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Tropical storm and environmental forcing on regional blue crab (*Callinectes sapidus*) settlement

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ABSTRACT

Global climate change is predicted to increase the frequency and magnitude of hurricanes, typhoons and other extreme cyclonic disturbance events, with little known consequences for recruitment dynamics of marine species that rely on wind-driven larval transport to coastal settlement and nursery habitats. We conducted a large-scale settlement study of the blue crab (*Callinectes sapidus*) in the Croatan-Albemarle-Pamlico Estuarine System (CAPES) in North Carolina, the second largest estuary in the US, during a 10-yr period that encompassed 35 tropical storms of varying magnitudes and tracks, to determine the effects of hurricane track, wind speed and direction as well as lunar-associated explanatory variables on spatiotemporal variation in settlement. The results suggest that much of the spatiotemporal variation in blue crab settlement within the CAPES is due to a combination of: (i) stochastic, meteorological events such as the number of tropical storm days during the fall recruitment season (~28% of the monthly variation explained), (ii) the frequency and duration of wind events blowing toward the southwest and, to a lesser degree, (iii) periodic events such as hours of dark flood tide. Tropical storms and hurricanes expand the blue crab nursery capacity of the CAPES. The benefits of hurricane-forcing to megalopal settlement was dependent upon the storm track, with highest settlement events generally associated with 'onshore' storm tracks that made landfall from the ocean and moved inland along a southeasterly/northwesterly path, or 'coastal' storms that followed a path roughly parallel to the coastline and were located <300 km offshore of the coast.

Key words: blue crab, larval dispersal, hurricanes, recruitment, settlement, tropical storms

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INTRODUCTION

Extreme variation in recruitment of many finfish and invertebrate fisheries (Caddy and Gulland, 1983; Sissenwine, 1984; Hare and Able, 2007) often masks the effects of overexploitation, thereby hampering management efforts (Ludwig *et al.*, 1993). The need to understand seemingly chaotic fluctuations in population sizes of animals and plants fuels efforts to identify the relative roles of intertwined external forcing and internal feedbacks on population dynamics (May, 1981; Higgins *et al.*, 1997; Cowen *et al.*, 2000; Hare and Able, 2007 and references therein). External environmental forcing has been linked to fluctuations in fish and invertebrate distribution and abundance patterns through several mechanisms, including change in decadal-scale temperatures influencing spawning and recruitment success, and change in wind regimes and subsequent oceanographic currents determining successful delivery of larvae to coastal nursery habitats (Ma, 2005; Criales *et al.*, 2006; Hare and Able, 2007 and references therein). One implication of global climate change is the predicted increasing frequency and magnitude of hurricanes, typhoons and other extreme cyclonic disturbance events (Webster *et al.*, 2005), with little known consequences for recruitment dynamics of marine species that rely on wind-driven larval transport to coastal settlement and nursery habitats.

The blue crab *Callinectes sapidus* supports the world's largest fishery for crabs (Lipcius and Eggleston, 2001) and represents North Carolina's most valuable commercial fishery (NC Blue Crab FMP 2004). Blue crab population size and commercial landings are declining in many areas throughout the East and Gulf

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coasts of the USA (Lipcius *et al.*, 2007). In this study, we use results from a 10-yr recruitment study of blue crab conducted in the Croatan-Albemarle-Pamlico Estuarine System (CAPES) to assess the effects of hurricane track, wind speed and direction, as well as lunar-associated explanatory variables, on spatiotemporal variation in megalopal settlement, to test hypotheses (elaborated below) about environmental influences, especially tropical storm forcing, on large scale blue crab settlement success.

Blue crab

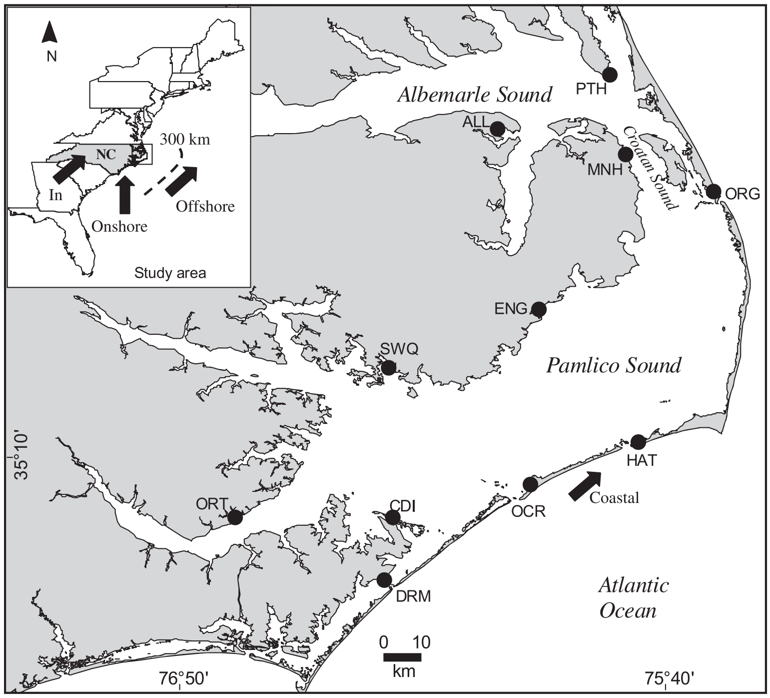
Like many marine invertebrates, the blue crab has a complex life cycle. Estuarine-dependent females migrate to estuary mouths to spawn such that larvae are advected seaward to high salinity continental shelf waters (Provenzano *et al.*, 1983). Larval development proceeds through a series of seven to eight zoeal (larval) stages over ~30 days, followed by metamorphosis to the post-larval or megalopal stage (Van Engel, 1958). Blue crab megalopae are likely transported shoreward by wind-driven Ekman circulation and into estuaries by means of barotropic flow moving in from the shelf (reviewed by Epifanio, 2007). Post-larval influx into Chesapeake Bay, USA, and Pamlico Sound, NC, USA, is correlated with wind speed and direction (Goodrich *et al.*, 1989; Mense *et al.*, 1995), whereas post-larval influx in the Newport River near Beaufort Inlet, NC, was not correlated with cross-shelf or along-shore wind speed; rather, settlement occurred with semi-lunar periodicity with highest settlement at the times of neap tides during quarter phases of the moon and increased with hours of dark flood tides (Forward *et al.*, 2004). The proposed explanation for the Newport river example was that (i) megalopae undergo flood tide transport for entrance into estuaries and up-estuary movement, and (ii) the behavior underlying flood tide transport is most effective when all the nocturnal flood tide occurs in darkness (Forward *et al.*, 2004). Blue crab megalopae may also use a combination of flood-tide currents and wind-driven currents in micro-tidal estuaries such as Pamlico Sound to reach shallow settlement habitats (Reyns *et al.*, 2007). Once within the estuary, blue crabs settle in beds of submerged aquatic habitat (e.g., seagrass or other complex habitats) where they undergo metamorphosis to the first benthic instar (J1) (Heck and Thoman, 1981; Orth and van Montfrans, 1987; Etherington and Eggleston, 2000). It is generally accepted that juveniles remain in these habitats until they reach the fifth to seventh instar (J5–7) stage and begin to migrate benthically into non-vegetated habitats (Orth and van Montfrans, 1987; Pile *et al.*, 1996). However, recent research in Pamlico Sound demonstrates that recently settled early juvenile blue crabs exhibit pelagic emigration (Etherington and Eggleston, 2000, 2003; Blackmon and Eggleston, 2001; Reyns *et al.*, 2007). This pelagic emigration is predominantly undertaken by the first juvenile stages and is density-dependent (Reyns and Eggleston, 2004).

The blue crab exhibits considerable variation in abundance between different regions along the Atlantic and Gulf coasts of the USA, as well as over time (Lipcius and Van Engel, 1990; van Montfrans *et al.*, 1995). This variation in abundance is particularly evident in North Carolina, where average annual population abundance can vary 20-fold between successive years or between local regions within a year (Eggleston *et al.*, 2004). Variable recruitment may be due to varying spawning stock biomass (Higgins *et al.*, 1997; Lipcius and Stockhausen, 2002), physical transport (Roughgarden *et al.*, 1988; Eggleston *et al.*, 1998), and survival of settled individuals in nursery habitats (Eggleston and Armstrong, 1995; Pile *et al.*, 1996). For the blue crab in NC, although recruitment dynamics of early juvenile blue crabs can be strongly density-dependent at the local scale, the population size of early juvenile blue crabs at the scale of Pamlico Sound appears to be limited by post-larval recruitment when overall population size is relatively low (Etherington and Eggleston, 2003; Eggleston *et al.*, 2004). Approximately 30% of the variation in blue crab settlement can be explained by variation in spawning stock biomass (Eggleston *et al.*, 2004). Moreover, megalopal settlement has been correlated with blue crab landings 2 yr later (Forward *et al.*, 2004). Thus, in North Carolina, recruitment dynamics of early juvenile blue crabs, and possibly adults, appears to depend upon spawning stock biomass in a given year and subsequent recruitment of post-larval blue crabs. Spatiotemporal variation in abundance of juvenile and adult crabs may be due, in part, to settlement patterns by postlarvae.

Study site

CAPES is the largest lagoonal system and second largest estuarine system (after Chesapeake Bay) in the USA (Fig. 1). The vast shallow waters of this system and its tributaries serve as nursery and adult habitat for numerous estuarine-dependent species, and support North Carolina's annual $1 billion fishing industry. Extensive seagrass beds line the sound-side of the barrier island chain and serve as primary nursery habitats for newly settled and early juvenile blue crabs (Etherington and Eggleston, 2000, 2003). The western

Figure 1. Map of Croatan-Albemarle-Pamlico Estuarine System (CAPES) in NC, USA. Post-larval collector sampling stations were located at Alligator River (ALL), Point Harbor (PTH), Manns Harbor (MNH), Oregon Inlet (ORG), Engelhard (ENG), Hatteras Inlet (HAT), Ocracoke Inlet (OCR), Swanquarter (SWQ), Oriental (ORT), Cedar Island (CDI) and Drum Inlet (DRM). Wind data were obtained from the National Weather Service Station at Cape Hatteras. Inset shows North Carolina (and study area) relative to the East Coast of the USA. Filled arrows illustrate storm track categories: (i) 'In' refers to 'inland' storms tracked west of central North Carolina, (ii) 'Onshore' refers to storms that made landfall from the ocean approximately perpendicular to the North Carolina coast, (iii) 'Offshore' refers to storms tracked greater than 300 km offshore, and (iv) 'Coastal' refers to storms tracked approximately parallel to coast and east of Central North Carolina to 300 km offshore.



and northern shores of the estuary contain complex vegetated and shallow detrital habitats that function as alternative juvenile nurseries (Etherington and Eggleston, 2000, 2003). The CAPES is separated from the ocean by a chain of barrier islands known as the 'Outer Banks'. There are three major inlets in this island chain that serve as sources of coastal water and larvae spawned offshore: Oregon Inlet, Hatteras Inlet, and Ocracoke Inlet (Fig. 1), as well as one smaller inlet, Drum Inlet, to the south, which connects Core Sound with the Atlantic Ocean. The entire CAPES system is relatively shallow, with a mean depth of 4 m and a maximum depth of 7 m. Circulation is dominated by wind-driven currents and freshwater input (Pietrafesa and Janowitz, 1988; Lin, 1992). Thermal stratification, salinity variations, astronomical tides and salt intrusions do not affect overall circulation significantly (Pietrafesa and Janowitz, 1988; Lin, 1992). Tidal phase in and around Pamlico Sound inlets are generally semi-diurnal, with tidal ranges of 60–130 cm (Pietrafesa *et al.*, 1986). Tidal range is negligible along the western shore of Pamlico Sound.

The winds over Pamlico Sound are highly variable over a broad energy spectrum, with significant peaks at daily, weekly, seasonal and interannual periods (Weisberg and Pietrafesa, 1983). In general, winds blowing towards the southwest characterize winter conditions, and winds towards the northeast characterize summer conditions; both of these wind fields occur during fall and spring transitions. These winds derive from synoptic scale frontal systems that transverse the region. Moreover, seasonal cyclonic storms are an important component of the climatology. During the mid-summer through fall, tropical storms or hurricanes have passed within 300 km of the North Carolina coast at a frequency of over three per year since 1996 (see below). Over the past 100 yr, more severe storms have struck the US Atlantic coast than anywhere else on Earth, with North Carolina second only to Florida in the number of storms that have made landfall (http://www.nhc.noaa.gov). This large-scale, exogenous forcing by tropical storms likely has a significant role in annual recruitment variation of megalopal blue crabs, but has not been tested.

Due to the shallow nature of the estuary, Pamlico Sound water level sets up/down with the onset of persistent winds within 4–6 h (Giese *et al.* 1985; Pietrafesa *et al.*, 1986; Pietrafesa and Janowitz, 1988). Of crucial interest to fishery and habitat managers are hydrodynamic model predictions of no to extremely low larval or post-larval recruitment to Albemarle Sound, which relies on inlets to the south for oceanic input (Xie and Eggleston, 1999). Albemarle Sound is one of the most productive fishery water bodies in North Carolina, accounting for an average of ~25% of the state's annual blue crab landings (Eggleston *et al.*, 2004). Model results show that when the wind is favorable for enhanced recruitment of larvae via enhanced inflow through inlets, these same winds induce an unfavorable pressure gradient in the CAPES, driving the flow within the CAPES south and away from Albemarle Sound (Xie and Eggleston, 1999). This southward flow would hinder the transport of larvae or postlarvae into Albemarle Sound. This prediction is consistent with the observed paucity of early juvenile stages of estuarine-dependent fish species in Albemarle Sound (Ross and Epperly, 1985). Nevertheless, the latter observation may also be associated with relatively low salinities (5–6 ppt) observed in this estuary, or low post-settlement survival. Recent evidence indicates that the time-to-metamorphosis from the megalopa to first benthic instar for blue crabs is approximately 3.5 days, whether salinity is 10 or 35 ppt (R. Forward and M. DeVries, Duke University Marine Lab., unpublished data).

According to hydrodynamic model predictions, winds blowing towards the southwest are favorable for post-larval transport through Oregon, Hatteras and Ocracoke Inlets, with subsequent delivery to expansive seagrass habitats on the sound side of these inlets. Water containing blue crab postlarvae is transported to the western parts of the CAPES during floods associated with intense extra-tropical or tropical cyclones (herein 'storms') that approach from the south during late summer and early fall, producing strong winds blowing towards the northeast (Xie and Eggleston, 1999). Thus, tropical storms approaching from the south may be the only events that transport significant numbers of estuarine-dependent larvae into Albemarle Sound. Despite strong circumstantial evidence and hydrodynamic model predictions for limited or non-existent larval and post-larval recruitment to Albemarle Sound, as well as enhanced larval and post-larval delivery along the western shore of Pamlico Sound during tropical storm events, these hypotheses remain untested.

In this study, we quantified daily settlement of blue crab postlarvae at 4–10 sites located throughout the CAPES over a 10-yr period to characterize spatio-temporal variation in settlement patterns. We tested the following hypotheses: (***H1***) monthly post-larval settlement of megalopal stage blue crabs to the CAPES will increase with the number of days that contain tropical storms or hurricanes during the recruitment season, (***H2***) settlement will be positively correlated with northeasterly wind speed and (***H3***) hours of dark flood tide, and (***H4***) settlement will be highest during the first quarter of the lunar phase under relatively dark conditions than later lunar phases. We also tested the hypotheses that (***H5***) settlement will be higher during fall than spring, and that (***H6***) there will be relatively low to no settlement in Croatan and Albemarle Sounds compared to Pamlico Sound based on hydrodynamic larval dispersal modeling predictions.

METHODS

Settlement study

During 1996–2005, blue crab settlement was measured at 4–10 sites spanning the entire length–width axes of Pamlico Sound (Fig. 1; Table 1). Three sampling stations were located along the 'eastern inlets' of the Outer Banks: Oregon Inlet, Hatteras Inlet, and Ocracoke Inlet (Fig. 1). Stations at Oregon and Hatteras Inlets were located at US Coast Guard facilities, which are approximately 3–4 km NNW and NE of the inlets, respectively. The Ocracoke station was located on the northwest shore of Ocracoke Island, and was located 4 km N of the inlet. Three sampling stations, Manns Harbor, Point Harbor and Alligator River, were approximately 20, 40 and 80 km NNW, respectively, of Oregon Inlet (Fig. 1). These stations are herein referred to as 'northern shore' stations. Two stations were established along the 'western shore' of Pamlico Sound at Engelhard and Swanquarter (Fig. 1). Engelhard is located 45 km SSW of Oregon Inlet, and 40 km WNW of Hatteras Inlet (Fig. 1). Swanquarter is located 60 km WNW of Hatteras and Ocracoke Inlets (Fig. 1). Finally, two stations were established along the 'southern shore' of Pamlico Sound at Oriental and Cedar Island (Fig. 1). Oriental is located near the mouth of the Neuse River and is located 60 km WSW of Ocracoke Inlet (Fig. 1). The Cedar Island station was located on the northern shore of 'West Bay', and is located 25 km WSW of Ocracoke Inlet (Fig. 1). Water depths at these

Table 1. Summary of post-larval blue crab settlement stations sampled within the CAPES during the fall recruitment period of 1996–2005.

		Blue crab settlement stations sampled by region										
		East				North			West		South	
Year	Sampling interval	ORG	HAT	OCR	DRM	ALL	PTH	MNH	ENG	SWQ	CDI	ORT
1996	1 Aug.–31 Oct.	X	X	X			X	X	X	X	X	X
1997	1 Aug.–31 Oct.	X	X	X			X	X	X	X	X	X
1998	1 Aug.–31 Oct.	X	X	X	X		X	X	X	X		
1999	1 Aug.–31 Oct.	X	X	X	X			X	X			
2000	1 Sept.–31 Oct.	X	X					X	X			
2001	1 Aug.–31 Oct.	X	X					X	X			
2002	1 Aug.–31 Oct.	X	X					X	X			
2003	1 Aug.–16 Sept.	X	X					X	X			
2004	1 Aug.–31 Oct.	X	X					X	X			
2005	1 Aug.–31 Oct.	X	X			X		X	X			

ORG, Oregon Inlet; HAT, Hatteras Inlet; OCR, Ocracoke Inlet; DRM, Drum Inlet; ALL, Alligator River; PTH, Point Harbor; MNH, Manns Harbor; ENG, Engelhard; SWQ, Swanquarter; CDI, Cedar Island; ORT, Oriental.

locations ranged from 1.5 to 3 m. Two sites were removed from the sampling protocol in 1998 (Oriental and Cedar Island) based on consistently low to no post-larval settlement, and one site was added to the sampling scheme (Drum Inlet) to improve spatial coverage within the southern portion of the system. One site (Alligator River) was sampled only in 2005 as an additional test of recruitment limitation north of Oregon Inlet. A core set of seven sites spanning the Inlet and Sound regions were sampled consistently during 1996–99. During 2000–2005, the number of core sampling stations was reduced from eight to four because settlement at certain stations during 1996–1999 was consistently non-existent or very sparse (see Results below), and because we wanted to consolidate sampling effort more efficiently to replicate inlet stations: Oregon and Hatteras, and replicate inshore stations: Manns Harbor and Engelhard (Fig. 1; Table 1). These four sites were selected from a total of nine sites that we originally sampled for megalopal settlement in 1996 because they provide a good estimate of the number of postlarvae entering the sound (inlet sites), as well as the number of megalopae that cross Pamlico Sound and reach western Sound sites (Etherington and Eggleston, 2003). Moreover, pelagic concentrations of megalopal and first benthic stage blue crabs in Pamlico Sound are positively correlated with blue crab settlement at Oregon and Hatteras Inlets, suggesting that settlement at Oregon and Hatteras Inlets provides a good proxy for megalopal influx to Pamlico Sound (Reyns *et al.*, 2007).

Sampling methodology

Standardized cylindrical artificial settlement substrates (van Montfrans *et al.*, 1995) were deployed daily (except where noted) from August 1 to October 31, 1996–2005. Substrates were constructed from 16.3 cm diameter × 7.5 cm length polyvinyl chloride (PVC) pipes covered by sleeves of 'hogs-hair' air-conditioning filter material (surface area = 0.26 m^2). The substrates were suspended below the surface of the water from docks, and deployed for a 24-h period. A total of three substrates were deployed from a dock at each location. Three to four substrates are necessary to stabilize the variance in settlement magnitude and accurately assess settlement patterns (Metcalf *et al.*, 1995). Substrates were sampled at a consistent time during the day (typically 1500–1600 h) by lifting the entire substrate into a 19-L bucket. Sleeves were then removed and replaced with rinsed, air-dried sleeves before redeployment of the substrates. Samples were processed by rinsing sleeves in freshwater and sieving the rinse water (van Montfrans *et al.*, 1990). Organisms were preserved in 70% ethanol and enumerated in the laboratory. *Callinectes sapidus* megalopae were distinguished from *Callinectes similis* using criteria established by Stuck and Perry (1982). These settlement substrates have been used extensively along the Atlantic and Gulf coasts of the USA to measure the relative magnitude of post-larval supply in blue crab settlement studies (e.g., van Montfrans *et al.*, 1995; Forward *et al.*, 2004). In addition to sampling blue crab settlement during the anticipated peak fall recruitment period for blue crabs in NC (1 August–31 October each year), we quantified settlement during spring of 2000 (8 April–4 June) at Oregon Inlet, and spring of 2004 (24 April–20 June) at Hatteras Inlet to test the general assumption that fall represents the primary blue crab post-larval settlement season in NC (e.g., Mense *et al.*, 1995; van Montfrans *et al.*, 1995).

Data analyses

The response variable, the average number of megalopae substrate^{-1} day^{-1} per site, was calculated for each 24-h period. During our study, sampling was abruptly terminated prior to 31 October in certain locations and years due to local evacuation and destruction by hurricanes. For example, daily sampling ceased at Swanquarter after early September in 1996 due to Hurricane Fran, and after early September in 2003 at Hatteras Inlet due to Hurricane Isabel. However, generally gaps in sampling did not exceed 3 days. Blue crabs remain in the post-larval stage for about 3–5 days (Wolcott and De Vries, 1994); therefore, to account for the accumulation of postlarvae on days not sampled, daily post-larval abundance was estimated by averaging the number of postlarvae collected on the day sampling resumed, over the total number of sampling days missed within a 5-day period. We examined how variation in blue crab settlement over time varied according to environmental factors such as wind speed and direction, and hours of dark flood tide with time series analyses (see below). The relationship between megalopal settlement and environmental factors was examined only for data collected at Oregon and Hatteras Inlets because settlement was too episodic at inshore stations for time series analyses, and because these inlets were consistently sampled from 1996 to 2005. We examined the relationship between spatial variation in settlement and the timing and track of named tropical storms and hurricanes for all sites and years (see below).

Tides, sunrise–sunset, and moon phase information were obtained from the WWW Tide and Current Predictor (http://tbone.biol.sc.edu/tide/sites_useastlower.html) and used to compute hours of dark flood tide and lunar phase for Hatteras and Oregon Inlets (http://tidesandcurrents.noaa.gov/). Storm data were obtained from the National Weather Service Atlantic Hurricane Archives (http://weather.terrapin.com/hurricane/index.jsp) and from notes taken during field sampling. Storm days were defined as the period when a named hurricane or tropical storm might have the greatest effect on winds and weather in North Carolina. This time was set as the period when the storm center was within a box bounded by 30–40° north latitude and 75–80° west longitude, which can influence water levels in Pamlico Sound (Lin 1992). Wind speed and direction data for Cape Hatteras was obtained from the NOAA National Weather Service (made available by State Climate Office of North Carolina at North Carolina State University).

Cross-correlation analyses were used to determine if settlement of blue crab postlarvae to Oregon and Hatteras Inlets was spatially synchronous, and to investigate the relationship between mean daily settlement at each inlet and daily-averaged wind speed, and hours of dark flood-tide. Wind data were averaged into daily records before being decomposed into several components: u (east–west), v (north–south), and the principal axes of variance where velocity fluctuations are at a maximum and minimum along the major and minor axes, respectively (Emery and Thomson, 2001). Prior to analyses, settlement records were $\log(x + 1)$-transformed to equalize variances, and detrended. To detrend the data, an autocorrelation function (ACF) was first used to identify cyclical patterns in post-larval settlement and temporal dependence in settlement pulses (Jassby and Powell, 1990). We then fit autoregressive, moving average (ARMA) models to the post-larval, wind, and hours of dark flood tide time series to remove periodicity and autocorrelation, and to reduce each series to white noise (randomness) (Dunstan, 1993). Model residuals that passed a Chi-squared test for white noise were used in the cross-correlations. We computed cross-correlations for lags of ±5 days; positive lags for correlations between settlement and environmental components represent the number of days blue crab settlement peaked after these events.

A two-way ANOVA was used to examine the effects of location (Oregon Inlet, Hatteras Inlet) and lunar quarter (1 = lunar days 27–4; 2 = lunar days 5–11; 3 = lunar days 12–19; 4 = lunar days 20–26) on mean settlement. These divisions of the lunar cycle accurately account for the amount of illumination and variation in tidal currents that megalopae would encounter (Mense *et al.*, 1995). Daily mean megalopae/settlement substrate values were normalized to the total number of megalopae collected that year. To generate the dependent variable, daily settlement values were averaged over each of the lunar phases within each month of each of the years. When necessary, crab settlement was log-transformed to normalize variances. Significant interaction effects were interpreted with Ryan's Q multiple comparison tests and lower-level ANOVA models. Lastly, for sites sampled all 10 yr (two inshore stations: Manns Harbor and Engelhard; two inlet stations: Oregon and Hatteras

Inlets), linear least-squares regression models examined the relationship between the number of settlement peaks (considered here as those exceeding twice the annual mean value within a site within a year; *sensu* van Montfrans *et al.*, 1995) at a given sampling site or region (Inlets versus Inshore), and the number of storm days.

RESULTS

During 1996–2005, settlement of blue crab megalopae in Pamlico Sound was highly episodic at a given sampling station within a year (Figs 2 and 3), often several orders of magnitude higher near inlets than inshore stations (except during certain hurricane tracks) (Figs 2 and 3), and up to several orders of magnitude higher during fall than spring (compare Figs 2 and 3 with Fig. 4). Of the annual megalopal influx to four sites that were consistently sampled from 1996 to 2005 (ORG, HAT, MNH, ENG), approximately 78% of the influx was associated with episodic settlement peaks (peak = 2× the annual mean) (Fig. 5); the number of settlement peaks was highest in September (160), followed by August (62) and October (45).

Spatiotemporal variation in settlement

Tropical storms

During this 10-yr study there were a total of 35 named tropical storms, 28 of which were hurricanes (Table 2). The frequency of named tropical storms ranged from 0 in 1997, which was an El Niño year, to eight in 2004. The largest number of storm days occurred during September (47 days), followed by August (29 days), and October (15 days) (Table 2). Thus, there was a wide range of monthly and annual tropical storm frequency, as well as varying storm tracks, with which to assess the effects of this large-scale forcing on blue crab estuarine settlement patterns. Of the annual settlement peaks at a given site during 1996–2005, a total of 65–85% were associated with named tropical storms or hurricanes (e.g., Fig. 5). There was a positive and statistically significant relationship between the number of tropical storm days within a given month, and the total monthly mean settlement at ORG, HAT, MNH, and ENG (Fig. 6).

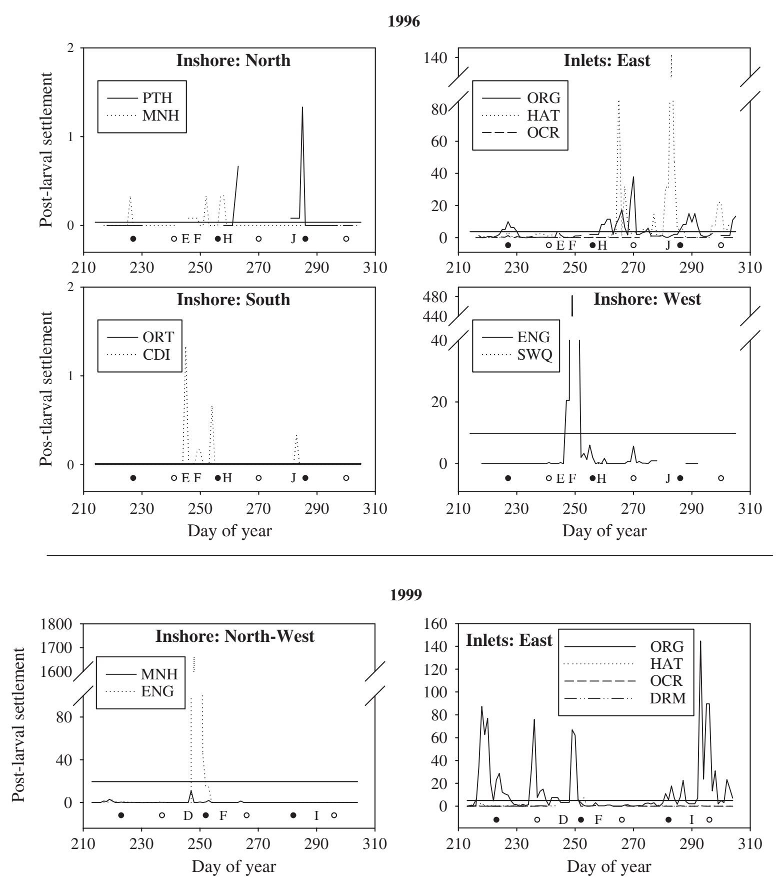


Figure 2. Blue crab post-larval settlement (average number collector^{-1} day^{-1}) by northern, eastern, southern and western regions within the CAPES during August–October 1996, as well as inshore and inlet regions in 1999. These years were chosen to illustrate settlement patterns during years of intense hurricane activity (see Table 2). PTH, Point Harbor; MNH, Manns Harbor; ORG, Oregon Inlet; HAT, Hatteras Inlet; OCR, Ocracoke Inlet; ORT, Oriental; CDI, Cedar Island; ENG, Engelhard; SWQ, Swanquarter. For 1996, E, Hurricane Edouard; F, Hurricane Fran; H, Hurricane Hortense; and J, tropical storm Josephine. For 1999, D, Hurricane Dennis; F, Hurricane Floyd; and I, Hurricane Irene. The thin horizontal line represents mean regional settlement over the sampling interval, while filled and open circles represent new and full moons, respectively. Note changes in scale of *y*-axis by region.

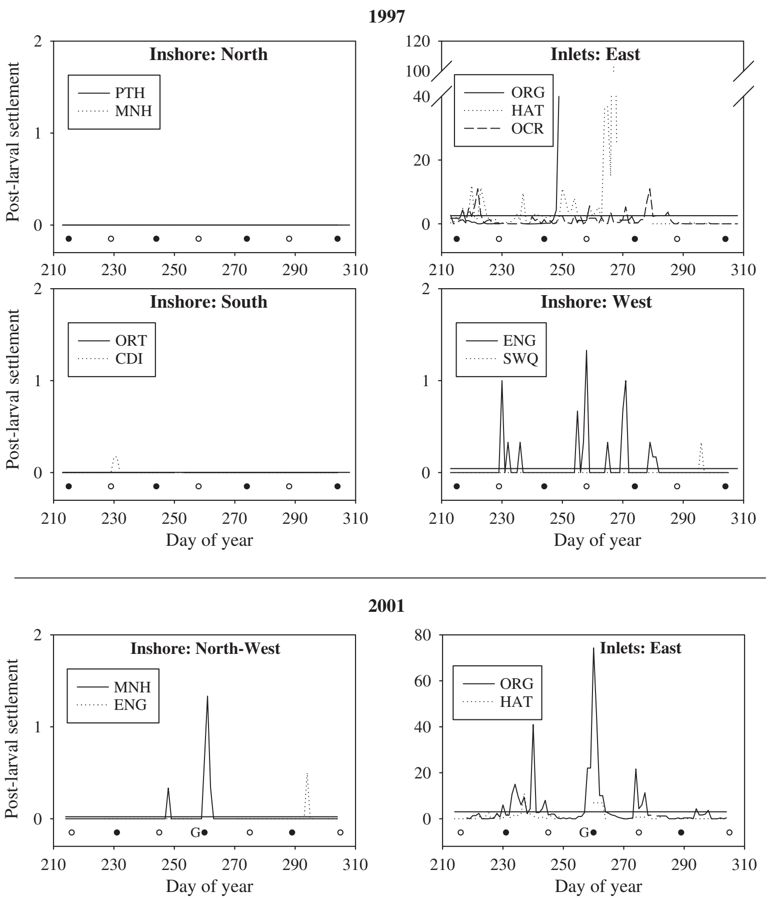
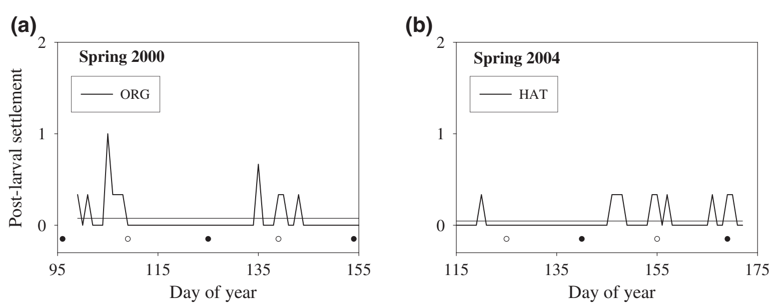


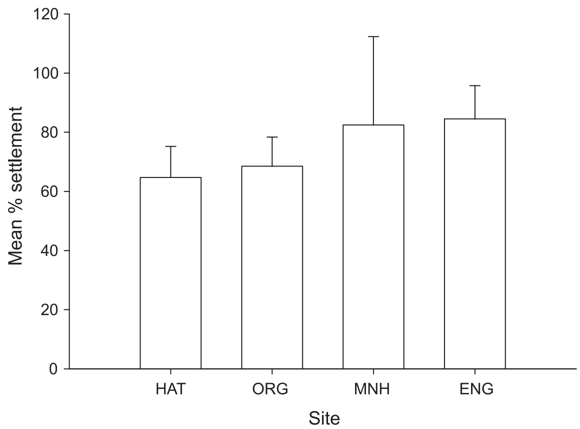
Figure 3. Blue crab post-larval settlement (average number collector^{-1} day^{-1}) by northern, eastern, southern and western regions within the CAPES during August–October 1997, as well as eastern and western regions in 2001. These years were chosen to illustrate settlement patterns during years of no storms (1997) to low numbers of storms (one in 2001). Sampling station abbreviations are the same as in Fig. 2. The thin horizontal line represents mean regional settlement over the sampling interval, while filled and open circles represent new and full moons, respectively. G, Hurricane Gabrielle in 2001. Note changes in scale of *y*-axis by region.

Figure 4. Blue crab post-larval settlement (average number collector^{-1} day^{-1}) at eastern inlet sites during spring 2000 and 2004. During 2000 (panel A), sampling was conducted from 8 April to 4 June at Oregon Inlet (ORG). During 2004 (panel B), sampling was conducted from 24 April to 20 June at Hatteras Inlet (HAT). The thin horizontal line represents mean settlement over the sampling interval, while filled and open circles represent new and full moons, respectively. Note changes in scale of *x*-axis by year.



The path of a hurricane's track, as illustrated on Fig. 1, influenced the number of settlement peaks at a given location, such that there was little to no blue crab megalopal settlement at inshore stations unless there was a tropical storm of a certain track. For example, along the western shore of Pamlico Sound at Engelhard, the highest percentage of settlement peaks (42%) were associated with 'onshore' storm tracks that made landfall from the ocean and moved inland along a southeasterly/northwesterly path, followed by 'coastal' storms that followed a path roughly parallel to the coastline and were located <300 km offshore of the coast (32% of peaks) (Fig. 7). The most striking examples of this pattern of high blue crab settlement

Figure 5. Mean percentage (+1 SD) of annual settlement occurring as peaks (i.e., two times the mean settlement) as opposed to non-peak days. Data represent means over 10 yr at each sampling station.



to Engelhard occurred when major hurricanes tracked onshore in 1996 (Fran), 1999 (Floyd/Dennis) and 2003 (Isabel). For example, mean settlement at western region stations ranged from 0 to 1 megalopae substrate^{-1} day^{-1} during low storm years (1997 and 2001), to 480–1700 megalopae substrate^{-1} day^{-1} during years with intense, onshore hurricanes (compare Figs 2 and 3). The lowest percentage of settlement peaks at Engelhard was associated with either 'offshore' storms that stayed >300 km offshore (4% of peaks), or 'inland' storms that tracked in a northerly path that was completely inland and located >300 km inshore of the coast (22% of peaks), as well as during 1997 (compare Figs 2 and 3). Along the western shore of Pamlico Sound at Manns Harbor, the highest percentages of settlement were also associated with 'offshore' (40%), 'onshore' (30%) and 'coastal' (25%) storms, with the lowest percentage of peaks associated with 'inland' storms (15%) (Fig. 7). Thus, a high percentage of settlement peaks at inshore sampling stations (e.g., ENG, MNH) were associated with onshore and coastal storms. Conversely, the lowest percentage of settlement peaks at the inlet stations were associated with onshore storms (6% of the peaks at ORG and 0% of the peaks at HAT), whereas a relatively high percentage of settlement peaks for the inlet stations were associated with offshore (38% of peaks at ORG and 41% of peaks at HAT) and coastal storms (39% of peaks at ORG and 44% of peaks at HAT), with offshore storms having little effect on settlement peaks at the inshore Engelhard site. Relatively low blue crab settlement at inlet stations during onshore storms suggests that these storms may force coastal water into Pamlico Sound so rapidly that megalopae are swept past inlet settlement areas and transported to more inshore habitats.

Recruitment limitation and settlement hotspots

In the absence of tropical storms, blue crab settlement north of Oregon Inlet during 1996–1998 was essentially non-existent, despite relatively high settlement at Oregon Inlet (compare 'Inlets: East' with 'Inshore: North' on Figs 2 and 3). Similarly, no megalopae or early juvenile blue crabs were detected in 2005 on artificial settlement substrates in the Alligator River, which was our northernmost station (Fig. 1). There was also little to no settlement during 1996–1998 at Cedar Island and Oriental in southern Pamlico Sound, and Swanquarter in western Pamlico Sound, irrespective of storm activity (Figs 2 and 3). During 1997 at Engelhard, minimal settlement was observed in the absence of tropical storms. Thus, in the absence of tropical storms, blue crab megalopae do not appear to disperse throughout the CAPES (this study), rather they appear to disperse via secondary dispersal as J1 stage crabs (Etherington and Eggleston, 2000, 2003; Reyns *et al.*, 2006, 2007).

Relative settlement and spatial coherence

During 1996, mean settlement at Oregon and Hatteras Inlets did not differ significantly from each other, but settlement at both were significantly higher than that observed at Ocracoke Inlet (one-way ANOVA; df = 5, 472, F = 14.25, P < 0.001, Ryan's Q multiple comparisons test; Fig. 2). Similarly, during 1997, mean settlement did not differ between Oregon and Hatteras Inlets, but settlement at Hatteras Inlet was significantly higher than at Ocracoke Inlet (one-way ANOVA; P < 0.001, Ryan's Q test; Fig. 3). When blue crab settlement at all the major inlets connecting Pamlico Sound and the Atlantic Ocean were sampled (ORG, HAT, OCR, DRM) in 1998, mean settlement varied significantly by inlet (one-way ANOVA; df = 3, 358, F = 42.3, P < 0.001), and was higher at Oregon Inlet than in the other inlets (Ryan's Q multiple comparisons test). Thus, mean settlement at Oregon and Hatteras inlets appears similar, and both were higher than mean settlement at Ocracoke Inlet.

Results of cross-correlation analyses between post-larval settlement at Oregon Inlet and Hatteras Inlet indicated that they were significantly correlated in 8 of 10 yr, with settlement at Oregon Inlet generally leading that at Hatteras by 0–4 days (Table 3). These results suggest that whatever the physical forcing mechanism influencing blue crab settlement, it appears to affect both Oregon and Hatteras Inlets in a similar manner, and affected Oregon Inlet before

Named storms	Year	Date	Track	No. of storm days
Irene (H)	2005	August 14	Offshore	<0.5
Katrina (H)	2005	August 23–30	Gulf of Mexico	*
Ophelia (H)	2005	September 10–17	Coastal	7.5
Wilma (H)	2005	October 25	Coastal	1
Alex (H)	2004	August 1–4	Coastal	4
Bonnie (H)	2004	August 12	Coastal	1
Charlie (H)	2004	August 14–15	Coastal	2
Frances (H)	2004	September 6–7	Inland	2
Gaston (H)	2004	August 27–31	Coastal	5
Hermine (TS)	2004	August 29–30	Offshore	2
Ivan (H)	2004	September 17–19	Inland	3
Jeanne (H)	2004	September 27	Inland	1
Henri (TS)	2003	September 7–8	Offshore	2
Isabel (H)	2003	September 17–18	Onshore	3
Cristobal (TS)	2002	August 5–8	Offshore	4
Edouard (TS)	2002	September 2–3	Offshore	2
Gustav (H)	2002	September 8–11	Coastal	4
Kyle (H)	2002	October 10–12	Coastal	3
Gabrielle (H)	2001	September 15–18	Offshore	4
Florence (H)	2000	September 11–13	Offshore	3
Gordon (H)	2000	September 18	Coastal	1
Helene (TS)	2000	September 22	Inland	1
Leslie (TS)	2000	October 5–7	Offshore	3
Michael (H)	2000	October 17–19	Offshore	3
Dennis (H)	1999	September 3–5	Onshore	3
Floyd (H)	1999	September 15–16	Coastal	2
Irene (H)	1999	October 17–18	Coastal	2
Bonnie (H)	1998	August 26–29	Coastal	4
Danielle (H)	1998	August 31–September 3	Offshore	4
Earle (H)	1998	September 3–5	Coastal	3
Georges (H)	1998	September 30–October 1	Coastal	2
No Storms	1997			0
Edouard (H)	1996	August 31–September 2	Offshore	3
Fran (H)	1996	September 5–7	Onshore	3
Hortense (H)	1996	September 3	Offshore	1
Josephine (TS)	1996	October 8–9	Coastal	2

*Although its track was not within our defined area of influence, Hurricane Katrina is listed because it was a large storm that influenced weather patterns in coastal North Carolina.

Table 2. Summary of named tropical storms (TS) and hurricanes (H) that moved within 30–40°N latitude and 70–85°W longitude from 1996 to 2005. Storms within this latitude and longitude can impact water levels within Pamlico Sound, NC. Tropical storms and hurricanes generally approach coastal NC from the south, southeast or southwest, and occasionally from the east-southeast ('onshore'). Track categories are : 'inland', tracked west of central North Carolina; 'coastal', tracked approximately parallel to coast east of central North Carolina to 300 km offshore; 'onshore', landfall from the ocean approximately perpendicular to the North Carolina coast; and 'offshore', tracked greater than 300 km offshore. During 1996–2005, there were a total of 35 tropical storms potentially influencing fall blue crab recruitment; of these, 28 were hurricanes.

Hatteras Inlet. The years in which there was no correlation (1996, 2004), or a negative correlation (1999), coincided with the presence of strong, onshore hurricanes, which may have disrupted regional megalopal forcing mechanisms.

During 1998, when all four inlet and four inshore stations were sampled, cross-correlation analyses indicated statistically significant spatial coherence in settlement between certain stations. For example, settlement at Oregon Inlet led settlement at Ocracoke by 1 day, and settlement at Ocracoke Inlet led settlement at Drum Inlet by 2 days (Table 4). From an across-sound perspective, mean settlement at Hatteras and Ocracoke Inlets led settlement at Engelhard and Swanquarter along the western shore of Pamlico Sound by 0–5 days (Table 4).

Temporal variation in settlement

Given that 63–85% of the settlement peaks observed in this study occurred during tropical storm days, we wanted to determine whether other stochastic (winds) or periodic (lunar phase, hours of dark flood-tide)

Figure 6. Relationship between the number of storm days within a given month (see Table 2) and the total monthly settlement (3 months per year) over 10 yr of sampling at four sites (ORG, HAT, ENG, MNH; $N = 30$). One outlier was eliminated (October 1999) because settlement at one site (ENG) was 1–2 orders of magnitude higher than experienced during the 10-yr time series (1996–2005).

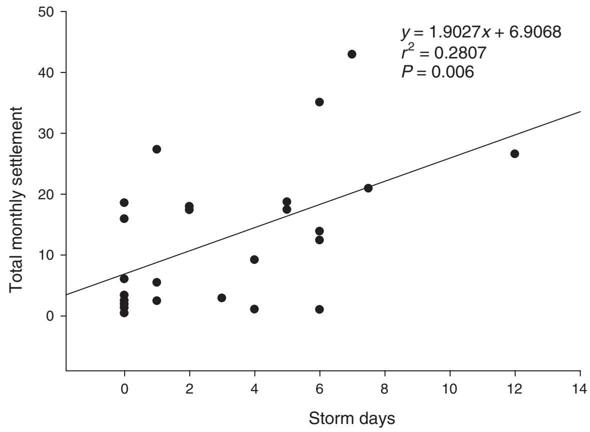
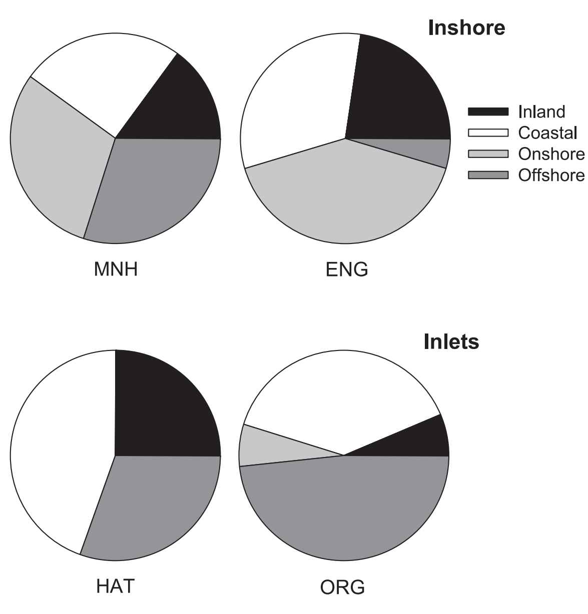


Figure 7. Percentage of storm settlement peaks associated with a given category of storm track during 1996–2005. See Fig. 1 for illustration and description of storm tracks.



factors explained additional variation in blue crab settlement peaks over time. Based on autocorrelation analysis, peaks in blue crab settlement were often temporally autocorrelated for 2–3 days ($P < 0.05$), indicating that pulses in settlement last for several days.

Table 3. Results of cross-correlation analyses between blue crab post-larval settlement at Oregon Inlet and settlement at Hatteras Inlet. Residuals of ARMA models were fit to log(x + 1)-transformed average daily post-larval settlement records from each inlet. Significant ($P < 0.05$) cross-correlation R-values are reported, with days (in parentheses) by which settlement at Oregon Inlet leads (+ values) or lags (− values) settlement at Hatteras Inlet.

Year	Post-larval settlement: Oregon and Hatteras Inlets
1996	ns
1997	0.28 (−1 day)
1998	0.20 (2 days)
1999	−0.21 (0 day)
2000	0.38 (1 day)
2001	0.27 (0 day)
2002	0.18 (4 days)
2003	0.33 (4 days)
2004	ns
2005	0.18 (2 days)

Wind

With the exception of 1999, winds during all years of this study alternated primarily between summer conditions (blowing toward the northeast) and winter conditions (blowing toward the southwest) (Fig. 8). The unusual wind pattern observed in 1999 may have been due to onshore Hurricanes Dennis, Floyd and Irene, which produced strong winds that were aligned primarily along the minor (east–west) axis of prevailing winds (http://www.nhc.noaa.gov).

There was a statistically significant cross-correlation between wind speed along the major axes of wind and daily variation in blue crab megalopal settlement in 6 of 10 yr at Oregon Inlet, and 8 of 10 yr at Hatteras Inlet (Table 5). In all cases but one (ORG in 2004), blue crab settlement was correlated with wind speed blowing toward the southwest, and settlement generally lagged wind speed by 1–3 days (Table 5). For example, at Oregon Inlet in 1998 and Hatteras Inlet in 2002, settlement peaks corresponded to reversals of winds from the southwest to blowing out of the northeast (Oregon Inlet = Days 246–248 and Day 298 on (Fig. 9a); Hatteras Inlet = Days 253–255 on Fig. 9b). In general, daily variation in blue crab settlement at Oregon and Hatteras Inlets was strongly correlated with wind speed blowing toward the southwest (Table 5).

Hours of dark flood tides

The hours of dark flood tide (HDFT) gradually increased during fall as the length of daylight decreased, and were higher during neap than spring

Table 4. Results of cross-correlation analyses between post-larval settlement at settlement stations in 1998 when the largest number of stations were sampled throughout Pamlico Sound. Residuals of ARMA models were fit to log(x + 1)-transformed average daily post-larval settlement records from each site. Significant (P < 0.05) cross-correlation R-values are reported, with days (in parentheses) by which settlement at sites in the row headings lead (+ values) or lag (− values) settlement at sites in the column headings.

	ORG	HAT	OCR	DRM	PTH	MNH	ENG	SWQ
ORG	–	0.20 (2 days)	0.19 (1 day)	−0.22 (0 day)	ns	−0.21 (−4 days)	ns	−0.29 (0 day)
HAT		–	0.31 (5 days)	ns	ns	ns	0.31 (5 days)	0.50 (0 day)
OCR			–	0.27 (2 days)	ns	ns	0.28 (1 day)	0.38 (2 days)
DRM				–	ns	ns	−0.24 (3 days)	0.19 (0 day)
PTH					–	0.66 (4 days)	0.33 (4 days)	ns
MNH						–	0.25 (0 day)	ns
ENG							–	0.36 (5 days)
SWQ								–

ns, Not significant.

tides. The relationship between daily variation in blue crab megalopal settlement and HDFT was weaker than the relationship between settlement and wind, and the pattern was not consistent between inlets. For example, there was a statistically significant cross-correlation between HDFT and daily variation in blue crab megalopal settlement in 4 of 10 yr at both Oregon and Hatteras Inlets; however, only 2 of 4 yr were the same, and not necessarily in the same years (Table 5). Moreover, blue crab settlement was positively correlated with HDFT in 3 of 4 yr at Oregon Inlet, whereas settlement at Hatteras Inlet was negatively correlated with hours of dark flood tide in all four cases (Table 5).

Lunar phase

In this study, mean blue crab settlement was highest during the first and second quarters of the lunar phase; however, the settlement patterns did not vary significantly according to lunar phase or sampling station (two-way ANOVA; lunar phase: df = 3, 198, F = 2.46, P = 0.064; sampling station (ORG, HAT): df = 1, 198, F = 0.068, P = 0.79), nor the interaction effect (P = 0.812).

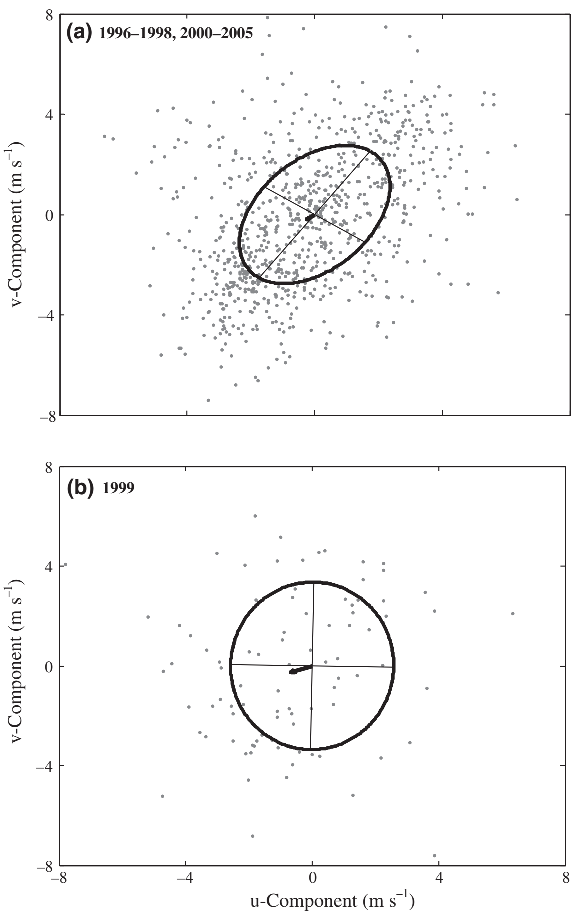
DISCUSSION

Tropical storms and hurricanes exert a strong effect on spatial variation in blue crab settlement, and appear to expand the nursery capacity of the CAPES for the blue crab by transporting megalopal-stage blue crabs across-sound (Etherington and Eggleston, 2000, 2003; Reyns *et al.*, 2006, 2007; this study). The benefits of hurricane-forcing to megalopal settlement is dependent upon the track of a given storm, with the highest recruitment events generally associated with 'onshore' storm tracks that made landfall from the ocean and moved inland along a southeasterly/northwesterly path, or 'coastal' storms that followed a path roughly parallel to the coastline and were located <300 km offshore of the coast. Over the past 100 yr, an average of three hurricanes a year have either made landfall or passed within 210 km of the NC coast during the period when blue crab megalopae are in the water column (http://www.nhc.noaa.gov). The contribution of this seemingly consistent, storm-driven larval transport mechanism to spatiotemporal variation in blue crab population dynamics appears important (Etherington and Eggleston, 2003; this study).

Spatiotemporal variation in settlement

There was consistently low to no blue crab settlement at inshore stations located in the northern (Alligator River, Point Harbor, Manns Harbor; Fig. 1) and southern (Cedar Island, Oriental; Fig. 1) regions of the CAPES. Conversely, inshore stations located along the central to northwest portions of Pamlico Sound, especially Engelhard, consistently displayed the highest settlement of all the inshore stations in this study. A recent biophysical study of blue crab post-larval dispersal in Pamlico Sound found that during wind events blowing toward the southwest, surface currents near Oregon and Hatteras Inlets were almost always directed towards the south–southwest, which would promote dispersal in this same general direction (Reyns *et al.*, 2006, 2007) and away from the northern region of the CAPES (Xie and Eggleston, 1999). The general paucity of blue crab settlement north of Oregon Inlet in this study is consistent with the notion of wind-driven recruitment limitation for Albemarle Sound (Xie and Eggleston, 1999). Tidal currents near Oregon Inlet are aligned along an axis that connects Oregon Inlet with the western sound near Stumpy

Figure 8. Principal axis of variance of daily-averaged wind velocity during the blue crab recruitment season (August–October, 1996–2005). Wind conditions were similar during 1996–1998 and 2000–2005 and were therefore combined to illustrate 'typical' fall wind patterns (a). Wind conditions during 1999 were considered 'non-typical' (b). See text for more details. Points represent u- (east–west) and v- (north–south) components of wind velocities. Major axis is denoted by a line extending along length of ellipse. Positive values denote north and east directions. Arrow represents magnitude of average wind direction.



Point, which is located just north of Engelhard (Reyns *et al.*, 2006, 2007). This alignment of wind-driven and tidal surface currents between Oregon Inlet and Stumpy Point, especially during southwestward winds, apparently enhances the supply of blue crab megalopae and first benthic instars to the northwestern region of Pamlico Sound, where relatively high concentrations of blue crabs were repeatedly observed during plankton cruises (Reyns *et al.*, 2006, 2007). The consistent supply of blue crab megalopae and first benthic instars via this 'Oregon Inlet-Stumpy Point dispersal pathway' may also explain why this region consistently experiences relatively high abundances of later-staged juveniles (Eggleston *et al.*, 2004). Similarly, episodic, storm-driven transport was a critical determinant of blue crab settlement during 1985–1987 in Chesapeake Bay (Goodrich *et al.*, 1989).

The apparent recruitment limitation in the southern region of Pamlico Sound observed in this study was unexpected given the general southwestward flow of currents towards Cedar Island and Oriental. Recruitment limitation in southern Pamlico Sound may be due to: (i) a 'recruitment shadow' (e.g., Roughgarden *et al.*, 1988), whereby the majority of blue crab megalopae settle near inlets and along the northwestern shore of Pamlico Sound, with few remaining to be transported to southern Pamlico Sound; (ii) a density-driven 'return flow' that flows northeastward along the bottom of Pamlico Sound in response to a northeasterly wind-driven set-up of water levels in the south, which might impede megalopal dispersal southwestward (R. Luettich, UNC-CH, pers. comm.), or (iii) both. These hypotheses remain to be tested.

Although the two primary inlets where we quantified blue crab post-larval settlement in this study are east-facing to some degree, slight differences in the orientation of these inlets exist (Oregon Inlet faces east-northeast, and Hatteras Inlet south–southeast, see Fig. 1). A three-dimensional baroclinic circulation model of the CAPES demonstrated how differences in the response of Oregon and Hatteras Inlets to wind forcing in terms of shelf–estuary exchange may result from the respective orientation of these inlets, leading to predictions that larval transport would be greatest through Oregon Inlet during southwestward winds (Xie and Eggleston, 1999). Settlement pulses of blue crab megalopae following southwestward wind events in this study were greater at Oregon Inlet than Hatteras Inlet as predicted, but in only 1 of 3 yr. While differences in the magnitude of settlement pulses at each inlet may reflect different geographical sources of larvae (or blue crab spawning cycles), the fact that we observed a nearly synchronous blue crab supply to Oregon and Hatteras Inlets suggests that temporal variability in post-larval blue crab abundance results, in part, from regional oceanographic processes occurring on the continental shelf, rather than localized processes specific to each inlet. The interaction between southward wind-generated shelf currents and the coastline makes transport into both inlets possible: nearshore currents in the region north of Cape Hatteras (where Oregon Inlet is located within the Middle Atlantic Bight) move southward, and currents south of Cape Hatteras (location of Hatteras Inlet within

Year	Wind and post-larval settlement		HDFT and post-larval settlement	
	Oregon Inlet	Hatteras Inlet	Oregon Inlet	Hatteras Inlet
1996	ns	−0.28 (−3 days)	ns	ns
1997	ns	−0.21 (2 days)	0.34 (−3 days)	−0.19 (2 days)
1998	−0.29 (1 day)	−0.26 (−1 day)	ns	−0.23 (−1 day)
1999	ns	ns	ns	−0.40 (−1 day)
2000	−0.29 (3 days)	ns	ns	ns
2001	−0.28 (2 days)	−0.24 (0 day)	−0.25 (−3 days)	ns
2002	−0.21 (1 day)	−0.37 (3 days)	0.18 (−3 days)	ns
2003	−0.35 (2 days)	−0.33 (0 day)	ns	ns
2004	0.33 (−2 days)	−0.19 (3 days)	ns	−0.19 (3 days)
2005	ns	−0.21 (−1 day)	0.18 (0 day)	ns

Table 5. Results of cross-correlation analyses of residuals of ARMA models fit to environmental variables and log(x + 1)-transformed average daily post-larval settlement. Significant ($P < 0.05$) cross-correlation R-values are reported, with days (in parentheses) by which settlement lags (+ values) or leads (− values) environmental variables. Wind, major axis of daily-averaged wind data, which was blowing from the northeast to southwest for negative R-values, and blowing from the southwest to northeast for positive R-values; HDFT, hours of dark flood tide at each inlet; ns, not significant.

South Atlantic Bight) are pushed towards the southwest (Werner *et al.*, 1999), such that currents are directed into both Oregon and Hatteras Inlets, respectively. Simulation models and settlement studies of blue crab megalopae both north and south of Cape Hatteras support the hypothesis that downwelling favorable (southward) wind events drive across-shelf transport, and that variation in the supply of megalopae to estuaries is a function of variation in winds over the adjacent continental shelf (Epifanio and Garvine, 2001; Epifanio, 2007, this study).

Temporal variation in settlement

The episodic nature of settlement observed in this study is characteristic of *C. sapidus* settlement, as measured with the same standardized approach in estuaries along the East and Gulf coasts of the USA (van Montfrans *et al.*, 1995; Rabalais *et al.*, 1995; Forward *et al.*, 2004; Epifanio, 2007 and references therein), with wind events toward the southwest and corresponding settlement events lasting for several days. Southwestward winds have also been associated with settlement peaks of blue crabs in another study within North Carolina but south of the CAPES (Mense *et al.*, 1995). Such wind events, which parallel the coastline, advect shelf surface water toward the coast (westward) through Ekman transport. This produces a rise (i.e., set-up) in coastal sea-level, downwelling shelf water, and drives a geostrophic alongshore current that flows southward (Blanton *et al.*, 1989). Within Pamlico Sound, southward winds cause a concurrent drop in sea level (i.e., set-down) along the sound-side of the barrier island coast, resulting in a pressure gradient force that drives a rapid current through the inlets (Pietrafesa and Janowitz, 1988). This coastal–estuarine circulation may develop within a day of persistent southwestward wind forcing (Pietrafesa and Janowitz, 1988; Blanton *et al.*, 1989). Southwestward winds are associated with the passage of frontal systems (Epifanio, 2007), and during each year of this study, northeasterly winds occurred ~50% of the time while increasing in frequency from fall to winter months. Previous work in the Chesapeake Bay showed that wind-driven inflow events occur, on average, 10 times during any given blue crab season (fall months) (Goodrich *et al.*, 1989). Therefore, meteorologically forced onshore flow appears to represent a regular feature on the continental shelf that promotes the shoreward movement of organisms in surface waters, rather than a fortuitous transport mechanism (Goodrich *et al.*, 1989; Epifanio, 2007; this study).

With the exception of the unusually large settlement events observed at Engelhard in association with Hurricanes Fran, Floyd and Isabel during this study, the magnitude of daily settlement measured (0–100 megalopae collector^{-1} day^{-1}) was consistent with the range of values observed in other studies along the East Coast of the USA (0–170 megalopae collector^{-1} day^{-1}; van Montfrans *et al.*, 1995). Settlement peaks of *C. sapidus* typically account for 50% or more of the annual settlement at a given site (van Montfrans *et al.*, 1995), and accounted for ~65–85% of the annual settlement in this study. The population-level consequences of episodic settlement peaks may be a reduction in predation- and cannibalism-induced mortality rates (van Montfrans *et al.*, 1995). Settlement and metamorphosis to the benthic stage that is timed to occur synchronously may reduce overall mortality, particularly in unvegetated habitats where predation and emigration rates appears to be linked to settlement density (Pile *et al.*, 1996; Moksnes *et al.*, 1997; Reyns and Eggleston, 2004). Thus, episodic settlement of blue crab megalopae may enhance its overall survival in Pamlico Sound.

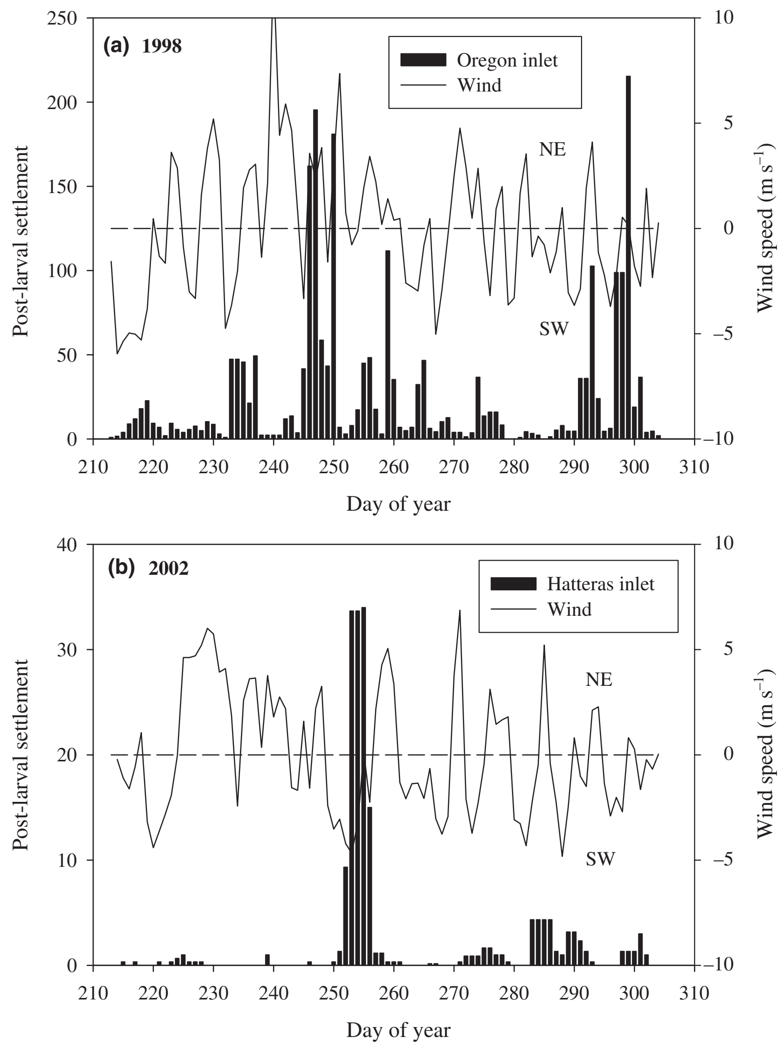


Figure 9. Relationship between post-larval settlement (average number collector day^{-1}) and daily-averaged major axis of wind variance. (a) Representative relationship between Oregon Inlet settlement and wind in 1998. (b) Representative relationship between Hatteras Inlet settlement and wind in 2002. Positive wind speeds indicate winds blowing toward the northeast and negative values indicate winds blowing toward the southwest.

Periodic phenomena may also explain temporal variation in megalopal settlement including the neap–spring tidal cycle (van Montfrans *et al.*, 1990; Forward *et al.*, 2004), equatorial tides (Rabalais *et al.*, 1995), lunar phase (Boylan and Wenner, 1993), residual in-flow at the bottom of an estuary mouth (Forward and Tankersley, 2001), and the timing of larval release from spawning areas (C. Epifanio, University of Delaware, pers. comm.). For example, during 3 of 7 yr in which settlement near Beaufort Inlet, NC, was quantified, there was a semi-lunar periodicity with settlement occurring at the time of neap tides during the quarter phases of the moon, and no relationship between wind forcing and settlement (Forward *et al.*, 2004). One possible reason for the lack of importance between wind forcing and megalopal settlement in the Newport River, NC, compared to inlets located along the Outer Banks of NC (this study), is the orientation of the Newport River relative to predominantly south and southwestward winds that occur during the fall blue crab recruitment season. The orientation of the Newport River and Beaufort Inlet is southward-facing, and winds blowing towards the south or southwest would force water out of the Newport River estuary, possibly inhibiting megalopal ingress into there. However, a more likely explanation is that the Newport River is a strongly tidal system, whereas the tidal signal near Oregon Inlet is greatly diminished within 2.5 km of the inlet, and hydrodynamics near Oregon and Hatteras Inlets are much more responsive to regional-scale wind forcing than tidal forcing (Nichols and Pietrafesa, 1997; Forward *et al.*, 2004).

Although egg-bearing, female blue crabs (sponge crabs) occur on inlet spawning sanctuaries in NC throughout spring, summer and fall (Medici *et al.*, 2006; Eggleston *et al.*, 2009), megalopal settlement at Oregon Inlet was fivefold higher in late summer–early fall than late spring–early summer. Given that a significant spawning stock-recruit relationship for the blue crab in NC (Eggleston *et al.*, 2004) reflects some degree of biological connection between these life stages and is not simply a statistical artifact, these results suggest that (i) the majority of spawning is taking place in August, (ii) similar levels of spawning are occurring throughout the spring–fall period but oceanographic conditions are more favorable to transport megalopae inshore during late summer–early fall, or (iii) both. The mechanism underlying consistently high settlement of blue crab megalopae in Pamlico Sound during early fall as opposed to late spring–early summer is likely due to upwelling-favorable wind conditions (northward winds) that would promote offshore transport during spring–summer spawning periods, and downwelling-favorable winds (southward) that promote onshore transport during fall (Epifanio, 2007). For example, computer simulations of blue crab larval dispersal indicated that unfavorable advection offshore towards the Gulf Stream was more important than biological mortality in determining loss of larvae hatched from the mouth of Delaware Bay (Epifanio and Garvine, 2001).

In conclusion, the generally positive benefits of hurricanes to estuarine blue crab settlement must be tempered by the magnitude of a given hurricane. For example, although Hurricanes Dennis and Floyd in 1999 delivered the highest settlement of blue crab megalopae to Pamlico Sound during our 10-yr study, these megalopae were transported primarily to the western shore of Pamlico Sound, where salinities dropped during this 100- to 500-yr flood event to record lows <5 ppt (Burkholder *et al.*, 2004). Given that (i) blue crab megalopae die in salinities below 10 ppt (D. Eggleston & G. Plaia, unpublished data), (ii) the blue crab population in Pamlico Sound appears recruitment-limited (Etherington and Eggleston, 2003; Eggleston *et al.*, 2004), and (iii) the extremely high settlement observed during 1999 did not lead to relatively high successive year classes (Eggleston *et al.*, 2004), we suggest that extreme freshwater events associated with particularly intense hurricanes may cause mass mortality of megalopae delivered by storm-driven transport. Both the frequency and intensity of hurricanes are expected to increase over the next several decades in the US South Atlantic (Landsea *et al.*, 1999; Webster *et al.*, 2005). Therefore, it is critical that adequate levels of spawning stock be maintained so that recruitment might be enhanced during storm-driven transport. Moreover, nursery areas in settlement 'hot-spots' near inlets and the central/northwestern region of Pamlico Sound must be protected to ensure recruitment success so that the population remains resilient to potential mass mortality of recruits under extreme freshwater inflow events.

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