ for wind direction [circular-circular correlation]; $r^2 = 0.80$ for wind speed). Hourly data were averaged over the 24 h (diel) period starting at 07:00 h the day before collection and ending at 06:00 h the morning of collection. This ensured that wind data corresponded to the approximate times of settlement on collectors each night (Tankersley et al. 2002, Ogburn & Forward 2009). Because specific alongshelf and across-shelf axes were difficult to identify, wind stress was calculated at 15° intervals beginning at 0° (winds from the north) (Large & Pond 1981). Calculating unidirectional wind stresses instead of combining positive and negative stress along an axis allowed for direct comparison of wind stress and relative abundance data. Cross-correlations between wind stress at each 15° interval and relative megalopal abundance were calculated for lags of 0 to –4 d.

Predicted tide height and time data were obtained from the software Tides and Currents (Nobeltec). To determine the relationship between relative coastal abundance and the semi-diurnal tidal cycle at the coastal site, maximum daily tidal range was calculated as the maximum difference between a low tide and subsequent high tide each day. A different method was needed for relating relative estuarine abundance to tides because of the behaviors associated with FTT. For this purpose, the duration of nighttime flood tide was calculated as the number of minutes of flood tide between sunset and sunrise during the night of collector deployment. When flood tides occurred in both evening and morning, only the tide of longer duration was used.

Prior to comparing relative abundance with tides, a 21 d moving average of relative abundance was calculated and subtracted from the raw relative abundance data to remove the seasonal trend. Cross-correlations between these residual data sets and tides were calculated at lags of 0 to –15 d. Due to significant autocorrelations for both relative abundance and tide time series in each year, 95 % CI were calculated both assuming independent points and autocorrelation. The most conservative value was used to determine significance (Wing et al. 1995).

Cross-Fourier analysis was used to determine the dominant period of covariance and squared coherence between relative abundance and tide data (Roegner et al. 2007). For periods with large cross-amplitudes, squared coherence can be interpreted as the percent of variation in relative abundance that is explained by variation in the duration of nighttime flood tide. Because data gaps prevent use of this analysis, all data gaps except one were filled using linear interpolation. In 2006 at the coastal site, the 10 d gap from 7 to 16 October was filled by adding in a previous 8 d period of low settlement (15 to 22 September) and using linear interpolation to connect it to the observed data. This was necessary because relative abundance was high at each end of the gap and linear interpolation would have resulted in a 2 wk period of constant high relative abundance that was uncharacteristic of the episodic nature of the relative abundance data. This manipulation makes it necessary to exercise caution when interpreting these data, but we felt that this was better than eliminating the data set from our analysis.

Observed water level and temperature data were obtained from NOAA's NDBC Stn BFTN7 located at the Duke University Marine Laboratory dock adjacent to the location of collectors. A daily water level anomaly value was generated by subtracting the predicted slack high water level after flood tide (Tides and Currents, Nobeltec) from observed values. This anomaly provided a relative measure of the effects of winds and rain on water inflow to the estuary. Daily water temperature was calculated at slack water after flood tide by averaging the hourly temperature value recorded nearest slack water for the 2 tides each day. The seasonal trend in temperature was removed for time series analysis by calculating residuals from a 21 d moving average. To determine the effect of winds on water level and temperature, the water level anomaly and residual temperature data were cross-correlated with positive and negative wind stress along the 15° (alongshelf) and 105° (across-shelf) axes.

## RESULTS

### Physical data

Winds were typically weak and from the south during summer and increased and shifted to predominantly from the northeast in fall. Winds from the northeast resulted in increased water level and decreased water temperature at slack water after flood tide, with the strongest correlations at lags of 0 and –1 d (Table 1). Winds from the southeast were also positively correlated with water level and negatively correlated with water temperature at lags of +1 and –1 d (Table 1).

Tides were semidiurnal with amplitude ranging from 0.33 to 1.49 m at the estuarine site. In 2004 and 2005, there were significant positive correlations between maximum daily tidal range and water temperature at slack water after flood tide at lags of −2 to −4 d, suggesting that positive temperature anomalies occurred between spring and neap tides.

## Relative coastal abundance

The relative abundance of *Callinectes sapidus* megalopae at the coast was episodic and characterized by a common broad period of peak abundance from July to October (Fig. 2, Table 2). Nightly relative abundance at the coast ranged from a low of 0 to a maximum of 6637 megalopae collector$^{-1}$. The relative abundance of J1 crabs was 1% (2006) to 3% (2005) of megalopal abundance. Relative J1 and megalopal abundances were significantly correlated at lags of 0 to −5 d, with the strongest correlations at 0 d (Table 3). There were no significant correlations between relative megalopal abundance and the proportion of juveniles in the total daily catch.

Relative megalopal abundance was weakly associated with wind stress and tides. Significant correlations between wind stress and relative coastal abundance occurred in each year, but the wind directions and signs of the relationships were inconsistent (Fig. 3). Low relative abundances at high wind stresses may have prevented the detection of significant relationships (Fig. 4). Relative abundance was significantly correlated with maximum daily tidal range in 2006, with high abundances occurring 2 to 5 d after minimum amplitude tides (Fig. 5). Periodicities around the semilunar cycle explained 29 to 39% of the variability in settlement (Fig. 5). Tidal range was not related to relative abundance in other years.

## Relative estuarine abundance

The relative abundance of *Callinectes sapidus* megalopae in the estuary was significantly but weakly correlated with relative coastal abundance in 2005 and 2006 at lags of −1 to −4 d (r < 0.25). The time of peak abundance was less variable than at the coast, occurring in September or October of each year (Fig. 2, Table 2). Relative estuarine abundance was also much lower than at the coast, ranging from 0 to 495 megalopae collector$^{-1}$. As at the coastal site, relative J1 abundance was 1 to 3% of relative megalopal abundance with significant correlations at lags of 0 to −5 d (Table 3). The 2 sites differed in that the percent of juveniles in the total daily catch at the estuarine site was significantly correlated with relative megalopal abundance at lags of −2 to −5 d (Table 3). During this period, J1 crabs made up as much as 50% of the catch.

There were significant positive correlations between relative abundance and wind stress in each year. In 2004, positive correlations were observed between relative abundance and winds from the northeast at lags of 0 to −4 d, winds from the southeast at lags of 0 to −1 d, and winds from the south at 0 d lag (Fig. 3). This pattern reflected a shift from downwelling to onshore winds that occurred just prior to the day of maximum settlement during each of the 4 high relative abundance events in September (Fig. 2). Relative abundance in 2005 was positively correlated with winds from the northeast at lags of −1 to −2 d, again suggesting a relationship between coastal downwelling and high relative estuarine abundance (Fig. 3). In 2006, there

Table 1. Time-series analyses between physical data. Lags represent the number of days temperature or water level data followed (negative values) or preceded (positive value) wind and tide data. Correlation coefficients (r) are given for significant comparisons (p < 0.05). Data analyzed are alongshelf (Along; 15° axis) and across-shelf (Across; 105° axis) wind stress, maximum daily tide range (Tide), water level anomaly at slack water after flood (Level), and water temperature at slack water after flood (Temp). ns: not significant

| Comparison | 2004 | | 2005 | | 2006 | |
|---|---|---|---|---|---|---|
| | Lag (d) | r | Lag (d) | r | Lag (d) | r |
| Along vs. Temp | ns | ns | 0 | −0.282 | ns | ns |
| | | | −1 | −0.242 | | |
| Across vs. Temp | 0 | −0.475 | 0 | −0.365 | 0 | −0.297 |
| | −1 | −0.345 | −1 | −0.391 | −1 | −0.377 |
| | −2 | −0.188 | −2 | −0.356 | −2 | −0.215 |
| | | | −3 | −0.299 | | |
| | | | −4 | −0.234 | | |
| Tide vs. Temp | −4 | 0.243 | −1 | 0.229 | ns | ns |
| | | | −2 | 0.298 | | |
| | | | −3 | 0.327 | | |
| | | | −4 | 0.272 | | |
| Along vs. Level | 0 | 0.387 | +1 | 0.319 | 0 | 0.331 |
| | −1 | | −1 | 0.188 | | |
| Across vs. Level | 0 | 0.387 | 0 | 0.303 | 0 | 0.263 |
| | −1 | 0.406 | −1 | 0.309 | −1 | 0.256 |
| | −2 | 0.178 | −2 | 0.309 | −2 | 0.256 |
| | | | −3 | 0.179 | | |
| Level vs. Temp | 0 | −0.289 | 0 | −0.179 | ns | ns |
| | −1 | | −1 | −0.307 | −1 | −0.258 |
| | −2 | | −2 | −0.235 | −2 | −0.202 |
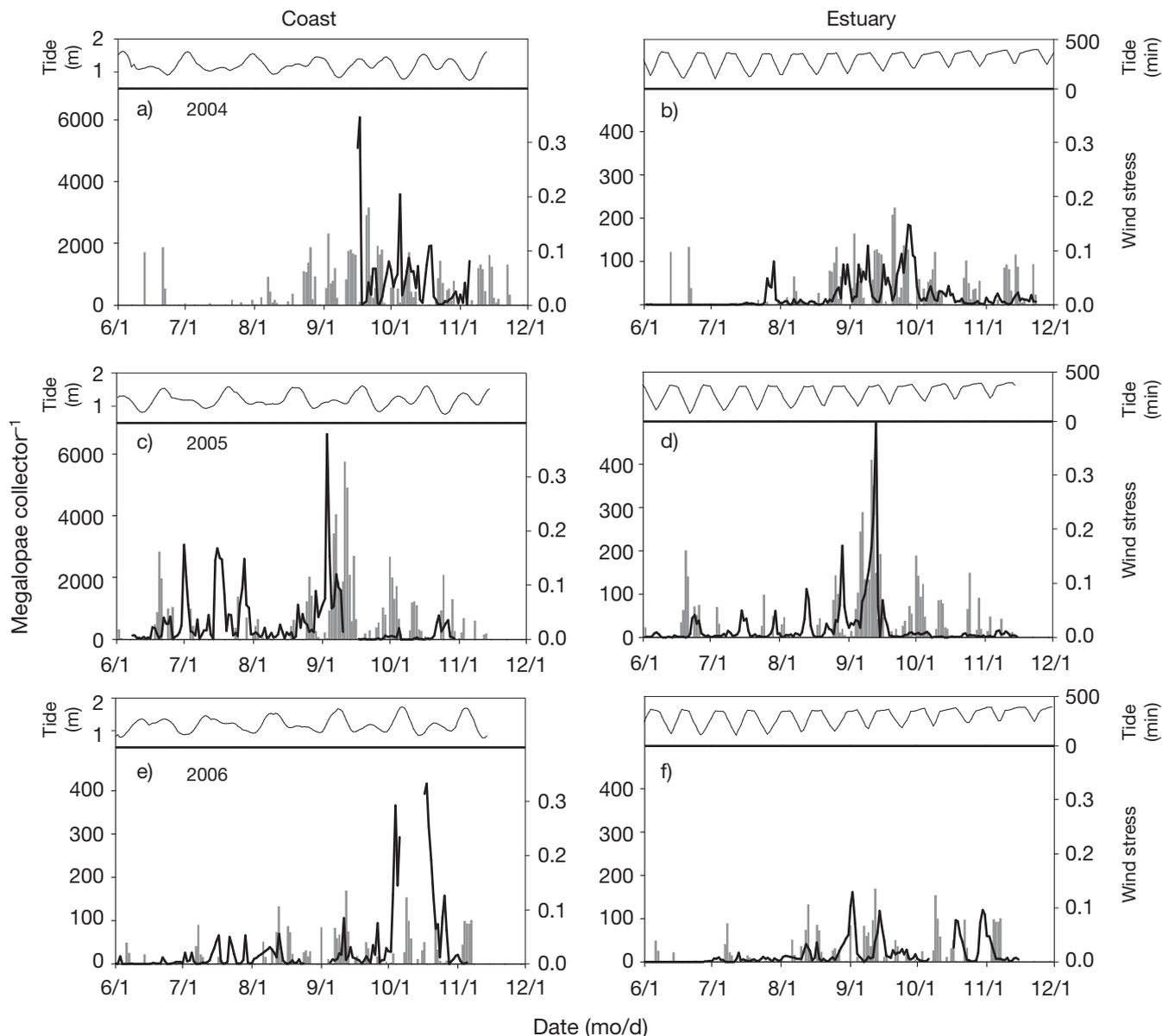
Fig. 2. *Callinectes sapidus*. Time-series of nightly relative megalopal abundance (black line; left axis), wind stress from 45° (gray bars; right axis), and tides (top panel) at the (a,c,e) coastal and (b,d,f) estuarine sites in (a,b) 2004, (c,d) 2005 and (e,f) 2006. Tide data are the maximum daily tidal range in meters (coast) and the duration of nighttime flood tide in minutes (estuary)

Table 2. *Callinectes sapidus*. Mean monthly relative abundance (megalopae collector$^{-1}$ night$^{-1}$) of megalopae at the coastal and estuarine sites. n/s: months not sampled

| Location | Year | Jun | Jul | Aug | Sep | Oct | Nov |
|----------|------|-----|-----|-----|-----|-----|-----|
| **Coast** | 2004 | n/s | n/s | n/s | 1221 | 738 | 410 |
| | 2005 | 223 | 1039 | 323 | 811 | 132 | 296 |
| | 2006 | 8 | 39 | 46 | 67 | 483 | 226 |
| **Estuary** | 2004 | 1 | 29 | 47 | 198 | 47 | 35 |
| | 2005 | 26 | 37 | 88 | 194 | 13 | 20 |
| | 2006 | 1 | 17 | 46 | 102 | 106 | 52 |

were positive correlations between winds from the east and relative abundance at lags of 0 to –2 d (Fig. 3). Winds from the southwest, which would be favorable for coastal upwelling, were negatively correlated with relative abundance in 2004 and 2005. Although the exact relationships between relative abundance and winds differed somewhat from year to year, the wind directions at which significant correlations were detected reflected the directions of the dominant wind events occurring in that year.

The duration of nighttime flood tide was significantly correlated with relative estuarine abundance each

Table 3. *Callinectes sapidus*. Time-series analyses of relative megalopal and juvenile crab (J1) abundance. Lags represent the number of days that data for relative J1 crab abundance (JUV) and the proportion of J1 crabs in the total catch (% JUV) followed relative megalopal abundance data. Correlation coefficients (r) are given for significant comparisons (p < 0.05). ns: not significant

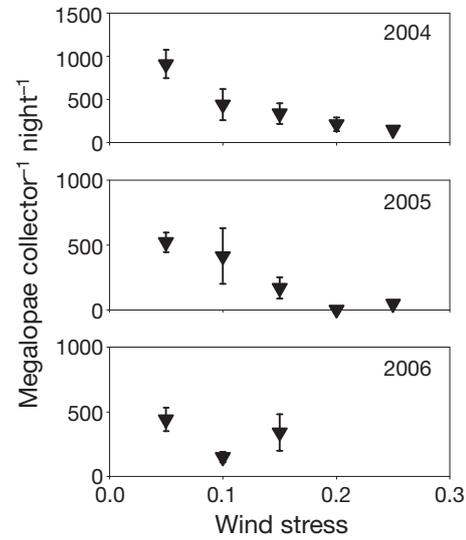| Year | Data | Coast | | Estuary | |
|------|------|-------|------|---------|------|
| | | Lag (d) | r | Lag (d) | r |
| 2005 | JUV | 0 | 0.687 | 0 | 0.579 |
| | | −1 | 0.501 | −1 | 0.489 |
| | | −2 | 0.305 | −2 | 0.403 |
| | | −3 | 0.195 | −3 | 0.630 |
| | | −4 | 0.216 | −4 | 0.601 |
| | | −5 | 0.169 | −5 | 0.594 |
| | % JUV | ns | | −2 | 0.368 |
| | | | | −3 | 0.261 |
| | | | | −4 | 0.249 |
| | | | | −5 | 0.230 |
| 2006 | JUV | 0 | 0.691 | 0 | 0.268 |
| | | −1 | 0.349 | −1 | 0.210 |
| | | −2 | 0.252 | −2 | 0.184 |
| | | −4 | 0.229 | −4 | 0.156 |
| | | −5 | 0.336 | | |
| | % JUV | ns | | −4 | 0.151 |
| | | | | −5 | 0.242 |



Fig. 4. *Callinectes sapidus*. Mean number (±1 SE) of megalopae collector$^{-1}$ night$^{-1}$ at the coast versus wind stress in the across-shore direction (0° axis). Wind stresses were grouped at intervals of 0.05
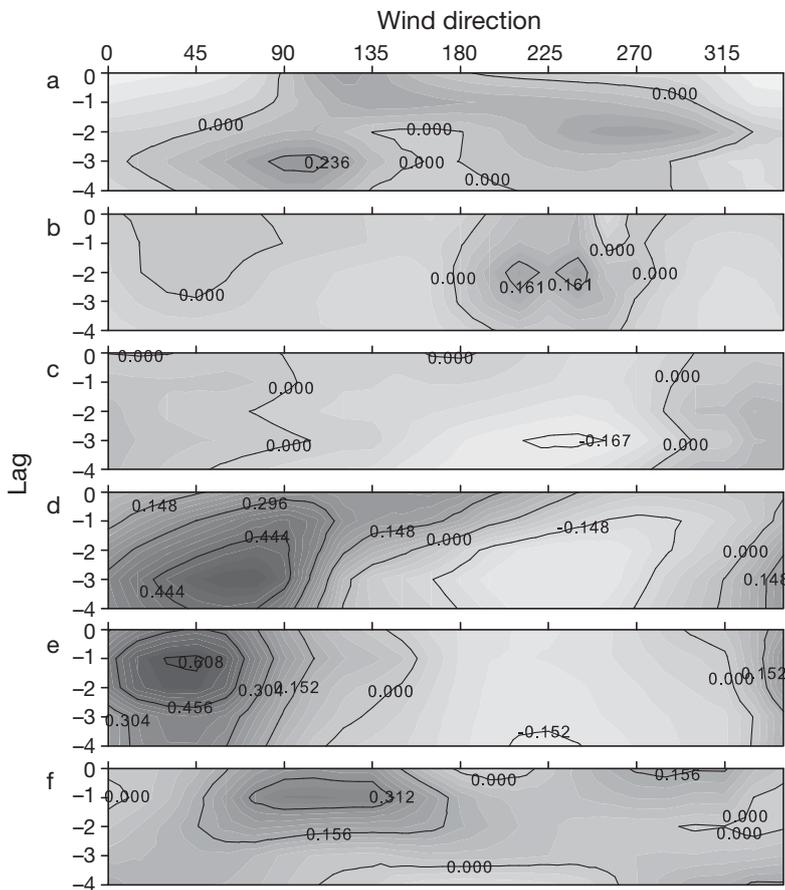


year, explaining 52 to 71% of the variability at periods of 14 to 14.8 d (Fig. 5). In September 2004, a series of 4 ingress events associated with downwelling-favorable winds altered the timing of ingress relative to nighttime flood tides, resulting in high relative abundances 2 to 5 d after the maximum duration of nighttime flood tides (Fig. 5). In 2005 and 2006, relative abundance was positively correlated with the duration of nighttime flood tide at a lag of 0 d, suggesting a close association between the timing of high relative abundance and nighttime flood tides (Fig. 5). Results of the cross-Fourier analysis for 2006 were consistent with those of 2004 and 2005, suggesting that filling the 10 d data gap did not adversely affect the

Fig. 3. Results of cross-correlation analyses between nightly relative megalopal abundance and wind stress at the (a,b,c) coastal and (d,e,f) estuarine sites in (a,d) 2004, (b,e) 2005 and (c,f) 2006. Wind stress was calculated at 15° intervals (0° indicates wind stress from the north). Lags indicate the number of days that relative abundance data followed wind stress data for each correlation. Correlation coefficients (contour plot) greater than the first positive interval or less than the first negative interval are significant (p < 0.05)
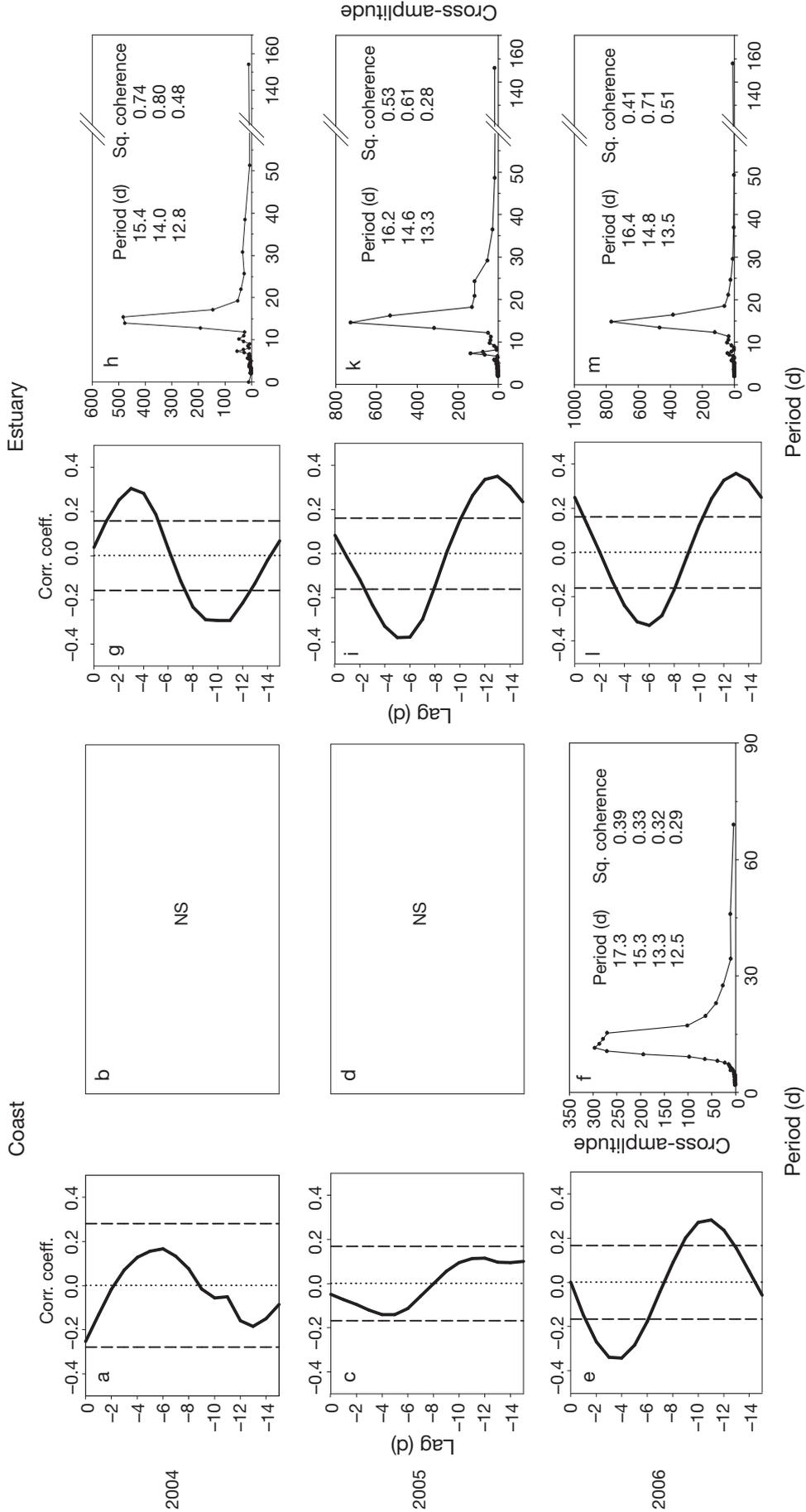
Fig. 5. Statistical comparison between maximum daily tidal range and the nightly relative abundance of megalopae at the 2 sites (a–f) coast and (g–m) estuary in (a,b; g,h) 2004, (c,d; i,k) 2005 and (e,f; l,m) 2006. Panels (a,c,e) and (g,i,l) are results of crosscorrelation analyses. Lags represent the number of days that relative abundance data followed tidal range data. Values outside the 95% CI (dashed lines) are significant. Panels (b,d,f) and (h,k,m) are results of cross-Fourier analyses. For (b) 2004 and (d) 2005 no significant correlations were observed (NS). Values for cross-amplitude, a measure of covariance of tidal range and relative abundance, are plotted and for squared coherence are presented in text. Squared coherence is an estimate of the percentage of variation in settlement at each period due to tidal range

nature of the relationship between relative abundance and the duration of nighttime flood tide. Estuarine ingress events that were not associated with winds from the northeast (e.g. the event of late July 2004) always occurred during nighttime flood tides.

## Hurricanes

Hurricanes passing over or near the study location were usually associated with high relative abundance in the estuary. In 2004, the 4 peaks in relative abundance from late August to early October were associated with 4 hurricanes (Frances, Gaston, Ivan and Jeanne) passing to the south or southwest of the study area resulting in downwelling-favorable winds along the coast (Fig. 2). The highest relative estuarine abundance observed during the study, on 13 September 2005, occurred before Hurricane Ophelia made landfall at Cape Lookout. Similarly, the highest relative abundance in 2006 occurred when Hurricane Ernesto passed just to the west of the study area.

## DISCUSSION

Recruitment of *Callinectes sapidus* postlarvae to US Atlantic and Gulf Coast estuaries has not been definitively associated with hypothesized mechanisms of transport to estuaries. Shoreward transport is primarily thought to occur in surface waters during coastal downwelling (Epifanio & Garvine 2001), but can also occur in frontal zones (Shanks et al. 2000) and possibly by internal waves (Shanks 1988). Estuarine ingress is facilitated by behaviors resulting in nocturnal FTT (Forward et al. 2003). The relative abundance of postlarvae settling on hog's hair collectors, however, has been shown to be related to a variety of wind events (Goodrich et al. 1989, Boylan & Wenner 1993, Blanton et al. 1995, Jones & Epifanio 1995, Mense et al. 1995, Olmi 1995, Rabalais et al. 1995, Morgan et al. 1996) and tidal (or lunar) phases (Olmi et al. 1990, van Montfrans et al. 1990, 1995, Boylan & Wenner 1993, Mense et al. 1995, Metcalf et al. 1995, Olmi 1995, Perry et al. 1995, Rabalais et al. 1995, Morgan et al. 1996, Shanks 1998, Forward et al. 2004) that are not always consistent with hypothesized transport mechanisms. Differences among these studies could be due to the various methods of data analysis used, annual variability or geographical differences in the dominant transport mechanisms.

The present study set out to clarify the relationships between the relative estuarine abundance of *Callinectes sapidus* megalopae and potential mechanisms of transport. Nightly settlement on hog's hair collectors

was monitored at a coastal site (to examine shoreward transport) and an estuarine site (to examine estuarine ingress) from 2004 to 2006. The coastal site was 3 to 4 km west of the inlet to the estuary and the estuarine site was 1.5 km inside the estuary. Data analyses focused on explaining the mechanisms that resulted in the few episodic estuarine ingress events that occurred each year.

Relative abundance at the coast was rarely correlated with environmental variables. Two significant difficulties with correlating relative coastal abundance and environmental variables were: (1) tropical cyclones and strong onshore winds generated waves large enough to break at the collector location and forced removal of collectors for 1 to several days and (2) relative abundance was generally low at high wind stresses (Fig. 4), limiting our ability to detect relationships between wind stress and relative abundance. The latter may have been due to megalopae swimming (and not settling on collectors) in response to turbulence in the water column (Welch et al. 1999), and could explain in part why relationships between wind stress and relative abundance have often not been detected, especially at sites exposed to high wave energy (e.g. Shanks 1998). There was a significant positive relationship between relative abundance and tidal amplitude in 2006, but not in other years. Because of the difficulties described above, we were unable to evaluate hypothesized mechanisms of shoreward transport using the relative coastal abundance data.

Relative estuarine abundance increased following winds from the northeast in 2004 and 2005, supporting the hypothesis that estuarine ingress of *Callinectes sapidus* megalopae occurs during coastal downwelling. Increased estuarine water levels and decreased water temperatures were also consistent with downwelling-induced barotropic flow of coastal water into the estuary during winds from the northeast. Relatively weak correlations between alongshore wind stress and water level ($r \leq 0.387$) were likely due to connections between the Newport River estuary and the Neuse River via Core Creek and Pamlico Sound via Core Sound, which complicate the response of Beaufort Inlet water level to wind forcing (Logan et al. 2000, Blanton et al. 1999b). In 2006, winds from the east were associated with high relative estuarine abundance due to the combination of ingress associated with winds from Hurricane Ernesto and weaker winds from the northeast. Without adequate coastal abundance data it was not possible to determine whether increases in relative abundance during downwelling were due to cross-shelf transport, barotropic inflow or both. Significant correlations between relative estuarine abundance and wind stress from the south and southeast in 2004 also lend support to the hypothesis that onshore

winds result in ingress. Shoreward transport at the surface on the inner shelf (~10 to 30 m) may be driven primarily by onshore winds when waves are small (Tilburg 2003, Fewings et al. 2008). Relative estuarine abundance did not increase following upwelling-favorable winds and was not consistently related to maximum daily tidal range, suggesting that relaxation of upwelling events and surface convergence zones above internal waves were not dominant mechanisms of shoreward transport in our study area.

The complex nature of the shoreline near the Newport River estuary prevented *a priori* identification of the exact wind directions relevant to coastal downwelling and/or upwelling. By correlating relative abundance with unidirectional wind stress calculated at 15° intervals we were able to associate high relative abundance with hypothesized mechanisms of shoreward transport and identify yearly differences in the wind events that resulted in high relative abundance. For these reasons, correlating raw abundance data with unidirectional wind stress from a range of directions may represent a more effective method for relating larval abundance to potential wind-driven transport mechanisms. Reanalysis of earlier studies could provide additional support for wind-driven shoreward transport of *Callinectes sapidus* megalopae.

One unexpected result of the present study was the apparent close relationship between relative estuarine abundance and both the timing and strength of winds during September and October. Off the North Carolina coast, monthly average winds are from the southwest in June and July, variable during a transition period in August, from the northeast during mariner's fall in September and October and from the northwest in November (Weber & Blanton 1980). Downwelling-favorable winds during mariners' fall, which reach a peak around the second week of September based on wave height records (Jahnke et al. 2008), correspond directly to the time of highest relative estuarine abundance. The magnitude of downwelling-favorable wind stress each year and the maximum number of megalopae collected during mariners' fall also appeared to

be related, but additional data are needed to evaluate this hypothesis.

Relative estuarine abundance was positively correlated with the duration of nighttime flood tides, supporting the hypothesis that estuarine ingress is facilitated by nocturnal FTT. The present study is the first to incorporate behaviors associated with FTT directly into statistical analyses of megalopal abundance. By calculating the duration of nighttime flood tides each night we were able to directly relate relative estuarine abundance to the predicted time of maximum estuarine ingress. In 2004, a 2 to 5 d lag in the relationship between the duration of nighttime flood tide and relative estuarine abundance was apparently due to a series of 4 downwelling wind events occurring at intervals approximating the semidiurnal tidal cycle but shifted by several days. Such wind-driven inflow events could be one reason why relative abundance has not always been associated with nighttime flood tides despite the importance of nocturnal FTT during estuarine ingress (e.g. Mense et al. 1995).

We propose a conceptual model to describe the environmental conditions under which estuarine ingress of *Callinectes sapidus* megalopae is most likely to occur (Fig. 6). Downwelling-favorable winds, especially strong winds lasting several days, are highly likely to result in estuarine ingress. Onshore winds also result in ingress, but do not appear to be as important as downwelling-favorable winds. The likelihood of ingress is lower for other wind directions except when winds are associated with hurricanes that pass near enough to increase barotropic inflow. The effect of winds on ingress is modified by tides such that the likelihood of ingress is enhanced during nighttime flood tides and decreased during nighttime ebb tides. The degree to which tides alter wind-driven ingress depends on the relative strengths of wind- and tide-driven water movements in a particular estuary. In the absence of favorable winds, FTT is sufficient for ingress assuming that a supply of megalopae is available near the inlet. This basic model of estuarine ingress can be applied throughout the range of *C.*
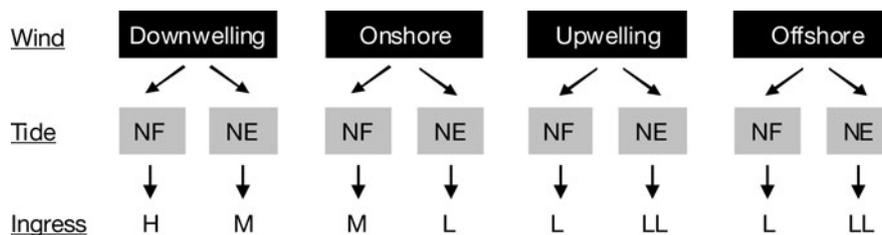


Fig. 6. Conceptual model describing the likelihood of estuarine ingress of megalopae under various environmental conditions. Tides are either nighttime flood tides (NF) or nighttime ebb tides (NE). The likelihood of ingress is indicated as high (H), medium (M), low (L) or very low (LL)

*sapidus* taking into account the orientation of the local shoreline and the relationship between the diel and tidal cycles. It may also be applicable for other species assuming that their behaviors are similar to those of *C. sapidus* megalopae.

Some megalopae may have been retained near the inlet for several days after estuarine ingress events. Megalopae entering the Newport River estuary are primarily in intermolt, but the proportion of premolt megalopae varies (Forward et al. 1996). Because molt-stage is not related to the likelihood of settlement (Hasek & Rabalais 2001), the proportion of J1 crabs in the daily catch can be considered a relative measure of the proportion of premolt megalopae. The proportion (but not the number) of J1 crabs in the estuary peaked 2 to 5 d after high megalopal abundances, suggesting that some megalopae were retained near the inlet for several days after ingress events and entered the estuary at an advanced stage of development.

In summary, we observed high relative estuarine abundances of *Callinectes sapidus* megalopae during coastal downwelling, tropical cyclones, onshore winds and nighttime flood tides. The seasonal pattern of estuarine ingress was related to the seasonal wind pattern, such that most megalopae were collected during a period of downwelling-favorable winds occurring in September and October. Relative coastal abundance was not consistently associated with environmental variables, probably due to behavioral responses to turbulence and our inability to sample during high waves. A conceptual model was proposed describing the likelihood of ingress under various environmental conditions.

## LITERATURE CITED

Blanton J, Wenner E, Werner F, Knott D (1995) Effects of wind-generated coastal currents on the transport of blue crab megalopae on a shallow continental shelf. Bull Mar Sci 57:739–775

Blanton J, Amft J, Luettich RA Jr, Hench JL, Churchill JH (1999a) Tidal and subtidal fluctuations in temperature, salinity and pressure for the winter 1996 larval ingress experiment—Beaufort Inlet, NC. Fish Oceanogr 8:134–152

Blanton J, Werner FE, Kapolnai A, Blanton BO, Knott D, Wenner EL (1999b) Wind-generated transport of fictitious passive larvae into shallow tidal estuaries. Fish Oceanogr 8: 210–223

Bookhout CG, Costlow JD Jr (1977) Larval development of

*Callinectes similis* reared in the laboratory. Bull Mar Sci 27:704–728

Boylan JM, Wenner EL (1993) Settlement of brachyuran megalopae in a South Carolina, USA, estuary. Mar Ecol Prog Ser 97:237–246

Costlow JD, Bookhout CG (1959) The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biol Bull 116:373–396

De Vries MC, Tankersley RA, Forward RB Jr, Kirby-Smith WW, Luettich RA (1994) Abundances of crab megalopae are associated with estuarine tidal hydrologic variables. Mar Biol 118:403–413

Epifanio CE, Garvine RW (2001) Larval transport on the Atlantic continental shelf of North America: a review. Estuar Coast Shelf Sci 52:51–77

Fewings M, Lentz SJ, Fredericks J (2008) Observations of cross-shelf flow driven by cross-shelf winds on the inner continental shelf. J Phys Oceanogr 38:2358–2378

Forward RB Jr, Rittschof D (1994) Photoresponses of crab larvae in offshore and estuarine waters: implications for transport. J Exp Mar Biol Ecol 182:183–192

Forward RB Jr, De Vries MC, Rittschof D, Frankel DAZ, Bischoff JP, Fisher CM, Welch JM (1996) Effects of environmental cues on metamorphosis of the blue crab *Callinectes sapidus.* Mar Ecol Prog Ser 131:165–177

Forward RB Jr, Tankersley RA, Welch JM (2003) Selective tidal-stream transport of the blue crab *Callinectes sapidus*, an overview. Bull Mar Sci 72:347–365

Forward RB Jr, Cohen JH, Irvine RD, Lax JL and others (2004) Settlement of blue crab *Callinectes sapidus* megalopae in a North Carolina estuary. Mar Ecol Prog Ser 269:237–247

Goodrich DM, van Montfrans J, Orth RJ (1989) Blue crab megalopal influx to Chesapeake Bay: evidence for a wind-driven mechanism. Estuar Coast Shelf Sci 29:247–260

Hasek BE, Rabalais NN (2001) A comparison of molt states of blue crab megalopae, *Callinectes sapidus* (Rathbun), sampled with artificial collectors and plankton nets. J Exp Mar Biol Ecol 265:15–27

Jahnke RA, Nelson JR, Richards ME, Robertson CY, Rao AMF, Jahnke DB (2008) Benthic primary productivity on the Georgia midcontinental shelf: benthic flux measurement and high-resolution, continuous *in situ* PAR records. J Geophys Res 113:C08022 doi:10.1029/2008JC004745

Johnson DR (1995) Wind forced surface currents at the entrance to Chesapeake Bay: their effect on blue crab larval dispersal and post-larval recruitment. Bull Mar Sci 57:726–738

Jones MB, Epifanio CE (1995) Settlement of brachyuran megalopae in Delaware Bay: an analysis of time series data. Mar Ecol Prog Ser 125:67–76

Large WG, Pond S (1981) Open ocean momentum flux measurements in moderate to strong winds. J Phys Oceanogr 11:324–336

Little KT, Epifanio CE (1991) Mechanism for the re-invasion of an estuary by two species of brachyuran megalopae. Mar Ecol Prog Ser 68:235–242

Logan DG, Morrison JM, Pietrafesa LJ, Hopkins TS, Churchill J (2000) Physical oceanographic processes affecting inflow/outflow through Beaufort Inlet, North Carolina. J Coast Res 16:1111–1125

Mense DJ, Posey MH, West T, Kincheloe K (1995) Settlement of brachyuran postlarvae along the North Carolina coast. Bull Mar Sci 57:793–806

Metcalf KS, van Montfrans J, Lipcius RN, Orth RJ (1995) Settlement indices for blue crabs megalopae in the York River, Virginia: temporal relationships and statistical efficiency. Bull Mar Sci 57:781–792

Miller JA, Shanks AL (2004) Ocean–estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae. Mar Ecol Prog Ser 271:267–279

Morgan SG, Zimmer-Faust RK, Heck KL Jr, Coen LD (1996) Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply. Mar Ecol Prog Ser 133:73–88

Ogburn MB, Forward RB Jr (2009) Ingress of brachyuran crab post-larvae to the Newport River estuary. Estuar Coast 32: 309–318

Olmi EJ III (1995) Ingress of blue crab megalopae in the York River, Virginia, 1987–1989. Bull Mar Sci 57:753–780

Olmi EJ III, van Montfrans J, Lipcius RN, Orth RJ, Sadler PW (1990) Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. Bull Mar Sci 46:230–243

Pearce AF, Phillips BF (1988) ENSO events, the Leeuwin Current, and larval recruitment of the western rock lobster. ICES J Mar Sci 45:13–21

Perry HM, Eleuterius CK, Trigg CB, Warren JR (1995) Settlement patterns of *Callinectes sapidus* megalopae in Mississippi Sound: 1991, 1992. Bull Mar Sci 57:821–833

Rabalais NN, Burditt FR Jr, Coen LD, Cole BE and others (1995) Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. Bull Mar Sci 57:855–876

Roegner GC, Armstrong DA, Shanks AL (2007) Wind and tidal influences on larval crab recruitment to an Oregon estuary. Mar Ecol Prog Ser 351:177–188

Shanks AL (1988) Further support for the hypothesis that internal waves can transport larvae of invertebrates and fish onshore. Fish Bull 86:703–714

Shanks AL (1998) Abundance of post-larval *Callinectes sapidus*, *Peneaus* spp., *Uca* spp., and *Libinia* spp. collected at an outer coastal site and their cross-shelf transport. Mar Ecol Prog Ser 168:57–69

Shanks AL, Roegner GC (2007) Recruitment limitation in Dungeness crab populations is driven by variation in atmospheric forcing. Ecology 88:1726–1737

Shanks AL, Largier J, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol Oceanogr 45:230–236

Tankersley RA, Welch JM, Forward RB Jr (2002) Settlement times of blue crab (*Callinectes sapidus*) megalopae during flood-tide transport. Mar Biol 141:863–865

Tilburg CE (2003) Across-shelf transport on a continental shelf: Do across-shelf winds matter? J Phys Oceanogr 33: 2675–2688

van Montfrans J, Peery CA, Orth RJ (1990) Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in the York River, Virginia: 1985–1988. Bull Mar Sci 46:214–229

van Montfrans J, Epifanio CE, Knott DM, Lipcius RN and others (1995) Settlement of blue crab postlarvae in western North Atlantic estuaries. Bull Mar Sci 57:834–854

Weber AH, Blanton JO (1980) Monthly mean wind fields for the South Atlantic Bight. J Phys Oceanogr 10:1256–1263

Welch JM, Forward RB Jr, Howd PA (1999) Behavioral responses of blue crab *Callinectes sapidus* postlarvae to turbulence: implications for selective tidal stream transport. Mar Ecol Prog Ser 179:135–143

Wing SR, Largier JL, Botsford LW, Quinn JF (1995) Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol Oceanogr 40:316–329