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Migratory Behavior of Ovigerous Blue Crabs *Callinectes sapidus*: Evidence for Selective Tidal-Stream Transport

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In the late summer and early fall, newly inseminated female blue crabs (Callinectes sapidus) *leave low-salinity areas of estuaries and migrate seaward to spawn near the entrance. We tested the hypothesis that migration of female* C. sapidus *to spawning grounds is facilitated by selective tidal-stream transport (STST). We monitored the swimming direction of adult crabs from a stationary platform located about 1 km inside the entrance to the Newport River Estuary (Beaufort, North Carolina). Swimming activity near the surface occurred primarily at night and most crabs avoided swimming against tidal currents. Eighty-one percent of the crabs observed moving down-estuary toward the inlet during ebb tide were ovigerous females. Of the 36 gravid females captured traveling in ebb currents, 97% possessed dark egg masses containing late-stage embryos. Conversely, nearly all (98%) adult crabs observed traveling in flood currents lacked egg masses, and all the females captured while migrating up-estuary exhibited signs of recent spawning. These observations indicate that ovigerous blue crabs use ebb-tide transport to migrate seaward to spawn and flood-tide transport to reenter the estuary shortly after larval release.*

Atlantic blue crabs (*Callinectes sapidus* Rathbun), like many brachyuran crabs, possess a complex life cycle that includes both estuarine and coastal migratory phases, making them ideal models for studying the intricacies of hydrodynamic transport, dispersal, and recruitment [see (1) and (2) for reviews]. Although populations of *C. sapidus* are found from Cape Cod to Brazil (3), their life history and ecology have been best studied in the estuaries of the western Atlantic and the Gulf of Mexico, where they support a significant commercial fishery. Adult blue crabs are widely distributed throughout the estuary, but their densities are greatest in regions of low salinity. Mating occurs in brackish areas from late spring to early fall. Following insemination, female crabs migrate seaward to high-salinity (euhaline) areas near the mouth of the estuary to spawn (4). Details of the duration of the down-estuary migration for individual crabs are lacking, but results of mark-recapture studies in larger estuaries of the western Atlantic indicate that newly inseminated crabs may take 3–4 months to travel 150–300 km to euhaline regions [see (5) for review]. Spawning occurs after crabs have reached the lower region of the estuary. Females extrude newly fertilized eggs onto the pleopods, forming a large egg mass, or "sponge," under the abdomen (4, 6). Newly oviposited egg masses are yellow-orange, but as embryonic development proceeds, they gradually turn dark brown and eventually black (4, 6). Larvae (zoea) are released at or near the time of nocturnal high tide and remain in surface waters where they are advected seaward to undergo development in the high-salinity waters of the continental shelf [see (2) for review]. Thus, the long-distance migration of female crabs to euhaline areas is thought to ensure the survivorship and development of the larvae, which are unable to tolerate the low-salinity conditions within the estuary (7).

Despite many accounts of newly inseminated crabs migrating to the mouths of bays and rivers to spawn [see (5) for review], details of the migratory behavior of fe-

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Abbreviations: STST; selective tidal-stream transport.

male crabs and the underlying mechanisms that contribute to down-estuary transport have not been investigated. Horizontal transport of migrating crabs most likely involves the integration of behavioral traits, including oriented swimming and vertical migration, with predictable physical and hydrographic processes such as tidal currents. Gross movements of migrating female *C. sapidus* have been inferred from mark-recapture studies [see (5) for review]. Unfortunately, these studies lack sufficient detail to accurately describe the temporal (lunar, tidal, and diel) and spatial patterns of movement or to elucidate the relevant physical and biological processes that influence transport.

Most recent models of hydrodynamic transport of marine and estuarine organisms with complex life cycles focus on the integration of physical processes with complex behaviors, especially tidally synchronized vertical migrations (*e.g.*, 1, 2, 8, 9). Although the exact behaviors and mechanisms that female blue crabs employ for down-estuary migration have not been identified, it is likely that females use ebb-tide currents to enhance the rate and efficiency of seaward transport. Selective tidal-stream transport (STST) is a common life-history trait of many estuarine-dependent organisms and involves appropriately timed vertical migrations into the water column to exploit tidal currents. Up-estuary migration is accomplished through flood-tide transport, in which animals ascend into the water column during flood tides and remain on or near the bottom during ebb tides. Similarly, seaward migration, or ebb-tide transport, involves vertical migrations toward the surface during ebb tides and maintenance near the bottom during flood tides. Although examples of ebb-tide transport are rare, many estuarine organisms, including crab megalopae and juveniles (*e.g.*, 10), have been shown to possess tidally timed activity patterns and vertical migrations that result in flood-tide (up-estuary) transport. The objective of the present study was to document the STST behavior of ovigerous female blue crabs and to examine the relationship between the direction of migratory movements and tidal currents.

During the summer of 1997, we monitored the frequency of adult blue crabs entrained in surface currents in Beaufort Inlet, North Carolina. The observation point—a stationary platform suspended from a bridge about 1 km inside the entrance to the Newport River Estuary—hung approximately 1 m above the water surface at high tide. It provided a convenient vantage point for monitoring the migratory activity of adult crabs as they traveled down-estuary toward the inlet or up-estuary toward more brackish regions. During two 24-h periods, on 13–14 August and 16–17 August 1997, we continuously surveyed the swimming direction (down-estuary or up-estuary) and reproductive state (ovigerous or non-ovigerous) of adult crabs traveling past the platform. An ovigerous crab was identified by its large egg mass and exposed semicircular abdomen. Since we were unable to differentiate between non-ovigerous female crabs and male crabs on the basis of observation alone, we used a dip net to capture crabs that came within a few meters of the platform and recorded their size (carapace width), sex, and egg mass color (if present). The study was repeated on 19–20 and 20–21 September 1997. On these dates, we restricted our observations to the hours between dusk and dawn since during the initial observation periods few crabs were spotted swimming near the surface during the day.

The results of the initial two 24-h observation periods are presented in Figure 1. Although fewer crabs were observed migrating during the September sampling periods, their movement patterns relative to tidal currents were similar to those recorded in August. Crabs swam primarily at night, and the frequency and swimming direction of those traveling past the platform was strongly correlated with the magnitude and direction of tidal currents (Fig. 1 and Table IA). Although blue crabs are excellent swimmers, most of the animals we observed appeared to be transported passively (*i.e.*, "treading water"), and few were seen displaying the stereotypical sideways posture and rapid 5th pereiopod movement associated with swimming in *C. sapidus* (11).

Most (81%) crabs observed moving down-estuary toward the inlet during ebb tide were ovigerous "sponge" crabs (Table IA). Since we were unable (based on observations) to accurately determine the sex of crabs without egg masses, the remaining 19% were either non-ovigerous female or male crabs. Of the 36 gravid females captured traveling in ebb currents, 35 (97%) possessed dark sponges (brown or black) containing late-stage embryos. Microscopic examination of the larvae inside the eggs revealed they were within 2–3 days of hatching. Only one crab carrying early-stage eggs (yellow-orange sponge) was captured swimming near the surface (Table IA) even though female crabs with newly oviposited egg masses frequently inhabit the area surrounding the platform from June to October (12; R. Tankersley, pers. obs.). Conversely, nearly all (98%) adult crabs observed traveling in flood currents lacked egg masses (Table IA). Moreover, all crabs captured while migrating up-estuary exhibited signs of recent spawning, including the discoloration of the abdomen near the site of egg attachment and the presence of egg-mass fragments on the pleopods (Table IB). Thus, the migratory behavior of *C. sapidus* females appears to be influenced by the presence of an egg mass and the developmental state of the embryos.

These observations support the hypothesis that ovigerous blue crabs undergo vertical migrations that are synchronized with tidal cycles and result in unidirectional seaward transport toward the entrance of estuaries (*i.e.*,

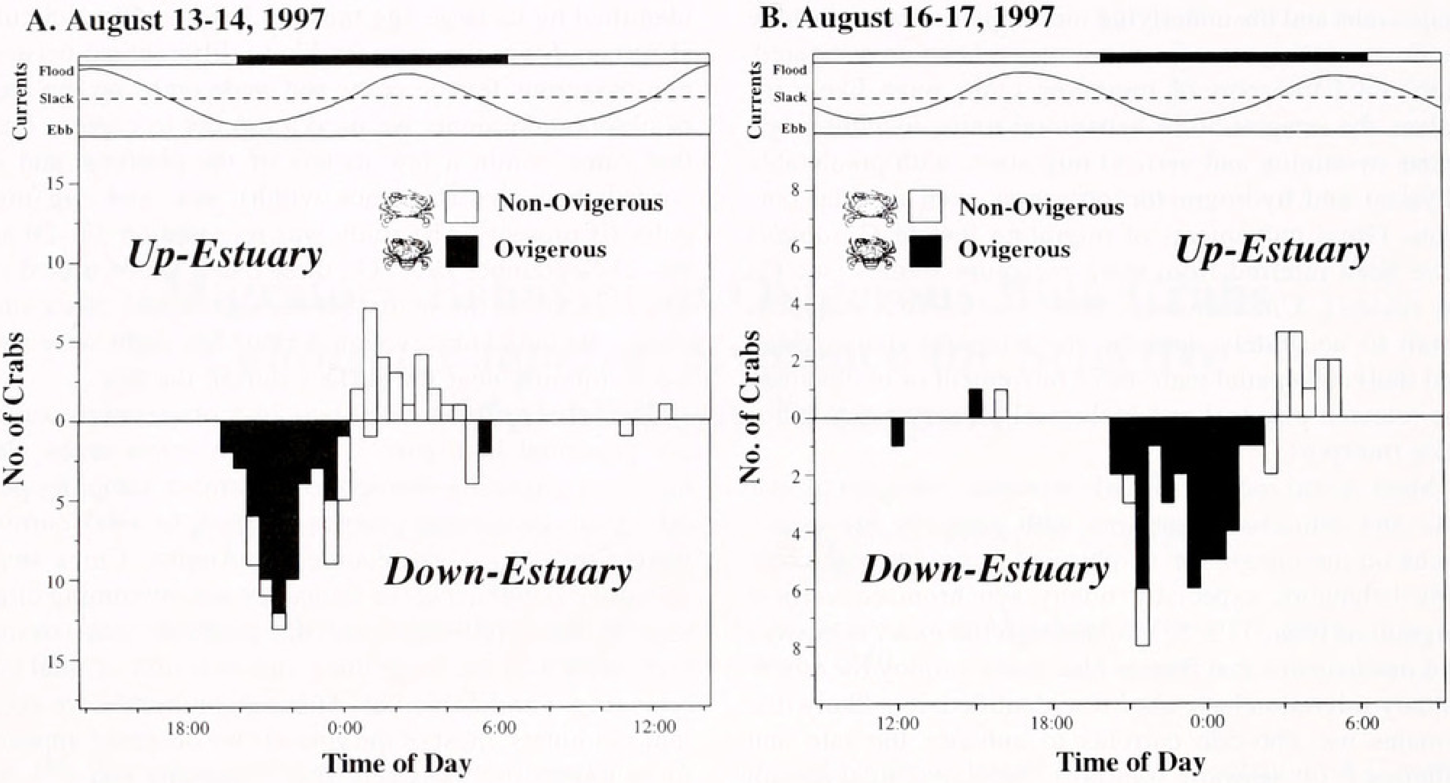

Figure 1. Frequency (plotted at 30-min. intervals) of adult blue crabs observed traveling either up-estuary or down-estuary near the surface during two 24-h observation periods (13–14 and 16–17 August 1997). Only crabs that entered a 6.8-m × 10.1-m rectangular area surrounding the observation platform were censused and included in the study. At night, the area surrounding the platform was illuminated with a diffuse overhead light that had no apparent effect on the swimming behavior or activity of migrating crabs. Secchi disk depths ranged from 1.0 m to 2.5 m. The light:dark cycle and direction and magnitude of tidal currents are depicted in the top panels. Tidal current velocities were obtained from the computer program Tides and Currents Pro 2.5 (Nautical Software, Inc.).

Table I

Number (in parentheses) and relative frequency of crabs traveling in flood and ebb currents

A. Observed crabs: From observations alone, only two categories of crabs could be distinguished

Direction of transport	Crab type: Non-ovigerous crabs	Crab type: Ovigerous females
Up-estuary (Flood tides)	98% (48)	2% (1)
Down-estuary (Ebb tides)	19% (24)	81% (103)
Log-likelihood ratio test: $G = 105.2$, df = 1, $P < 0.0001$		

B. Captured crabs: Crabs caught for closer examination could be separated into four categories

Direction of transport	Crab type: Pre-ovigerous females	Ovigerous females	Post-spawning females	Males
Up-estuary (Flood tides)	0% (0)	0% (0)	86% (6)	14% (1)
Down-estuary (Ebb tides)	5% (2)	88% (36)	0% (0)	7% (3)
Log-likelihood ratio test: $G = 35.7$, df = 3, $P < 0.0001$				

Note: Associations between crab type (*i.e.*, sex and reproductive condition) and direction of transport (up-estuary and down-estuary) were tested using a log-likelihood ratio test (G-test). Table values represent the pooled observations from four sampling periods in August and September 1997.

ebb-tide transport). The results also suggest that after spawning, female crabs reverse direction and move up the estuary in a saltatorial fashion (*i.e.*, flood-tide transport). A change in the direction of migration requires that the mechanisms responsible for synchronizing the vertical migratory behavior of female crabs with the appropriate tidal currents must shift 180° (*i.e.*, $\approx$6 h) following larval release. Alternatively, ovigerous and post-spawning crabs may rely on different mechanisms or cues to time their forays into the water column.

This migratory pattern is apparently not unique to the Newport River Estuary. In an extensive mark-recapture study conducted in the St. Johns River, Florida, Tagatz (13) found that females with developing eggs migrate from the river to the ocean just prior to larval release. Ovigerous crabs collected within the river had primarily yellow-orange egg masses, whereas most of those collected near the river's mouth and in coastal waters had dark brown or black sponges. Blue crabs that had recently possessed sponges were also observed reentering the lower 40 km of the river and developing a second sponge. Tagatz (13) also reported that several sponge crabs tagged in coastal waters lacked egg masses when they were recaptured in the river within a couple of weeks of their release.

Based upon our observations of the migratory behavior of ovigerous blue crabs in the Newport River Estuary and the results of previous mark-recapture studies [see (5) for review], we have developed a conceptual model for the seaward migration of female blue crabs for spawning. The model is divided into two phases—a long-distance down-estuary phase in which newly inseminated non-ovigerous crabs travel seaward toward the lower reaches of the estuary (Phase I; Fig. 2), and a shorter distance spawning phase in which ovigerous crabs migrate from euhaline areas to the entrance of the estuary and coastal waters to release larvae (Phase II; Fig. 2). Although the timing of various components of the model may differ among estuaries, we believe that the sequence of events is similar.

Phase I (down-estuary migration) is initiated when, shortly after mating, newly inseminated crabs migrate seaward from brackish water toward the mouth of the estuary. Male crabs remain in low-salinity regions and do not migrate. Down-estuary migration of the females most likely occurs at night and is facilitated by STST on ebb tides. Depending upon the size of the estuary and their distance from the mouth, individual crabs may take weeks to months to complete their down-estuary migration. Upon reaching high-salinity regions, female crabs cease ebb-tide transport as their ovaries and eggs complete development. Crabs that mate in late spring may reach euhaline areas in time to spawn (*i.e.*, undergo Phase II) that same year (6). Crabs reaching the lower estuary in late fall overwinter near the mouth of the estuary and spawn the following spring.

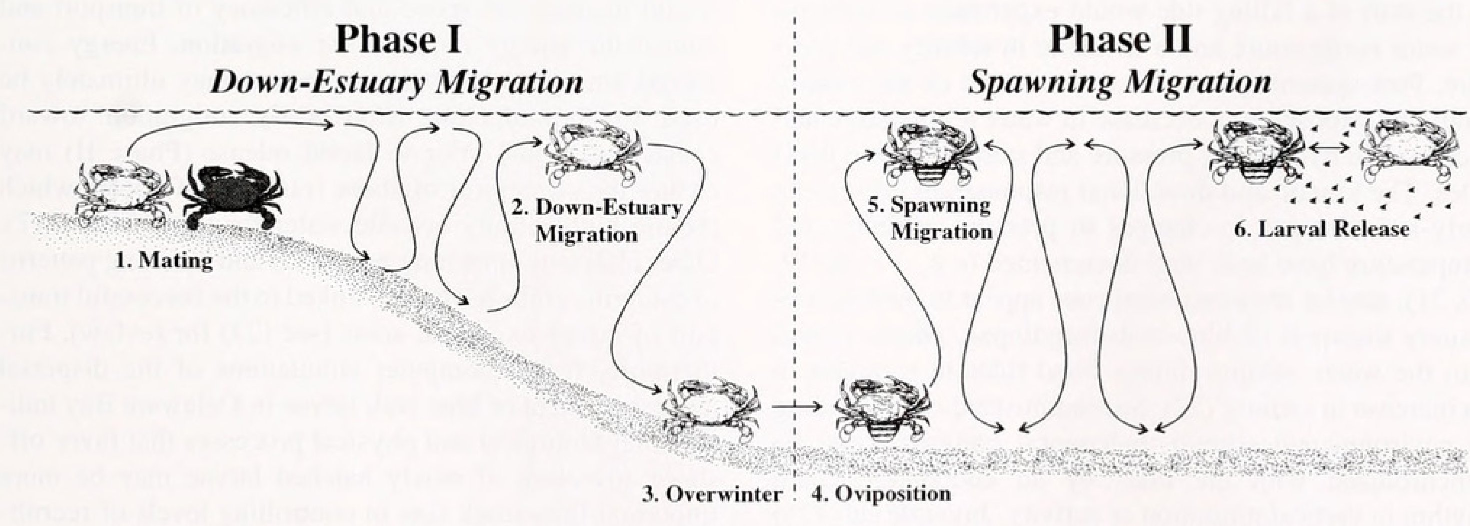

Figure 2. Diagram of the proposed conceptual model of the migratory behavior of female blue crabs. The model is divided into two phases, a down-estuary phase (Phase I) and a spawning phase (Phase II). (1) From late spring to early fall, adult crabs mate in the brackish regions of the estuary (dark crabs represent males; light crabs represent females). (2) Following insemination, female crabs migrate seaward using selective tidal-stream transport (STST) on nocturnal ebb tides. Male crabs remain in low-salinity areas. (3) After reaching euhaline regions, female crabs cease STST and may overwinter near the mouth of the estuary. (4) Spawning is initiated by the attachment of the egg mass (sponge) to the underside of the abdomen. About 10–12 days following extrusion of the sponge, female crabs with late-stage eggs migrate to the mouth of the estuary and possibly into coastal waters using STST on nocturnal ebb tides. (5) At the entrance to the estuary, larvae are released near the time of high tide at night. Shortly after larval release, female crabs reenter the estuary using STST on flood tides. Since some female crabs are capable of producing more than one brood, steps 4–6 may be repeated several times during a single season.

Phase II (spawning migration) of the model is initiated by the oviposition of fertilized eggs under the abdomen. Sponge crabs with early-stage eggs remain in the lower portion of the estuary and do not engage in STST. About 10–12 days after oviposition, female crabs with late-stage eggs migrate vertically toward the surface during nocturnal ebb tides and are transported seaward toward the entrance of the estuary and possibly into coastal waters. Upon reaching the mouth of the estuary, ovigerous females release their larvae near the time of nocturnal high tide. Due to the number of eggs in the egg mass, larvae may be released over several consecutive nights, as has been observed for the lobsters *Homarus gammarus* (14) and *Nephrops norvegicus* (15). Subsequently, post-spawning crabs reenter the estuary by migrating toward the surface during nocturnal flood tides. Since female blue crabs are capable of producing more than one egg mass (4, 5), individual crabs may undergo multiple spawning migrations in a single season.

The success of tidal-stream transport depends upon the time of entry into and exit from the water column, the length of time in the water column, and the animal's vertical position relative to tidal currents (8, 9, 16). Therefore, to be effective, vertical migrations underlying STST must be precisely timed with the correct tidal currents (8, 9). There are two alternative mechanisms that crabs might use to achieve this synchrony. First, these behaviors could be cued by a change in hydrologic variables, which is associated with the tides. Ovigerous crabs on the bottom at the start of a falling tide would experience an increase in water temperature and a decrease in salinity and pressure. Post-spawning crabs near the mouth of the estuary would be exposed to a decrease in water temperature and increases in hydrostatic pressure and salinity during flood tides. The kinetic and directional responses of crustacean early-larval stages to changes in pressure, salinity, and temperature have been well documented (*e.g.*, 17, 18, 19, 20, 21); similar environmental cues appear to mediate up-estuary transport of blue crab megalopae, which ascend into the water column during flood tides in response to an increase in salinity (22). Second, instead of responding to environmental stimuli, behavioral patterns could be synchronized with the tides by an endogenous tidal rhythm in vertical migration or activity. Juvenile eels (23) and fiddler crab postlarvae (24) have circatidal rhythms in swimming activity that appear to underlie STST. Regardless of the underlying mechanism, vertical migratory behaviors contributing to seaward transport toward the mouth of the estuary seem to be restricted to gravid female crabs carrying late-stage embryos (Table IB). Similarly, up-estuary migration on flood tides seems to be restricted to post-spawning females (Table IB). Male blue crabs and females with yellow-orange egg masses containing early-stage embryos do not appear to undergo STST. Thus, we hypothesize that only egg-bearing females with dark sponges and crabs that have recently released larvae should respond to environmental cues associated with changing tidal conditions or possess an endogenous tidal rhythm that regulates swimming or activity and could be used for saltatory down-estuary or up-estuary transport.

Larvae of most estuarine crabs are hatched at specific times in the diel, tidal, and semilunar or lunar cycles. Although larval release for most brachyurans is under endogenous control, the timing may be controlled by the female, the developing embryos, or both [see (25) for review]. In the subtidal crabs studied (*Rhithropanopeus harrisii* and *Neopanope sayi*), egg hatching is mediated by communication between the larvae and the female (26, 27, 28). Near the time of hatching, substances released by the developing embryos induce ovigerous crabs to exhibit stereotypic larval release behaviors, including rhythmic pumping of the abdomen. Pheromones responsible for triggering this pumping response have been well studied [see (29) for review], and it is possible that similar substances released by the late-stage eggs may initiate the ebb-tide transport behaviors exhibited by ovigerous blue crabs.

Our conceptual model suggests that the transport behaviors responsible for down-estuary migration from brackish water (Phase I) are similar to those that produce the spawning migration (Phase II). Nevertheless, the adaptive value of STST during each phase may be different. For newly inseminated female crabs (Phase I), STST on ebb tides may be an energy-saving strategy since it would increase the speed and efficiency of transport and reduce the energy required for migration. Energy conserved during down-estuary transport may ultimately be used for reproduction. Conversely, migration toward coastal areas just prior to larval release (Phase II) may ensure the successful offshore transport of zoeae, which require high-salinity oceanic water for development (7). Other elaborate spawning behaviors and hatching patterns of estuarine crabs have been linked to the successful transport of larvae to coastal areas [see (23) for review]. Furthermore, recent computer simulations of the dispersal and recruitment of blue crab larvae in Delaware Bay indicate that biological and physical processes that favor offshore advection of newly hatched larvae may be more important than stock size in controlling levels of recruitment of older larvae or juveniles to adult habitats (30). Thus, hydrologic or meteorologic factors that either promote or impede STST by ovigerous females may have a significant impact on the reproductive success of the crabs and may be partially responsible for annual fluctuations in recruitment.

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