## SETTLEMENT OF BLUE CRAB (C. SAPIDUS RATHBUN) MEGALOPAE VARIES OVER DISTANCE AND TIME IN ARANSAS-REDFISH BAY, TEXAS

A Thesis by PHILIP FOWLER

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## PHILIP I. FOWLER

This thesis meets the standards for scope and quality of Texas A&M University-Corpus Christi and is hereby approved.

Kim Withers, PhD Chair Blair Sterba-Boatwright, PhD Committee Member

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## ABSTRACT

Blue crab (*Callinectes sapidus* Rathbun) are both a keystone species and an important fishery throughout its U.S. range. Extensive research of the life history and ecology of blue crab has been undertaken. However, limited research into postlarval recruitment dynamics in Texas estuaries has been conducted, providing impetus for this study. To describe the spatiotemporal occurrence and use of the Aransas-Redfish Bay Complex (ARBC), Texas, by blue crab megalopae, settlement was monitored via passive collectors at five sites along the periphery of the complex for 40 weeks (24 h week<sup>-1</sup>) from August 2012 through September 2013. Barometric pressure, flood time, fractional illumination, salinity, water temperature, and wind direction and speed were determined for each sampling period. Regression of a zero-inflated negative binomial model of settlement indicated that date, location, and east-west wind strength were significantly influential on settlement of blue crab megalopae.

Settlement was episodic and varied over time with a majority of settlement, 63.5%, occurring during 2012 sampling dates. Settlement occurred at low levels at all sites from August 2012 through March 2013, becoming confined to the site located within the Aransas Pass from April through August 2013. Peak settlement events (mean count  $\geq 25.2$  day<sup>-1</sup>) were observed in all months of the study except for January, August, and September 2013. Significant differences in mean settlement with distance from the tidal inlet was found with 97% of settlement occurring within 8.2 km of the Aransas Pass tidal inlet and 94% of settlement occurring along the Aransas Ship Channel. The greatest numbers of megalopae were collected within the Aransas Pass, accounting for 71% of

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total megalopae count. Settlement occurred primarily on ESE-SE mean winds between 6-9 m sec<sup>-1</sup>. Peak settlement events coinciding with predominantly SSE-ESE winds, but varied by site, dependent upon wind speed from a given direction.

The results of this study indicate that 1) blue crab megalopal settlement within the ARBC exhibits intra- and interannual variation consistent with related studies; 2) surface currents associated with onshore wind forcing primarily drive blue crab megalopal settlement within the ARBC; and 3) that settlement is secondarily driven by location, with vegetated bottom closer to the Aransas Pass tidal inlet serving as preferential nursery grounds.

# DEDICATION

For my mother, who always encouraged my sense of discovery.

For my wife, who is the bedrock that allows me to pursue my sense of discovery.

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#### **Background & Relevance**

Blue crab (*Callinectes sapidus* Rathbun) are both a keystone species and an important commercial fishery in the United States. Although blue crab populations and fisheries outside of Texas have been extensively researched, most notably along the US Atlantic coast, research pertinent to Texas populations has been limited and primarily confined to bay systems of the upper Texas coast. A more thorough knowledge of its lifecycle in Texas is essential to understanding not only its ecological roles and contributions, but how best to manage exploited populations. Additionally, of the research on Texas blue crabs, little effort has been dedicated to investigating megalopal recruitment dynamics. The overall goal of this study was to investigate the spatial and temporal distributions of blue crab postlarval megalopae in the Aransas-Redfish Bay.

#### **Ecological Importance**

Blue crabs are an essential component of the Gulf of Mexico coastal ecosystem and an economically important marine species. Economic importance, however, is only one facet of the ecosystem services provided by blue crabs. Blue crabs are important in regulating community and trophic structure (Hines 2007). Furthermore, as benthic opportunistic omnivores and detrital scavengers, blue crabs are an important component of nutrient and energy cycling within the systems they reside (Hill et al. 1989; Perry and McIlwain 1986) due to their varied diet (Laughlin 1982; Hill et al. 1989; Hines 2007; Lipcius et al. 2007; Perry and McIlwain 1986). Primary food sources include detritus, infaunal prey such as polychaetes and bivalves, epifaunal prey such as bivalves, gastropods, other crustaceans, including blue crabs, and carrion (Baldwin and Johnson

2009; Hines 2007; Sutton and Wagner 2007). As a result, blue crab foraging can have both direct and indirect affects upon not only trophic linkages, but also community structure. For example, consumption of grazing gastropods help to maintain seagrass and salt marsh integrity through predator release for grazed species (Hines 2007).

Over 60 finfish species prey on blue crabs at various life stages (Sutton and Wagner 2007). In the Gulf Coast region, fish such as the red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*) and sheepshead (*Archosargus probatocephalus*) are a few of the species that feed on blue crabs and are economically important commercial and recreational fishing targets (Perry and McIlwain 1986; Guillory and Prejean 2001). In Chesapeake Bay, blue crabs comprise over 50% of the diet of cobia (*Rachycentron canadum*) (Hines 2007). While finfish comprise the majority of natural blue crab predators, at least 15 species of birds, as well as reptiles and mammals also prey upon blue crab (Hines 2007). The endangered whooping crane (*Grus americana*) is dependent upon blue crab when overwintering along the Gulf of Mexico (GOM)(Greer 2010; Hunt and Slack 1989; Pugesek et al. 2008; Pugesek et al. 2013). Likewise, the Kemp's Ridley sea turtle (*Lepidochelys kempii*) feeds solely upon juvenile blue crabs in the Lower Chesapeake Bay (Hines 2007).

#### **Reproduction and Estuary Reinvasion**

Blue crabs are an estuarine-dependent species that exhibit a bimodal life history: an estuarine juvenile-adult stage and a pelagic larval stage. After their single mating just prior to the terminal molt, inseminated and ovigerous females migrate from low to higher salinity waters close to tidal passes to facilitate egg development and where larvae can escape from estuary via advection on ebb tides (Carr 2004; Epifanio et al. 1984;

Tankersley et al. 1998). Daugherty (1952) reported that, although spawning can occur year round, two peak spawning events occur per year in Texas: March-April and again in July-August. Blue crab larvae exist as pelagic nekton, principally in the surface waters over the shelf, for up to six weeks before reinvading the estuary as megalopae (Lipcius et al. 2007; Tilburg et al. 2007). During the larvae's pelagic existence it will undergo development through 7-8 larval zoeal stages before molting into postlarval megalopae, an intermediate stage between larvae and first crab juvenile (Costlow and Bookhout 1959; Lipcius et al. 1990; Tankersley and Forward 2007; van Montfrans et al. 1990).

Ingress into the bays occurs by passive, advective transport from shelf surface waters to the mouths of tidal inlets (Brookins and Epifanio 1985) whereupon the megalopae undertake predominately nocturnal selective tidal-stream transport (STST) (Epifanio et al. 1984; Forward and Rittschof 1994; Tankersley et al. 1994; Welch and Forward 2001; Tankersley et al. 2002), most often around the new and full moons (Lipcius et al. 1990). Many larval marine organisms use STST (reviewed in Welch and Forward 2001). However, unlike many of these STST-using organisms, blue crab megalopae exhibit negative phototaxis, and do not adhere to a circatidal rhythm of reinvasion and settlement (Luckenbach and Orth 1992; Tankersley and Forward 1994; Welch and Forward 2001; Tankersley et al. 2002). Rather, ingress occurs primarily during nighttime hours that coincide with flood tides, with the greatest ingress occurring when slack flood tides occur shortly after nightfall (Tankersley et al. 2002).

During ebb and slack tides, megalopae remain resting on bottom structure or partially buried in the bottom (Welch and Forward 2001). Increasing salinity during flood tides induces megalopae to return to the water column and engage in active vertical

swimming to get nearer the surface (Tankersley and Forward 1994; Tankersley et al. 1995; Welch and Forward 2001). However, increased salinity alone is not an adequate cue for continuous swimming that would allow them to maintain their vertical position in the water column (Welch and Forward 2001). Increasing turbidity in the upper water column due to increasing flood tide current induces the megalopae to swim continuously, which allows them to maintain their vertical position within the faster surface waters, facilitating advance into the upper estuary (Welch and Forward 2001; Welch et al. 1999). As the flood tide wanes, the corresponding decrease in turbulence and salinity cue the megalopae to discontinue active swimming and to settle to the bottom or other suitable structure where they can shelter from ebb tides thus avoiding extraction from the estuary (Tankersley and Forward 1994; Welch et al. 1999; Welch and Forward 2001). Competent megalopae that have successfully reinvaded the estuary will selectively settle into preferred habitat, predominantly the first available seagrass beds (Orth and van Montfrans 1987; Welch et al. 1997; Williams et al. 1990; van Montfrans et al. 2003) regardless of spatial complexity (Bell et al. 1986), although salt marsh habitats can act as primary nurseries in Texas where seagrass is lacking (Thomas et al. 1990).

#### **Essential Fish Habitat**

Structurally complex habitats with substantial amounts of submerged aquatic vegetation are important to many estuarine-dependent species, including blue crabs, at various points in their life history (Beck et al. 2001; Heck and Thoman 1981; Nañez-James 2009; Neahr et al. 2010; Rozas and Minello 1998). The importance of these habitats is cosmopolitan (Beck at al. 2001), although structural preference (i.e., preference for vegetation type) varies by species, life stage and location. For estuarine-

dependent species, structurally complex habitats are essential because they serve as nurseries for larvae that reinvade the estuary after time offshore, protecting them from predation and supporting their rapid growth into juveniles that subsequently recruit into the local population (Beck et al. 2001; Hines 2007; Rozas and Minello 1998). Submerged aquatic vegetation, such as seagrass and salt marsh, provides adequate food supply and increased structural complexity that affords protection from predation (Heck et al. 2003; Lipcius et al. 2007; Orth et al. 1984; Reese et al. 2008; Rozas and Minello 1998; Stunz and Minello 2001) and the capacity to support higher species densities and taxonomic richness (Beck et al. 2001; Connolly and Hindell 2006; Heck et al. 2003; Orth et al. 1984). Within estuaries of the south-central Texas coast, the highest densities of juvenile spotted seatrout (Cynoscion nebulosus) were found in seagrass compared to nonvegetated bottoms (Neahr et al. 2010; Rozas and Minello 1998). Juvenile southern flounder (Paralichthys lethostigma), red drum (Sciaenops ocellatus) (Brown et al. 2005; Nañez-James 2009; Stunz et al. 2001) and recruiting penaeid shrimp (i.e., *Farfantepenaeus* aztecus, F. duorarum) also prefer vegetated bottoms. Likewise, blue crab megalopae and juveniles are often found in seagrass and marsh habitats at densities greater than they are found in nonvegetated habitats (Heck and Thoman 1981; Heck et al. 2001; Orth and van Montfrans 1987).

#### **Population Dynamics**

In the latest stock assessment of blue crab in Texas waters conducted by the Texas Parks and Wildlife Department, the fishery was judged "senescent" (Sutton and Wagner 2007) and commercial landings continue to decline. Reduced abundance of blue crabs may be due in part to increasing prevalence of the blue crab parasite *Hematodinium* (Lee

and Frischer 2004), which results in up to 50% mortality of infected individuals (Coats 1999). Additional factors contributing to decline include overexploitation, overcapitalization, habitat degradation and fragmentation, reduced freshwater inflow, and bycatch mortality (Jackson et al. 2001; Fogarty and Lipcius 2007; Sutton and Wagner 2007).

Declines may also be due to constraints on recruitment. Mature female blue crab exhibit high fecundity, producing from 700,000 to 6 million eggs in the first brood, dependent on size at maturity, and declines through subsequent broods (Jivoff et al. 2007). Eggs per brood, egg viability and number of broods per season or lifetime are the primary factors affecting fecundity. Additionally, brood production is variable and varies from brood-to-brood and within, as well as with sperm quality and quantity. However, reduction in mean carapace width of mature females has been observed throughout the blue crab's natural range (Abbe 2002; Hammerschmidt et al. 1998; Lipcius and Stockhausen 2002), which limits ovary size and brood size (Jivoff et al. 2007). Thus, an associated decline in individual fecundity could be contributing to a decline in recruiting postlarvae via a negative feedback loop, even though compensatory individual fecundity responses at reduced abundances slow, but do not halt, depensatory fecundity response for blue crab in the Chesapeake Bay region (Lipcius and Stockhausen 2002).

While little is known about pre-settlement mortality of blue crab larvae and postlarvae (Lipcius et al. 2007), post-settlement mortality of megalopal and young juvenile blue crabs has been investigated. Rabalais et al. (1995) showed that mean megalopae settlement into GOM estuaries is an order of magnitude higher than Atlantic estuaries. However, juvenile density did not differ significantly between locations

(Rabalais et al. 1995), indicating that post-settlement mortality is higher in GOM estuaries. Indeed, Heck and Coen (1995) concluded that greater predation rates occur within GOM estuaries and could account for the similar juvenile densities observed throughout the blue crab's range. While both fish and invertebrates prey upon megalopae and young juveniles, post-settlement mortality is primarily a density-dependent function of habitat quality, i.e., related predator release, and size or molt stage (Lipcius et al. 2007), with a majority of mortality occurring via cannibalism (Heck and Coen 1995; Lipcius et al. 2007; Moksnes et al., 1997; Pile et al. 1996; Ruiz et al. 1993). It can be hypothesized that increased post-settlement predation, cohort or otherwise, of megalopae and young juveniles due to habitat degradation and/or changing climate could be a contributing factor in overall population decline throughout the blue crab's range.

## **Objectives**

Blue crab megalopae settlement often occurs at their first encounter of suitable habitat once within the boundaries of the estuary. This study was designed to test the hypothesis that settlement of blue crab megalopae decreased with increasing distance from the Aransas Pass tidal inlet and that settlement would vary over time. Additionally, given that salinity within the Aransas-Redfish Bay complex can remain at or above the salinity requirements of blue crab larvae, it has been hypothesized that *in situ* spawning may be occurring. If so, a detectable signal of equal or greater settlement should be evident at increasing distances form the tidal inlet.

The results of this research will form a foundation by which further studies of megalopal settlement within the Aransas-Redfish Bay complex can be more thoroughly examined. Additionally, it will contribute greatly to knowledge of the life history of blue

crab in Texas because much of the current fishery management of the species based on knowledge of its life history in areas such as Chesapeake Bay in Maryland and Virginia.

#### **Study Area**

The Aransas-Redfish Bay complex (ARBC; Fig. 1) is a shallow (average depth = 3 m) estuary characterized by seagrass-dominated tidal flats interspersed with pockets of nonvegetated bottom and fringed by intertidal *Spartina alterniflora* marsh (Nañez-James et al. 2009). There is a salinity gradient within the complex from the euhaline Aransas Pass tidal inlet to the poly- to mesohaline tertiary Mission Bay (Pollack et al. 2011 & 2012), although within the Aransas-Redfish Bay complex salinity can remain on average  $\geq$  20 (Chen 2010) and near oceanic closer to the Aransas Pass tidal inlet (Pollock et al. 2012).

Blue crab megalopae were collected from five sites along the periphery of the ARBC (Fig. 1). The study area was chosen due to its relationship to the tidal bore that enters the system through the Aransas Pass tidal inlet, along the Aransas ship channel, where it trifurcates into the Lydia Ann, Corpus Christi and Aransas Ship Channels (Fig. 1). The Aransas Ship Channel between Port Aransas, Texas and Aransas Pass, Texas, provides a portion of the tidal bore to the Aransas-Redfish Bay complex and the Intracoastal Waterway (ICW) running along the coast from Ingleside, Texas to Rockport, Texas (Fig. 1). Since a great majority of Texas coastal lands are private property, site selection was made as a result of granted property access.

Site A, located at Palm Harbor RV Park, Rockport, Texas (27.968661°, -97.088586°; Fig. 1), was characterized by a shallow seagrass flat at an approximate depth of 2.5 m and projecting ~3 m from the bulkhead before sloping into the ICW (Fig. 2). Site B, located at Brown Water Marine Services, Ingleside, Texas (27.853039°,



**Fig. 1** Sampling locations. Site A, Palm Harbor RV Park, Rockport, Texas; Site B, Brown Water Marine Service, Ingleside, Texas; Site C, Private residence, Aransas Pass, Texas; Site D, University of Texas Fisheries and Mariculture Laboratory, Port Aransas, Texas; Site E, UTMSI Research Pier, Port Aransas, Texas.



**Fig. 2** Mean percent seagrass cover 2012-2013. Red represents greater mean percent seagrass cover, green represents the least percent seagrass cover and no color indicates no measurable seagrass cover. Source data from Texas Statewide Seagrass Monitoring Program, University of Texas at Austin.

-97.171050°; Fig. 1), did not have visible seagrass flats immediately adjacent to the bulkhead (Fig. 2). Rather, water ~3.5 m deep was immediately accessible at the bulkhead. Spoil islands and seagrass flats were present across the ICW (Fig. 2). Site C was located at a private residential pier (27.879811°, -97.0977°; Fig. 1) projecting ~20 m into the Aransas Ship Channel from its western shore in water ~5 m deep. It was characterized by

a shallow tidal flat extending ~10 m from shore, interspersed with pockets of seagrass (Fig. 2) and fringed with sporadic clusters of *Spartina alterniflora*. Located at the University of Texas Fisheries and Mariculture Laboratory, Port Aransas, Texas (27.839456°, -97.072586°; Fig. 1), Site D was situated in water ~1 m deep over a nonvegetated sand flat interspersed with rock (Fig. 2). Site E (27.838122°, -97.050219°), located at the terminal end of the research pier of the University of Texas Marine Science Institute, Port Aransas, Texas, was situated within the Aransas Pass Channel approximately 40 m from the southern jetty wall in water ~6 m deep. No visible signs of vegetated bottom were apparent.

#### **Materials and Methods**

Blue crab megalopae were collected using a standard "horse/hogs hair" sampling device as described in Metcalf et al. (1995). Traps consisted of polyvinylchloride (PVC) pipe measuring 38.1 cm in height by 15.2 cm in diameter. A 2.5 cm thick covering of HVAC filter medium (American Air Filter, Ontario, CA #385-821-001) encompassed the outside surface providing ~1,819.4 cm<sup>2</sup> of sampling surface area per trap. Unlike Metcalf et al. (1995), only floating, subsurface traps were deployed due to the shallow nature of some of the sites located within the ARBC. Traps were constructed so that the top edge would remain ~10 cm below the surface.

Sampling was conducted for 40 weeks beginning August 2012 proceeding through the end of September 2013. Sampling periods occurred weekly for a single twenty-four hour period except for those falling on holidays that limited site access, prevented retrieval within the time window or where unavailable due to closure. However, sampling of Site B was restricted to 34 weeks due to a lack of access towards the end of the study. Additionally the loss of a single trap at Sites D and E occurred on September 7, 2012 and November 2, 2012, respectively. As such, aggregate count data for those dates and sites were multiplied by 4/3 to account for the missing trap data. Furthermore, the placement of a submerged light in close proximity to a single strap at Site E on October 5 and 19, 2012 resulted in count values that were orders of magnitude higher than the other three traps at the site. As such, the data for that particular replicate trap were excluded and the aggregate count data for that site and date were multiplied by 4/3. That trap was then relocated to a position away from the possible influence of the submerged light. All sampling locations were accessed on foot.

Four traps were deployed at each site for a total of n=20 samples per sampling period day and n=800 samples over the 40 week sampling period (n=680 for Site B). Traps were deployed and retrieved at approximately 1500 GMT ( $\pm$  1 hr) and within a three-hour window ending at approximately 1800 GMT ( $\pm$  1 hr). Sample media were processed and specimens retrieved as described in Metcalf et al. (1995). Recovered specimens were placed into 25% formalin for 24 hours, rinsed with freshwater, drained, and placed into 45% isopropyl alcohol post-fixation. Identifiable specimens were enumerated and classified appropriately as blue crab megalopae or lesser blue crab (*C. similis*) megalopae as described in Ogburn (2011). First crab stages of blue crab were counted as megalopae since it was presumed that they had settled onto the traps as premolt megalopae (Forward et al. 2004; Tankersley 2002). Sample counts were aggregated per site as individual trap independence was lacking due to having to deploy the traps in tethered pairs and of insufficient distance from one another.

Salinity (PSU) and water temperature (°C) were manually measured at each sampling site during retrieval. Barometric pressure (BP; hPa), wind speed (m s<sup>-1</sup>) and wind direction (degrees) data were retrieved from the National Data Buoy Center's monitoring buoy Station 42020 (LLNR 1330) located approximately 111 km SSE of Corpus Christi, Texas. Wind direction and wind speed means for each 24 h sampling period were calculated and then converted to north-south (NS) and east-west (EW) wind vectors. Wind direction cannot be used in linear statistical models since these models would not treat 0° and 359° as nearly identical wind directions. Lunar fractional illumination data was retrieved from the US Naval Observatories' Astronomical Applications Department. Flood time (FTM; minutes) was calculated using data from

Texas Coastal Ocean Observation Network's (TCOON) monitoring station DNR ID 009, located within the Corpus Christi Ship Channel (27.839750, -97.072740) approximately 35 m from the bulkhead at Site D, as the amount of time traps were deployed between slack before flood tide and slack before ebb tide.

#### **Statistical Analysis**

Because the count data of blue crab megalopae consisted of 65% zeros, development of a zero-inflated model was chosen to mitigate estimation bias and to account for overdispersion as a result of excess zeros, which are in excess of the number of zeros expected from a Poisson distribution. Zero-inflated models are mixture models composed of a binomial regression model that predicts occurrences of zeros, while a simultaneous Poisson or negative binomial regression predicts occurrences of count frequencies. Comparisons by AICc of a full zero-inflated Poisson (ZIP) and full zeroinflated negative binomial (ZINB) models showed that a ZINB model of settlement was superior to a ZIP model. Logistic regression of a full binomial presence-absence model was used to elucidate the most important factors contributing to the excess zeros as a starting model for the inflation portion of a ZINB model. Additionally, comparisons of the available identity link functions of the binomial model were made to determine the best function to implement within the ZINB model, finding that a Complementary Log-Log (cloglog) identity link function was superior to either a logit or probit identity link function. An initial ZINB model formula consisting of a full count model (number of megalopae as explained by site, T, salinity, BP, FI, FTM, date, NS and EW) and inflation model derived from the aforementioned logistic regression was constructed (number of megalopae as explained by site, date, BP, T and EW). Model simplifications were made

using marginal ANOVA backwards regression ( $\alpha = 0.05$ ), resulting in a final,

parsimonious model. Appropriate post-hoc analysis was undertaken as necessary.

#### Results

## **Abiotic Conditions**

Salinity varied by site (Fig. 3), ranging from 22-41 (mean = 35.2, sd = 2.6). Sites closest to the tidal inlet (Sites D and E) exhibited the least variability, likely due to the proximity to the more consistently stable GOM, while sites farthest from the tidal inlet exhibited larger variability around the mean (Fig. 3). Hypersaline conditions were observed at all sites, although the highest salinities and greatest frequencies of hypersalinity occurred at sites farthest from the tidal inlet (Sites A and B). Maximum salinity of 41 was observed at Site A on August 17, 2012 and again at Site B on December 21, 2012.

Water temperature ranged from 14-34 °C (mean = 25.4 °C, sd = 5.2 °C). Water temperatures for all sites were high relative to the mean from August to early November 2012 and again from May to September 2013 (Fig. 3). Variation of water temparature was rather consistant with respect to the mean across all sites. Maximum water temperature of 34 °C was observed at Site A, August 9, 2013.

Barometric pressure (BP) ranged from 1006.496 to1026.904 hPa (mean = 1015.432 hPa, sd = 4.566 hPa). Maximum BP was observed December 21, 2012. Minimum BP was observed February 22, 2013.

Flood time (FTM) ranged from 312-1074 minutes (mean = 706.2 minutes, sd = 176.4 minutes). Maximum FTM was observed September 21, 2012. Minimum was observed February 22, 2013.

Mean Fractional Illumination (FI) was 0.476 (~ first quarter/last quarter lunar phases) in a range of 0-1. Sampling during full (FI = 1) and new (FI = 0) lunar phases



**Fig. 3** Salinity and water temperature (°C) by site, August 17, 2012 – September 27, 2013. Dashed lines = mean salinity/water temperature. Salinity range = 22-41 PSU; water temperature range = 14-34 °C.

occurred five times, respectively. No sampling events occurred on dates of absolute first or last quarter lunar phases (FI = 0.5).

Mean wind direction and speed ranged from  $62.2-303.3^{\circ}$  and  $2.3-12.4 \text{ m sec}^{-1}$ , respectively. Mean wind direction was from the SSE (139.7°; sd = 42.1°). Mean wind speed was 6.3 m sec<sup>-1</sup> (sd = 2.0 m sec<sup>-1</sup>). East-West wind strength (EW) ranged from -10.9-8.0 (mean = 3.2; sd = 3.6). North-South wind strength (NS) ranged from -7.9-6.192 (mean = -3.4; sd = 3.0).

## **General Settlement**

Blue crab megalopae settlement varied by site and exhibited episodic pulses of peak settlement (Fig. 4). Mean settlement ranged from  $0.471\pm1.619$  to  $42.875\pm90.337$  (mean±1 SD) megalopae per site (Table 1). Settlement was primarily confined to Sites C and E. Site B exhibited the lowest settlement, while Site E exhibited the highest (Table 1), accounting for 71.1% of total megalopae count; 41.7% of all settlement events (n=28); and contributing 28.6% to the overall mean megalopae count.

#### ZINB Model Summary

No significant relationship of barometric pressure, fractional illumination, flood time, North-South wind strength, salinity or water temperature with blue crab megalopae settlement was evident. Of the remaining available predictors of settlement, only date (P= 1.42e-10), EW (East-West wind strength; P = 0.0128) and site (P = 6.29e-15) were significant predictors of count (Table 2); date was the only significant predictor of excess zeros (P = 0.0787; Table 2). However, the borderline significance of date in the inflation component of the model indicates that it may be a proxy for an unmeasured predictor of settlement that varies over time, i.e., precipitation. Goodness-of-fit was determined via visual rootogram analysis and as can be seen in Figure 5 the model predicts zero counts substantially well. Prediction of count bins  $\geq$  1, however, varies; count bins of 1, 5 and 6 tend to be overestimated, while other non-zero count bins tend to be underestimated.

The probability of observing presence or true absence of blue crab megalopae was predicated upon date, site and EW (Table 2). Significant differences in settlement by site indicate that settlement was dependent upon distance from the tidal inlet. However, the



**Fig. 4** Blue crab megalopae settlement on four passive collectors August 17, 2012 to September 27, 2013. Count values are absolute. Mean site count indicated by dashed horizontal line.

Site					
	А	В	С	D	Е
Mean	1.425	0.471	14.225	2.225	42.875
SD	4.904	1.619	43.469	6.463	90.337
Min (Median) Max	0 (0) 28	0 (0) 8	0 (0) 193	0 (0) 36	0 (4) 349

**Table 1** Descriptive statistics of Blue crab megalopae settlement on four passive collectors August 17,2012 to September 27, 2013.

log(# of megalopae) as explained by site, date, and EW					
	Estimate	Std. Error	z value	Pr(>   z  )	
(Intercept)	3.7206	0.3631	10.247	< 2.00E-16	
site A	-3.9935	0.5584	-7.152	8.58E-13	
site B	-5.4294	0.654	-8.301	< 2.00E-16	
site C	-2.2222	0.5362	-4.144	3.41E-05	
site D	-4.1515	0.5845	-7.103	1.22E-12	
date	-1.4195	0.2213	-6.414	1.42E-10	
ew	0.6216	0.2498	2.489	0.0128	
Zero-inflation model coefficients (binomial with cloglog link):					
(Intercept)	-2.2771	1.2364	-1.84177	0.0655	
date	0.8536	0.4854	1.758	0.0787	

**Table 2** Final ZINB summary. Reference site level = Site E.



**Fig. 5** Rootogram of ZINB model goodness-of-fit. Red line is expected model counts. Bars are binned counts. Count values not reaching 0 square root frequency overestimate bin count; values exceeding 0 square root Frequency underestimate bin count.

affect of distance on settlement covaried with the date of sampling, with a decreasing probability of observing settlement at any particular site over the course of the study (Table 2). Likewise, the effect of distance on settlement covaried with EW, with an increasing probability of observing settlement with increasing East-West wind strength (Table 2).

The probability of observing zero megalopae was predicated on sampling date (P = 0.0787), with the probability of predicting overall absence increasing over time, regardless of site or source of zeros (Fig. 6). Likewise, the probability of observing excess zeros (false absence) increased over time from 2.6% at the start of the study to 33.5% at the end of the study (Fig 6), regardless of site, indicating that distance was not an important factor in determining the probability of observing excess zeros. The probability of observing true zeros (true absence), however, typically increased over time before decreasing in late spring or early summer, dependent upon site, with varying levels of maximum probability that did not return to their baseline probabilities (Fig. 6). Collectively, as can be seen in Figure 6 and Table 2, these results indicate that differences in settlement by site exist, but that the importance of distance from the tidal inlet was not essential to predicting excess zeros.

## **Temporal Distribution**

Blue crab megalopae settlement was date dependent ( $P_{count} = 1.42e-10$ ;  $P_{zero} = 0.0787$ ) and varied across time (Fig. 7) with a majority of settlement, 63.5%, occurring during 2012 sampling dates. Sites C and E exhibited settlement in a near cyclic periodicity of three weeks from August 24 to October 5, 2012 (Fig. 7). However, this



Fig. 6 Zeros predicted by count model across sampling dates per site by zero classification with mean EW = 0.

observation could be an artifact due to sampling events not occurring August 31 and September 28, 2012.

Peak settlement events (mean count  $\geq 25.2 \text{ day}^{-1}$ ; van Montfrans et al. 1995) occurred throughout the study (Table 3), but were predominately isolated to Site E (Fig. 7, Table 3). The absence of sampling events due to both aforementioned issues with site access (see Materials and Methods) and unplanned absences of sampling events, notably between December 14, 2012 and January 16, 2013, obfuscate any possible cyclic periodicity of settlement for this study.

Site(s)	Date	Count
С	August 24, 2012	193
A,C & E	September 14, 2012	28, 158, 287
Е	October 5, 2012	143
C & D	October 19, 2012	137, 36
Е	November 20, 2012 December 7, 2012 February 8, 2013 February 22, 2013 E March 22, 2013 April 12, 2013 May 24, 2013 June 14, 2013	345 27 349 161 39 93 41 74
	July 12, 2013	58

**Table 3** Peak blue crab megalopae settlement on four passive collectors August 17, 2012 to September 27, 2013. Peak settlement is defined as two times mean settlement. Count values are absolute.



Fig. 7 Mean blue crab megalopae settlement by date per site. Dashed line represents peak mean settlement. Peak mean settlement is defined as settlement  $\geq 6.3 \text{ day}^{-1}$ .

## **Distance from Tidal Inlet**

Because site is a proxy for the distance from the tidal inlet (Fig. 8), significant differences in mean settlement with distance from the tidal inlet were found (P = 6.29e-15). Comparison of Tukey-adjusted Least Square Means (LSM) per site indicated that Site E settlement was significantly different than all other sites, excluding Site C, which was not significantly different than all other sites (Fig. 9). The majority (97%) of settlement occurred within 8.2 km of the tidal inlet (Sites C, D and E; Fig. 8). However, Sites C and E accounted for 96.2% of the 97%, indicating that ingress occurred primarily along the long axis of the Aransas Ship channel (including Aransas Pass), with infrequent departures to Site D (see Fig 1).

#### **East-West Wind Strength**

A significant relationship was found between settlement and EW (P = 0.0128; mean = 3.2, sd = 3.6), but not NS (mean = -3.4, sd = 3.0; Table 2). Settlement occurred primarily on ESE-SE mean winds between 6-9 m sec<sup>-1</sup> (Figure 10). Peak settlement events coincided with predominantly SSE-ESE winds (Fig. 10), but varied by site, i.e., settlement at Site E was greatest on SSE mean winds, while Site C exhibited the greatest settlement on ESE mean winds (Fig. 10). Additionally, the influence of wind direction on settlement was dependent upon wind speed from a given direction. As mean wind direction shifted from SSE to ESE, settlement either increased (Sites A, C and D) or decreased (Sites B and E) at lower mean wind speeds (Fig. 10), indicating that the influence of wind speeds on site-specific settlement becomes more pronounced as distance from the tidal inlet increases.



**Fig. 8** Mean blue crab megalopae settlement per site. Area under circle is proportional to mean settlement per site. With the exception of Sites A and B, site labels are centered within their respective circle of mean settlement. Dotted white line represents an artificially selected tidal inlet demarcation corresponding to the ends of the Aransas Pass jetties. Straight-line bearing distances from the midpoint of the tidal inlet demarcation line are: A = 16 km; B = 13.6 km; C = 8.2 km; D = 3.84 km; and E = 1.7 km.



Fig. 9 Tukey-adjusted Least Square Means site comparisons with SE bounds. Color indicates Tukey HSD between sites.



**Fig. 10** Blue crab megalopae absolute count by wind direction and speed. Numbered radii indicate 24 h mean wind speed (mean =  $6.301 \text{ m s}^{-1}$ ; range =  $2.3-12.392 \text{ m s}^{-1}$ ). Overall mean megalopae count = 12.608. Count values  $\ge 25.2$  = peak settlement events (2\*count mean).

## **Fractional Illumination**

A clear concave pattern of settlement can be seen in Figure 11, indicating that although no significant relationship of settlement with FI was found, settlement predominantly occurred around new (FI=0) and full (FI=1) moon phases, diminishing until a moderate increase around FQ/LQ. Although sampling dates were not structured to coincide with an equal representation of lunar phases, sampling events were undertaken under relatively equal distribution of phases before and after FQ/LQ (55 % vs. 45%, Fig. 11).



**Fig. 11** Blue crab megalopae settlement in relation to lunar fractional illumination (FI). FI is scaled from 0-1: 0 = new moon phase (NM); 0.5 = quarter moon phases (FQ/LQ); 1 = full moon phase (FM)

#### Discussion

Understanding the recruitment dynamics of estuarine-dependent species is necessary for the proper management of those species and the proper conservation of habitats essential to their respective life cycles. Part of this understanding must include the delineation of the use of estuarine habitats by recruiting larval organisms and the contributing abiotic and biotic factors. As such, a lack of research describing such habitat selection and use by recruiting blue crab megalopae in estuaries of south-central Texas provided impetus for this study.

### **Temporal Distribution**

The distribution of blue crab megalopae settling in the ARBC also varied temporally. Mean settlement occurred at consistently low numbers throughout this study, interspersed with episodic pulses of peak settlement (mean count  $\geq 25.2$  day<sup>-1</sup>) occurring August-October and December 2012, as well as early February 2013 (see Fig. 8). Megalopal settlement in the GOM typically occurs around two months after spawning (Lochmann et al. 1995), which would indicate that regional blue crab spawns contributing to the peaks in this study occurred July-August, October and December 2012. This differs from Daugherty (1952) and More (1969), who reported that two peak spawning events occur per year for Texas blue crabs: March-April and again in July-August, although mild winter water temperatures and an absence of freezes allow yearround spawning to occur. However, both Daugherty (1952) and More (1969) indicated that blue crab larvae circulate in nearshore waters for approximately a month, whereas more recent research indicates a two-month nearshore residency (Lochmann et al. 1995). The two peak settlement events of February 2013 are most likely the result of December 2012 spawning rather than overwintering zoea from a late October 2012 spawn. While blue crab zoea can delay ecdysis at water temperatures  $\leq 15$  °C (More 1969), water temperatures as measured at the closest National Data Buoy Center's monitoring buoy (Station 42020; LLNR 1330) did not decline to 15 °C during the last quarter of 2012.

With the exception of Site E, an appreciable decline in mean megalopal settlement was observed in 2013. Other studies have also observed inter- and intra-annual variation in blue crab megalopae settlement (Goodrich et al. 1989; Rabalais et al. 1995). However, an increase in drought severity between years of this study (Fig. 11) may have contributed to a modification in seagrass coverage (Fig. 12), altering the availability of preferred settlement habitat, potentially increasing predation upon megalopae at internal ARBC sites (Coen et al. 1981; Heck and Thoman 1981; Orth and van Montfrans 1987). Furthermore, although the drought was punctuated by a decrease in salinity at each study site beginning in March 2013 (see Fig. 3), notably at Sites A-C, megalopae were rarely collected below a salinity of 32.6 (mean - 1 SD) throughout the study. This is perhaps a more plausible explanation for the observed decline in settlement given that the typical megalopal response to falling salinities is to settle out of the water column to suitable structure. Therefore, penetration of fresher water into the lower estuary would promote a reduction of settlement at sites furthest from the tidal inlet and a concurrent greater settlement at sites closer to the tidal inlet.



**Fig. 12** Texas Gulf watershed drought status, August 2012-2013. Modified from the US Drought Monitor. The U.S. Drought Monitor is jointly produced by the National Drought Mitigation Center at the University of Nebraska-Lincoln, the United States Department of Agriculture, and the National Oceanic and Atmospheric Administration. Map courtesy of NDMC-UNL.



**Fig. 13** Percent seagrass cover within the study area for 2012 (left) and 2013 (right). Modified from Texas Statewide Seagrass Monitoring Program, University of Texas at Austin.

## **Distance from Tidal Inlet**

Supporting evidence of the hypothesis that blue crab megalopae settlement within the Aransas-Redfish Bay Complex (ARBC) decreases with increasing distance from the Aransas Pass tidal inlet was found. A majority (97%) of sampled megalopae settled at study sites closest to the Aransas Pass tidal inlet ( $\leq$  8.2 km; see Fig. 6). This finding is consistent with other local studies that have found that larval settlement and/or juvenile densities of various species were greatest closest to tidal passes. Bushon (2006) found similar patterns of greater settlement and occupation of seagrass beds closest to the Aransas Pass and Packery Channel tidal inlets by juvenile red drum and southern flounder, but not for juvenile blue crabs or penaeid shrimp. Likewise, Nañez-James (2009) found that newly settled southern flounder in Aransas-Copano Bay, Texas (USA) were more abundant in submerged vegetation closest to the Aransas Pass tidal inlet.

Other studies of blue crab megalopae settlement and early juvenile distribution observed the same settlement and use patterns as those shown in this study. In a comparison of blue crab megalopae settlement within four GOM estuaries, Rabalais et al. (1995) also found decreasing settlement of blue crab megalopae with increasing distance into the estuary. Morgan et al. (1996) observed settlement occurring primarily within the lower Mobile Bay system in Alabama (USA). And patterns of settlement consistent with those observed in this study were also found for the lower Chesapeake Bay (Orth and van Montfrans 1987; Heck and Thoman 1984). Likewise, densities of juvenile blue crab in West Bay and Christmas Bay, Texas were greater in seagrass and salt marsh, respectively, than nonvegetated bottoms (Thomas et al. 1990). Megalopae entering the estuary are often in premolt phase between megalop and first crab (Forward et al. 2004;

Tankersley 2002), so it is reasonable to conclude that megalopae would exhibit the same or similar habitat preferences as early juvenile blue crab since both benefit from the refuge from predation and food availability that vegetated bottoms afford (Beck et al. 2001; Hines 2007; Rozas and Minello 1998) even though post-settlement megalopae and young juvenile mortality due to cohort cannibalism is high (Heck and Coen 1995; Lipcius et al. 2007; Moksnes et al. 1997; Pile et al. 1996; Ruiz et al. 1993). Thus, it would benefit ingressing megalopae to settle as quickly as possible upon entry into the estuary to avoid increased predation risk from remaining within the water column or by settling on nonvegetated bottom.

Decreasing settlement with distance from the tidal inlet did not occur linearly along the distance gradient: Site D, although second nearest to the tidal inlet, did not exhibit settlement exceeding that of Site C where mean settlement was nearly an order of magnitude greater. This observation was not entirely unexpected given the lack of vegetated bottom or fringing salt marsh to provide appropriate settlement cues and suitable substrate to settle upon (see Fig. 2). On ebb tides, blue crab megalopae respond to chemical cues of estuarine vegetation by settling into submerged vegetation or onto other suitable structure to avoid extraction from the estuary (Tankersley and Forward 1994; Welch et al. 1999; Welch and Forward 2001). But it remains unclear if megalopae can detect these chemical cues on flood tides, and if so, if they could then actively avoid settlement in non-preferential habitats given their limited swimming speed (Goodrich et al. 1989) with which to counter the horizontal flow of flooding surface currents. A more likely explanation for this observation is that majorities of ingressing megalopae are not afforded the opportunity to disseminate into the Corpus Christi and Lydia Ann ship

channels. Rather, the megalopae are likely entrained in a parcel of flooding surface water (Welch et al. 1999) that aligns with and travels through the Aransas Pass tidal inlet and progresses along the Aransas Pass ship channel (see Fig. 1).

### **East-West Wind Strength**

East-West wind strength was significantly influential on the observed megalopal settlement patterns of this study. With few exceptions, settlement occurred on predominately onshore SSE to ESE winds across all sites and all ranges of mean wind speeds (2.3-12.39 m sec<sup>-1</sup>). Southeasterly winds prevail along the GOM (Rabalais et al., 1995) and prevail an average of 227 days out of the year on the south-central coast of Texas (climate data, gov.noaa.ncdc:C00684, from NCDC; www.ncdc.noaa.gov), which produces conditions favorable to ingress through the Aransas Pass due to its southeastnorthwest alignment (see Figures 1 and 4). In low tidal amplitude estuaries and lagoons, wind forcing can be an important component of up-estuary advancement of ingressing megalopae (Brown et al. 2004; Goodrich et al. 1989; Rabalais et al. 1995). Wind forcing influenced settlement of fish and crustacean larvae through the Cedar Bayou inlet, a natural, but ephemeral, tidal inlet dividing San Jose and Matagorda Islands north of the Aransas Pass (King 1971). Rabalais et al. (1995) found no significant difference in mean settlement by wind direction in the Galveston Bay complex (Texas, USA), but settlement did predominately occur on SSE winds in study year 1991. Likewise, Goodrich et al. (1989) found settlement into Chesapeake Bay to be correlated with onshore wind forcing events.

Few megalopae were collected on wind directions other than southeasterly, indicating that larval supply to mouth of the tidal inlet, ingress and/or settlement could be

impeded for other wind directions. Northerly winds could facilitate extraction of megalopae from the estuary before settlement can occur or could cause stacking of megalopae within the pass, increasing predation risk of "stalled" megalopae. Westerly, and to a lesser extent southerly, winds could alter the circulation of late stage zoea and pre-ingressing megalopae, reducing larval supply to the mouth of the Aransas Pass tidal inlet.

Additionally, the effects of EW wind strength on megalopae settlement do not occur in isolation of other abiotic factors affecting settlement. Brown et al. (2004) found that variations in red drum larval supply to the Aransas Pass tidal inlet were a result of an interaction of water level and wind forcing. Unfortunately, water levels could not be measured or obtained for all of the study sites, and thus, were not available for analysis. Because larval red drum undergo STST (Holt et al. 1989), it reasonable to conclude that including water level in the analysis could have revealed a similar interaction affecting the settlement of blue crab megalopae through the Aransas Pass tidal inlet.

## Salinity

While a relationship of settlement with salinity has been found in previous studies (Perry et al. 1995; Rabalais et al. 1995), no significant relationship was found in this study. Freshwater input into Texas bays and estuaries mirrors a precipitation gradient that decreases with decreasing longitude (Longley 1994; Tolan 2007). Thus, freshwater input into the ARBC is on average order of magnitudes lower than those in the upper Texas coast (Longley 1994; More 1969), the northern GOM (Rabalais et al. 1995; More 1969) and the Atlantic coast (Benson 1981). Combined with appreciably higher levels of surface evaporation (Longley 1994; Pollack et al. 2011), salinities are often 20 or greater

in the ARBC (Chen 2010). Since salinity is a primary cue for resting megalopae to ascend into the water column by resting megalopae during STST (Tankersley and Forward 1994; Tankersley et al. 1995; Welch and Forward 2001) near constant salinities across tidal phases may be expected to inhibit ingress into and settlement within the ARBC by limiting detection of tidal phase changes. However, recent research has indicated that blue crab megalopae ingressing into the Mission-Aransas Estuary–which includes the eastern portion of the ARBC–exhibit positive ascension response to a change in salinity that is half that of ingressing megalopae in North Carolina, USA (Bittler 2013).

## **Fractional Illumination**

Unlike studies along the northwestern GOM and the Atlantic Coast that found a significant relationship of settlement with lunar phase (Rabalais et al. 1995; van Montfrans et al. 1990 and 1995), quantified in this study as fractional illumination, no significant relationship to settlement was found in this study. However, settlement did exhibit partial concurrence with the findings of Rabalais et al. (1995), who found greatest settlement in Galveston Bay, Texas (USA) occurred primarily around new moon phase (FI = 0); ca. full moon phase (FI=1) in the York River, Virginia (van Montfrans et al. 1990); and ca. both new and full moon phases in Wilmington and Pamlico Sound, North Carolina (Mense et al. 1995). The non-significance of a relationship between settlement and FI, however, was not unexpected: Texas coastal tides are mixed (diurnal and semi-diurnal) and typically of low amplitude and are greatly influenced by alongshore and onshore wind-forcing (Lipcius et al. 2007; Rabalais et al. 1995; Smith 1977) as opposed to those of the northeastern GOM and Atlantic coast tides that are more diurnally lunar-influenced (Rabalais et al. 1995; Smith 1977). It can be posited that this lack of

significant relationship—in combination with appreciable wind-forced tides along the south-central Texas coast and an accompanying appropriate level of turbidity that increases light attenuation within the water column—may afford blue crab megalopae the opportunity to ingress into the ARBC on flood tides outside of expected nocturnal patterns of STST.

## In situ spawning

More (1969) reported *in situ* spawning within the Galveston Bay, Texas when salinity was above 20. Since salinities within the ARBC and adjacent bay systems are normally  $\geq 20$  (Chen 2010) an additional hypothesis of this study posited that *in situ* spawning by ovigerous female blue crabs might be occurring since the salinity requirements of zoea larvae will have been met (Costlow and Bookhout 1959; Costlow 1967). If so, it was postulated that the occurrence of *in situ* spawning could be detected as an equal or greater proportion of megalopae being collected from sites farthest from the tidal inlet (Sites A and B). Clearly, settlement at these sites was orders of magnitude less than sites closest to the tidal inlet (see Table 2). Additionally, outside of a proportional equivalency, or greater, settlement at these sites, it became unclear how to identify the source of the collected megalopae as being from *in situ* or *ex situ* spawning. A more appropriate method for testing this hypothesis would be to quantify the density of early stage zoea larvae at increasing distances from tidal inlets. Given the current knowledge of blue crab life history, the detection of early stage zoea in the upper estuary would indicate that: a) freshwater inflow has diminished to a level that modifies the reproductive regimen of the local blue crab population, and b) a possible deleterious effect on

recruitment could be occurring due to higher rates of predation on zoea occurring than they would typically would be exhibited in the GOM (Tankersley and Forward 2007).

In closing, given the sparse research into the settlement patterns of blue crab megalopae into estuaries of south-central Texas, the results of the study form a solid foundation from which to further elucidate these settlement patterns and the contributing factors. Evidence from this study indicates that megalopal settlement into suitable habitats of the ARBC exhibits an inverse relationship with distance from the Aransas Pass tidal inlet and this relationship varies with East-West wind strength and time of year. Because these habitats are predominately submerged aquatic vegetation consisting of seagrass and salt marsh that are used as nursery habitats by not only blue crabs but by a range of commercially and ecologically important species, it is imperative that conservation efforts be focused upon them.

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