Journal of Experimental Marine Biology and Ecology 440 (2013) 149–155

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Endogenous swimming activity rhythms of postlarvae and juveniles of the penaeid shrimp Farfantepenaeus *aztecus*, *Farfantepenaeus duorarum*, and *Litopenaeus setiferus*

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ARTICLE INFO

Article history:
Received 15 June 2012
Received in revised form 18 December 2012
Accepted 19 December 2012
Available online 17 January 2013

Keywords:
Farfantepenaeus aztecus
Farfantepenaeus duorarum
Litopenaeus setiferus
Endogenous rhythms
Selective tidal-stream transport
Recruitment

ABSTRACT

Selective tidal-stream transport is commonly used by marine animals to migrate between oceanic and estuarine habitats as they undergo ontogenetic migrations, but behaviors used to accomplish these migrations may differ among species, life history stages, or locations. The ecologically and commercially important brown shrimp, *Farfantepenaeus aztecus*, pink shrimp, *Farfantepenaeus duorarum*, and white shrimp, *Litopenaeus setiferus*, undergo ontogenetic migrations between spawning locations on the continental shelf and juvenile nursery habitats in estuaries. This study evaluated the role of endogenous rhythms in vertical swimming activity in Flood Tide Transport (FTT) of postlarvae entering estuaries and the potential for shifts in behavior between the postlarval and juvenile stages. Brown and pink shrimp postlarvae exhibited circatidal rhythms in vertical swimming activity with period lengths of approximately 12.4 h that coincided with the time of early flood tide in the field, whereas white shrimp postlarvae did not exhibit an endogenous rhythm in swimming activity. Pink shrimp juveniles (20-40 mm total length) exhibited a distinct circadian activity rhythm with a mean period length of 23.8 ± 3.7 h and peak swimming during the time of night in the field. Juvenile brown and white shrimp exhibited relatively weak circatidal activity rhythms with peak vertical swimming around the times of ebb and early flood tide in the field, respectively. These results suggest that 1) brown and pink shrimp postlarvae exhibited endogenous activity rhythms that would enhance FTT, 2) white shrimp postlarvae likely depend on environmental cues associated with flood tide to accomplish FTT, and 3) pink shrimp are unique among these three species in exhibiting a shift from a circatidal to a nocturnal swimming activity rhythm between postlarval and juvenile stages.

1. Introduction

Estuarine-dependent marine species often use a horizontal movement called selective tidal-stream transport (STST) that takes advantage of tidal currents to complete ontogenetic migrations between oceanic and estuarine habitats. The larvae of shelf-spawning species commonly use STST to migrate into estuaries during flood tide (Flood Tide Transport, FTT) against the net outflow of water, and juveniles or adults return to the ocean on ebb tide (Ebb Tide Transport, ETT) (Forward et al., 2003). Researchers report species-specific differences in behaviors and environmental cues used to accomplish STST for a growing number of species (Forward and Tankersley, 2001; López-Duarte et al., 2011) as well as within-species differences under different tidal regimes (López-Duarte and Tankersley, 2007) or during different developmental stages (Darnell et al., 2010; Forward et al., 2007). These underlying mechanisms influence estuarine-dependent species' population dynamics and responses to oceanic and environmental variables. Comparable experimental techniques for investigating these mechanisms are essential to distinguishing species and life history stage differences.

Selective tidal-stream transport is accomplished through behavioral responses to environmental cues associated with the flood/ebb tidal cycle or endogenous activity rhythms timed to a particular tidal phase. Endogenous activity rhythms are cyclical variations in activity that persist under constant conditions for at least five cycles (free running rhythms) and have period lengths near those of environmental cycles (Forward and Tankersley, 2001). The combinations of behaviors that comprise STST have been described in detail for only a few species such as the blue crab *Callinectes sapidus*. Blue crab postlarvae (megalopae) are transported shoreward by wind-driven currents (Ogburn et al., 2009, 2012) and move from planktonic to benthic habitats in response to changes in water chemistry (Forward and Rittschof, 1994). Megalopae swim up into the water column during nighttime flood tides in response to increasing salinity, remain swimming in response to turbulence, and descend at the end of flood tide as turbulence declines (Forward et al., 2003). Upon reaching estuarine nursery habitats via FTT, megalopae

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0022-0981/$ – see front matter
http://dx.doi.org/10.1016/j.jembe.2012.12.007

Table 1
List of endogenous rhythm experiments including the shrimp species and life history stage of individuals used for each experiment, sampling site, the start date of the experiment, the number of individuals tested, and the temperature and salinity during sampling at the collection site. Shrimp species are brown shrimp *Farfantepenaeus aztecus*, pink shrimp *Farfantepenaeus duorarum*, and white shrimp *Litopenaeus setiferus*. Experiments with postlarvae were conducted using groups of 25 individuals.

Species	Stage	Site	Date	N	Temp	Sal
F. aztecus	Postlarvae	GA	24 March 2011	25 (group)	19	28
F. aztecus	Juveniles	GA	28 April 2010	6	24	21
F. duorarum	Postlarvae	FL	4 June 2009	25 (group)	29	50
F. duorarum	Postlarvae	FL	15 August 2009	25 (group)	34	37
F. duorarum	Juveniles	FL	15 August 2009	1	34	37
F. duorarum	Juveniles	FL	7 August 2010	6	33	40
L. setiferus	Postlarvae	GA	15 July 2009	25 (group)	29	30
L. setiferus	Juveniles	GA	8 July 2009	1	29	23
L.setiferus	Juveniles	GA	26 July 2010	6	32	22

molt to the juvenile phase and undergo a shift in endogenous vertical swimming activity from predominantly daytime activity as megalopae to nighttime activity as juveniles (Forward et al., 2007) before dispersing within estuaries at night (Reyns and Eggleston, 2004). Thus, STST can involve a series of complex behaviors including endogenous activity rhythms, responses to environmental cues, and ontogenetic shifts in behavior.

This study investigates STST in the ecologically and commercially important penaeid shrimp: brown shrimp (*Farfantepenaeus aztecus* Ives), pink shrimp (*Farfantepenaeus duorarum* Burkenroad), and white shrimp (*Litopenaeus setiferus* Linnaeus). These species support important fisheries in the United States from North Carolina to Texas and in the southern Gulf of Mexico and are important components of estuarine ecosystems (Beseres and Feller, 2007; Gleason and Wellington, 1988; McTigue and Zimmerman, 1991; Minello and Zimmerman, 1983; Schwamborn and Criales, 2000). Species distribution differs. The brown shrimp is most abundant in relatively muddy sediments in Texas and Bay of Campeche; the pink shrimp is most abundant in sandy sediments found in Dry Tortugas, Florida Bay, Bay of Campeche, and parts of North Carolina; and the white shrimp is most abundant in muddy sediments in Georgia, north Florida, Louisiana, Tabasco, and Bay of Campeche (Williams, 1984). Causes of these distributional differences are poorly understood but could include differences in larval transport, habitat or prey preferences, salinity tolerance, and competition.

Field studies of brown, pink, and white shrimp provide evidence that they, like blue crabs, use STST to complete ontogenetic migrations. Each species spawns on the continental shelf, and larvae develop in offshore waters while approaching coastal areas (Munro et al., 1968; Rogers et al., 1993). Larval development is rapid, approximately 30 d, and larvae pass through five nauplii, three protozoeae, three mysis, and three to six postlarval stages (Cook and Murphy, 1971; Dobkin, 1961). Larval migration from spawning to nursery grounds occurs in a succession of stages affected by tidal currents, winds, and specialized larval behaviors (Criales et al., 2007; Rogers et al., 1993). Postlarvae are caught in estuarine water columns in highest numbers during nighttime flood tides (Copeland and Truitt, 1966; Criales et al., 2011, 2006; Duronslet et al., 1972; Roessler and Rehrer, 1971; Wenner and Beatty, 1993; Wenner et al., 2005, 1998; Williams and Deubler, 1968). Pink shrimp postlarvae may also occur in the upper water column during daytime flood tides (Criales et al., 2007). Postlarvae settle in nursery habitats (seagrass beds or emergent marsh or mangrove fringe) and transition to the juvenile phase (Heck et al., 2003; Zimmerman et al., 2002). They grow rapidly in nursery habitats (Browder et al., 2002; Heck et al., 2003) and return to the ocean as late juveniles or subadults (Costello and Allen, 1966; Fry, 1981; Fry et al., 1999) during nighttime ebb tides (Criales et al., 2011; Hughes, 1972).

Table 2
Shrimp species, life history stage, means and standard deviations of period lengths of significant free running rhythms, number of replicates used to calculate each mean (N), and the phase of the tidal or diel cycle at field collection sites during the time of peak swimming in the laboratory. Each replicate for postlarvae indicates one group of 25 individuals.

Species	Stage	Period (h)	N	Time of peak swimming
F. aztecus	Postlarval	12.5/25.0	1	Early flood tide
F. aztecus	Juvenile	12.3 ± 0.6	6 of 6	Ebb tide
F. duorarum	Postlarval	12.7 ± 0.2	2	Early flood tide
F. duorarum	Juvenile	23.8 ± 3.7	7 of 7	Night
L. setiferus	Postlarval	None	1	None
L. setiferus	Juvenile	12.3 ± 0.4	2 of 7	Early flood tide

Limited prior experimental investigation suggests an influence of endogenous behavior in the STST of at least two of these shrimps. Possible endogenous swimming activity rhythms have been observed in brown and pink shrimp postlarvae (Hughes, 1972; Matthews et al., 1991). Both brown and pink shrimp postlarvae swim more actively in dark conditions and in response to increasing salinity, whereas swimming is reduced by light and decreasing salinity (Hughes, 1968; Matthews et al., 1991). On the other hand, Keiser and Aldrich (1976) did not observe endogenous activity rhythms in either postlarval brown or white shrimp. Large, late-juvenile pink shrimp exhibit a circadian activity rhythm by burrowing during the day and becoming active and feeding during the night (Fuss and Ogren, 1966; Hughes, 1968). Some prior studies failed to meet the criterion of sustained cyclical activity for at least five cycles, and none included precise calculations of the duration of activity rhythms.

This comparative study addressed endogenous activity rhythms with two primary hypotheses. The first was that postlarval brown, pink, and white shrimp exhibit circatidal endogenous rhythms in vertical swimming activity that promote transport into estuaries during nighttime flood tides (FTT). The second was that, between postlarval and small juvenile phases, a shift will occur in either period length of activity rhythms or timing of peak activity with respect to the tidal or diel cycle.

Study objectives were to: 1) determine whether brown, pink, and white shrimp postlarvae and juveniles exhibit endogenous rhythms in vertical swimming activity, 2) compare activity rhythms to local tidal and diel cycles, and 3) compare activity rhythms among the three species to describe species-specific behaviors underlying STST of penaeid shrimp. Endogenous activity rhythms that contribute to STST may be fundamental components of ontogenetic migrations key to their life history. Behavioral differences might help to improve species management by explaining observed habitat and distribution differences and year-to-year variation in abundance.

2. Materials and methods

2.1. Field collections

Pink shrimp postlarvae (9.1–11.5 mm total length [TL]) and small juveniles (20–40 mm TL) were collected in western Florida Bay during summer in 2009 and 2010. Both postlarvae and juveniles were collected during nighttime flood tides from a tidal channel (Joe Kemp) using channel nets (850 μm mesh net with 500 μm mesh cod end) deployed from a small boat at 30-min intervals. Salinity and temperature were measured in the field using a YSI 85. Postlarvae and juveniles were sorted at an Everglades National Park facility near the Flamingo dock and transported by car on the same night to the University of Miami's Rosenstiel School of Marine and Atmospheric Sciences (RSMAS). For the 4 June 2009 experiment, postlarvae were held in flow-through seawater tanks and fed brine shrimp nauplii once daily prior to experimentation (<24 h). For the 15 August 2009 and 7 August 2010 experiments, postlarvae and juveniles were shipped to Savannah State University (SSU) in Savannah, GA on American Airlines, arriving in the lab at SSU approximately 8 h after