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Developmental shift in the selective tidal-stream transport behavior of larvae of the fiddler crab *Uca minax* (LeConte)

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Following hatching, larvae of the fiddler crab *Uca minax* (La Conte) are exported from the adult habitat in estuaries to coastal and shelf waters where they undergo development prior to re-entering estuaries as postlarvae (megalopae). Studies of the spatial distribution of both newly hatched zoeae (Stage I) and megalopae indicate they undergo rhythmic vertical migrations associated with the tides for dispersal and unidirectional transport (selective tidal-stream transport) both within estuaries and between estuaries and the nearshore coastal ocean. We tested the hypothesis that *U. minax* zoeae possess a circatidal rhythm in vertical migration that facilitates offshore transport in ebb tidal flows, while postlarvae (megalopae) return to estuaries using a similar flood-phased endogenous rhythm. We also determined if the expression of the rhythm was influenced by the salinity conditions zoeae and megalopae experience as they transition between low-salinity regions of estuaries and high-salinity coastal waters. Stage I zoeae were collected by holding ovigerous female crabs in the lab until hatching. Megalopae were collected from the plankton and identified to species using molecular techniques (PCR-RFLP). Under constant laboratory conditions, both zoeae and megalopae exhibited endogenous circatidal rhythms in swimming that matched the principal harmonic constituent of the local tides (12.39±0.07 h; $\overline{X}$ ±SE). Upward swimming in Stage I zoeae occurred 2.5-4 h after high tide near the time of expected maximum ebb currents in the field. Rhythmic swimming of megalopae occurred slightly earlier in the tide (2.5±0.09 h after high tide; $\overline{X}$ ±SE) but was not entirely synchronized with flood currents, as expected. Salinity conditions had no apparent effect on the expression or pattern of the rhythms. Results indicate that this circatidal rhythm forms the behavioral basis of selective tidal-stream transport (STST) in early stage *U. minax* zoeae, but does not undergo a sufficient phase shift to account for vertical distribution patterns exhibited by megalopae in the field.

1. Introduction

Like most marine benthic invertebrates, marine decapod crustaceans often possess complex life cycles that include both a benthic adult phase and a series of planktonic larval stages that serve as the primary means of dispersal (McConaugha, 1992; Levin and Bridges, 1995; Queiroga and Blanton, 2005). Studies of brachyuran crabs inhabiting estuaries indicate that the larvae of some species are retained and complete development within the estuary before settling and recruiting to adult populations (see Forward and Tankersley, 2001; Queiroga and Blanton, 2005 for review). In most other taxa, larvae (zoeae) hatch near the adult habitat and migrate down-stream to the coastal ocean where they complete development prior to re-entering the estuary as postlarvae (megalopae) (e.g., Christy and Stancyk, 1982; Brookins and Epifanio, 1985; Levin, 1986; Morgan, 1995; Queiroga et al., 1997; Garrison, 1999).

Seaward transport of zoeae from parental habitats and eventual export from estuaries to adjacent shelf areas is facilitated by a variety of behavioral mechanisms including (1) release of larvae by ovigerous females near the time of high tide (Forward, 1987) and (2) vertical migration of zoeae toward the surface during strong ebb currents (e.g., Wheeler, 1978; Christy, 1982; Christy and Stancyk, 1982; Dittel and Epifanio, 1982; Lambert and Epifanio, 1982; McConaugha et al., 1983; Provenzano et al., 1983; Epifanio et al., 1984, 1989; Sulkin, 1984). However, these mechanisms are only advantageous for short-distance migrations during the brief period following release. Larvae that remain within the water column are transported in the opposite direction when the tide turns, resulting in little or no net displacement. Nevertheless, the coupling of tidally-timed vertical migrations with the phasing of tidal currents, a behavioral mechanism known as selective tidal-stream transport (STST) (see Forward and Tankersley, 2001; Gibson, 2003 for reviews), facilitates unidirectional transport within estuaries and exchange between estuaries and coastal areas. During STST, organisms take advantage of strong, directional tidal currents and vertical shear

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gradients by ascending toward the surface during one phase of the tide and descending and remaining on or near the bottom during the alternate phase. Timing of vertical migrations affects the direction and efficiency of transport and flux of larvae between the estuary and the coastal ocean (Pochelon, 2005). Vertical migratory behavior in which the active or upward-swimming phase occurs during ebb flows is known as ebb-tide transport (ETT) and results in rapid down-estuary movement. Similarly, flood-phased vertical migrations (flood-tide transport, FTT) induce up-stream movement and reinvasion of estuaries from coastal areas (Forward and Tankersley, 2001).

Behaviors associated with STST can be under exogenous or endogenous control. Upward and downward migration in the water column may be cued by environmental factors that change predictably with the tide, including changes in pressure, temperature, salinity, and turbulence (see Forward and Tankersley, 2001 for reviews). For example, megalopae of the blue crab *Callinectes sapidus* utilize flood-tide transport (FTT) to return to nursery habitats within estuaries. An increase in salinity triggers upward swimming near the beginning of flood tide and a decline in turbulence near the time of slack-before ebb cues descent toward the bottom (Tankersley and Forward, 1994; Forward et al., 1995; Tankersley et al., 1995). Alternatively, STST behaviors may be controlled by an endogenous clock with a period that matches the local tidal regime. The circatidal clock is also synchronized with the tides so that the active phase (period of upward migration and swimming into the water column) coincides with the appropriate tidal phase (ebb vs. flood). Circatidal rhythms that underlie STST for estuarine retention or reinvasion have been reported for several larval stages, including the copepod *Eurytemora affinis* (Hough and Naylor, 1992), zoeae of the mud crab *Rhithropanopeus harrisii* (Cronin and Forward, 1979, 1983; Forward and Cronin, 1980) and fiddler crab *Uca* spp. megalopae (Tankersley and Forward, 1994). Endogenous control of vertical migratory behaviors used for transport seaward during ebb tides (i.e., ETT) has been documented in juvenile glass eels *Anguilla rostrata* (Wippelhauser and McCleave, 1988), juvenile plaice *Pleuronoctes plastessa* (Gibson, 1973), spot *Leiostomus xanthurus* and pinfish *Lagodon rhomboids* larvae (Forward et al., 1998), ovigerous blue crab females *Callinectes sapidus* (Forward et al., 2003), trilobite larvae of the horseshoe crab *Limulus polyphemus* (Ehlinger and Tankersley, 2006), and zoeae of the shore crab *Carcinus maenas* (Zeng and Naylor, 1996a,b,c) and the sand fiddler crab *Uca pugilator* (López-Duarte and Tankersley, 2007a,b).

Among the fiddler crab species (*Uca* spp.) inhabiting intertidal coastal habitats and estuarine marshes along the Atlantic coast of the United States, the red-jointed fiddler crab *U. minax* is considered to be the most freshwater tolerant (Barnwell and Thurman, 1984; Brodie et al., 2005). Adults are generally found in oligohaline regions of estuaries, including the banks of brackish and freshwater tidal creeks, where the salinity is generally <5 (Barnwell and Thurman, 1984; Thurman, 2003). Yet, zoeae are unable to tolerate low salinity conditions near the adult habitat and are exported from estuaries to undergo development in shelf waters (Christy and Stancyk, 1982; Houser and Allen, 1996). Thus, following hatching *U. minax* larvae enter the water column and migrate considerable distances to coastal areas to complete development. Seaward transport and export from estuaries to the coastal ocean may be augmented by STST that is mediated by an ebb-phased circatidal rhythm, as has been documented for other species of fiddler crabs (López-Duarte and Tankersley, 2007a,b; López-Duarte et al., in preparation). Following zoeal development, the megalopa stage reinvades estuaries. Previous studies suggest STST is also involved in their up-estuary migration (DeVries et al., 1994) and the behavior may be controlled by a flood-phased endogenous rhythm in vertical migration (Tankersley and Forward, 1994). This apparent reversal in the direction of STST between developmental stages (Stage I zoeae vs. megalopae) is noteworthy as it requires the timing system of the underlying behavior to switch from one tidal phase to the other – a phase-shift of ≈6.2 h (or 180°) in areas with semi-diurnal tides.

The purpose of the present study was to determine if *U. minax* zoeae and megalopae possess endogenous tidal rhythms in vertical swimming that underlie STST; therefore facilitating both their export from (Stage I zoeae) and reinvasion (megalopae) of estuaries. The predicted pattern for zoeae is upward vertical migration during periods of ebb currents and downward swimming during periods of flood currents. Megalopae are hypothesized to possess a similar rhythm that is delayed or phase-shifted by 180° (≈6.2 h in areas with semidiurnal tides) so that the active phase is synchronized with flood currents. Previous studies of the vertical distribution and reinvasion of estuaries by fiddler crab megalopae indicate that STST is involved in their up-estuary migration prior to settlement in adult habitats (DeVries et al., 1994; Tankersley and Forward, 1994). However, in these earlier studies megalopae were pooled and categorized as *Uca* spp., as they are morphologically indistinguishable in the plankton (Sandifer, 1975; O'Connor, 1990). Thus, STST associated behaviors could not be attributed to a single species and were assumed to be common among all congeners inhabiting the estuary (DeVries et al., 1994; Tankersley and Forward, 1994). In the current study, the differences in the salinity tolerances of fiddler crab megalopae were used to overcome this limitation. *Uca minax* megalopae were collected from a low salinity/near-freshwater region of the estuary that was beyond the salinity tolerances of other fiddler crab species (Barnwell and Thurman, 1984; Thurman, 2003). Moreover, the identity of *U. minax* postlarvae in samples was verified using a recently developed restriction fragment length polymorphism (RFLP) protocol that is capable of discriminating between the three most common species (i.e., *U. pugilator*, *U. pugnax*, and *U. minax*) inhabiting the study estuary (Behum et al., 2005).

The hypothesis that the expression of circatidal rhythms underlying STST in fiddler crabs is influenced by the salinity gradient experienced by zoeae and megalopae as they travel between high-salinity coastal areas and low-salinity regions within the estuary was also tested. The prediction was that rhythmic swimming behaviors of zoeae would stop or be suppressed in salinity conditions characteristic of coastal areas (salinity 35) as the behavior is energetically costly and no longer has any apparent ecological significance. Similarly, circatidal rhythms underlying FTT in megalopae were expected to be exhibited by *U. minax* megalopae in euhaline and brackish conditions that are common throughout most of the estuary, but the behavior should cease at salinities indicative of the adult habitat (salinity<5) where settlement occurs.

2. Materials and methods

2.1. Collection of Zoeae and Megalopae

The study was conducted during July 2004-2006 using *Uca minax* zoeae and megalopae from the Winyah Bay Estuary, South Carolina, USA (Fig. 1). Newly hatched Stage-1 zoeae were obtained by holding (<24 h) ovigerous females in the laboratory until hatching. Gravid crabs were collected by hand from an intertidal marsh/mud flat area near the Old Hwy 17 Bridge (33°22'12''N; 79°15'58''W) on the Great Pee Dee River, South Carolina, USA, approximately 20 km from the entrance to the estuary (Fig. 1). Salinity in the area is generally around 5. Crabs were maintained in individual glass bowls (19 cm dia.×6 cm) containing 1 L of filtered seawater at 24 °C and were exposed to a photoperiod that approximated the natural light/dark (L:D) cycle at the time of collection. Salinity of the incubation water depended upon the test conditions used to monitor larval swimming (see description below). Developmental stage of the embryos in the egg mass was determined using procedures of DeVries et al. (1983) and Brown and Loveland (1985). Only crabs with embryos that were within 24 h of hatching (i.e., late-stage embryos) were used in experiments. Following larval release, newly hatched zoeae from the same egg mass were transferred to filtered (<5 μm) seawater (at test salinity, see description