A behavioral mechanism for dispersal in fiddler crab larvae (genus *Uca*) varies with adult habitat, not phylogeny

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Abstract

The genus *Uca* (fiddler crabs) includes both estuarine and coastal species, the zoeae of which must travel varying distances to reach the sea. Rapid seaward transport following hatching may be facilitated by tidal currents through an ebb-phased circatidal rhythm in vertical swimming by larvae. Assuming there is a cost to vertical swimming, we predicted that endogenous swimming rhythms would be stronger in zoeae of species that live far up estuaries (oligohaline and mesohaline areas) and weaker or absent in coastal species and that adult ecology, not phylogeny, would best explain interspecific variation in vertical swimming rhythms. Both predictions were confirmed. Ovigerous females of 15 *Uca* species in 4 subgenera were collected from 10 locations along the Atlantic and Gulf Coasts of the United States and the Pacific and Caribbean coasts of Panama. Swimming activity of zoeae-1 larvae was recorded under constant conditions for 72 h. Regardless of subgenus, estuarine species exhibited ebb-phased circatidal swimming rhythms that persisted for several cycles and matched the tidal patterns at the collection sites, while the swimming of coastal species was arrhythmic. Species-specific differences in the proximity of adult habitats and hatching areas to the sea accounted for differences in larval behavior that promotes seaward transport. Vertical swimming rhythms of larvae may have evolved together with other traits that permit estuarine living.

Many invertebrate and fish species that spawn in estuaries develop offshore and then return to estuaries, where they settle and recruit to adult populations (reviewed by Young 1995; Forward and Tankersley 2001; Queiroga and Blanton 2005). Dispersal of larvae offshore may minimize their exposure to physiologically stressful conditions and to abundant predators in shallow upper estuarine waters (reviewed by Morgan 1987; Morgan and Christy 1997; Christy 2003). Many estuarine brachyuran crab species facilitate offshore transport by releasing larvae near the time of high tide on the larger-amplitude nocturnal spring tides (reviewed by Christy 2011). Once in the water column, larvae remain near the surface and are dispersed rapidly down-estuary away from adult habitats by ebbing currents (Christy and Stancyk 1982; Epifanio et al. 1984, 1989).

Down-estuary movement can be assisted by the coupling of vertical swimming of larvae with the phase of tidal currents (i.e., selective tidal-stream transport [STST]; reviewed by Forward and Tankersley 2001; Gibson 2003). During STST, predictable changes in the horizontal direction and vertical distribution of tidal currents are used to achieve unidirectional (seaward or shoreward) transport. One kind of swimming behavior that enhances down-estuary transport is an ascent of larvae during the ebb-phase of the tides, resulting in horizontal advection seaward by strong surface currents and a descent into slower bottom currents during the flood-phase, which reduces up-estuary displacement (Forward and Tankersley 2001). Ebb-phased vertical swimming results in ebb-tide transport (ETT), whereas flood-phased vertical swimming promotes up-estuary migration or flood-tide transport (FTT) (Forward and Tankersley 2001).

Vertical swimming underlying STST can be controlled by changes in pressure, salinity, temperature, or turbulence associated with the tide, or swimming activity can be under endogenous control (Forward and Tankersley 2001). Circatidal rhythms mediating STST behaviors have been reported in juvenile glass eels *Anguilla rostrata* (Wipplehauser and McCleave 1988), juvenile plaice *Pleuronoctes plastessa* (Gibson 1973), spot *Leiostomus xanthurus* and pinfish *Lagodon rhomboids* larvae (Forward et al. 1998), ovigerous female blue crabs *Callinectes sapidus* (Forward et al. 2003), fiddler crab *Uca* spp. megalopae (Tankersley and Forward 1994), and newly hatched larvae of both the horseshoe crab *Limulus polyphemus* (Ehlinger and Tankersley 2006) and the shore crab *Carcinus maenas* (Zeng and Naylor 1996a,b,c). More recent studies indicate that zoeae of the fiddler crabs *Uca pugilator* (López-Duarte and Tankersley 2007a,b; Morgan and Anastasia 2008) and *Uca minax* (López-Duarte and Tankersley 2009) also exhibit a circatidal rhythm, in which peaks in larval swimming occur near the expected time of ebb tide in the field. Adults of both species live within estuaries, yet their larvae are transported rapidly to the sea (Christy and Stancyk 1982; Brodie et al. 2007). Hence, these circatidal rhythms together with precise timing of larval release are thought to facilitate rapid down-estuary transport (López-Duarte and Tankersley 2007a,b, 2009). However, it is unknown whether vertical swimming that facilitates ETT is widespread among species of *Uca* or whether it varies with phylogeny or

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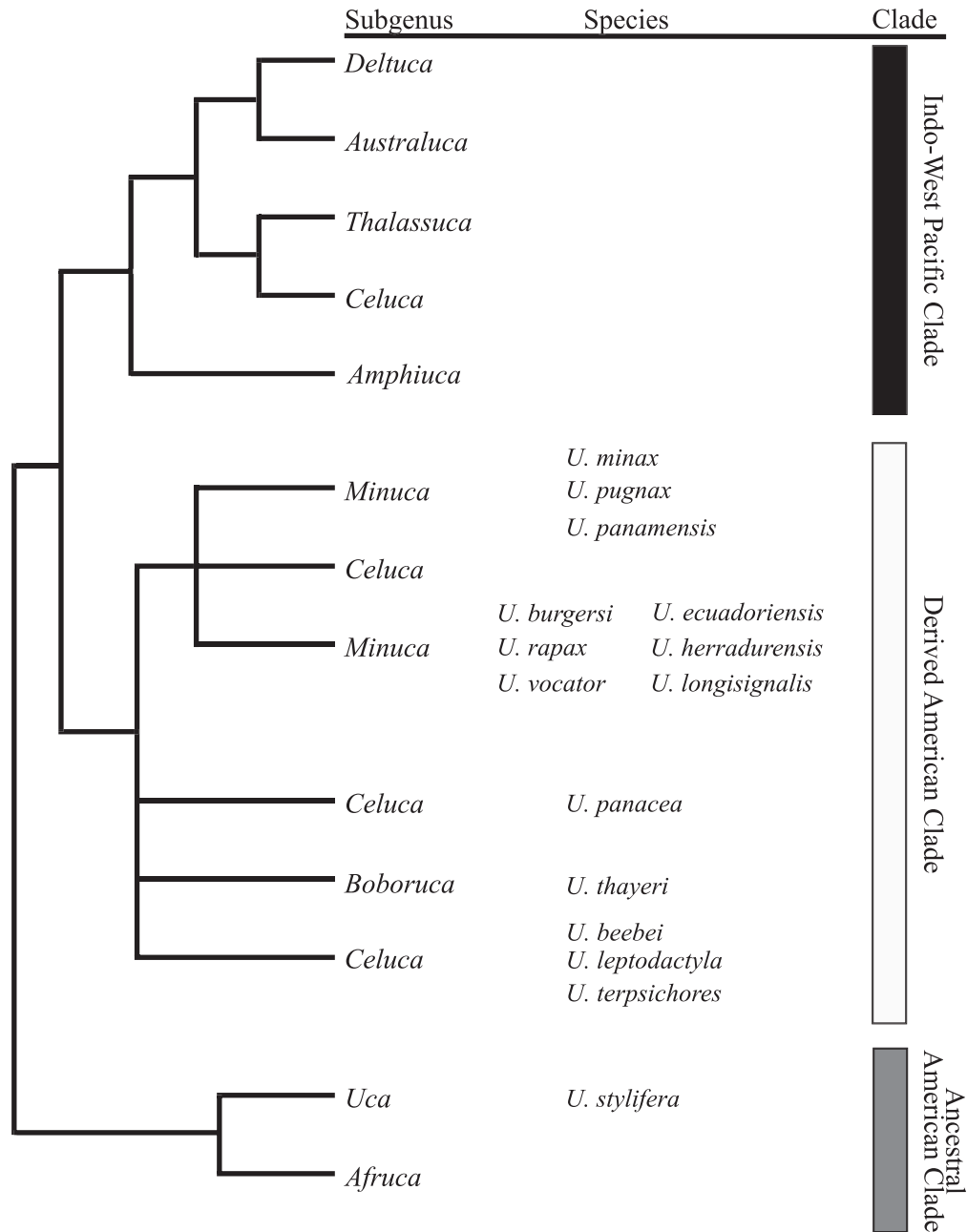
Fig. 1. *Uca* spp. phylogeny includes the 15 species examined in this study. Consensus tree is modified from Sturmbauer et al. (1996) and is based on a set of independent molecular characters (16S ribosomal deoxyribonucleic acid) for nine subgenera (28 species).

with adult habitat. We explored these two hypotheses for the first time in this study.

Fiddler crabs (*Uca* spp.) inhabit tropical to warm temperate coasts and estuaries worldwide (Crane 1975), and around 100 species have been described to date (Rosenberg 2001). The genus *Uca* has been historically divided into three clades (Fig. 1). Molecular analysis by Sturmbauer et al. (1996) indicates that the subgenera *Uca* and *Afruca* (American ancestral clade) split from the other species ca. 22 million yr B.P. The remaining species divided further into two groups ca. 17 million yr B.P. These are usually referred to as the derived American and the Indo-west Pacific clades (Sturmbauer et al. 1996). Subgenera of the derived American clade include *Boboruca*, *Celuca*, and *Minuca* (Rosenberg 2001; Fig. 1).

Twelve species of fiddler crabs are known to inhabit the Atlantic and Gulf of Mexico coasts of the United States (Barnwell and Thurman 1984), and an additional species (*Uca major*) occurs on the Caribbean coast of Central America (Crane 1975). In contrast, 27 species live on the Pacific coast of Central America, i.e., more than on any other coastline of comparable extent in the world (Crane 1975). Fiddler crabs occur in the intertidal and supratidal zones on protected coasts and throughout estuaries, and, in

general, a given species will be found on sediments with specific characteristics. Hence, the location of a species is determined largely by the physical and biotic processes that control sediment transport, deposition, and accumulation within its range (Crane 1941, 1975). In conjunction with their sediment preferences, fiddler crab species differ as adults in salinity preferences and tolerances (Thurman 2002, 2003). Thus, with few exceptions, species can be reliably assigned to oligohaline, mesohaline, or euhaline areas within the same estuary. Species-typical sediment and habitat distributions of fiddler crab species appear to be more closely related to their osmoregulatory ability and salinity tolerance than their phylogenetic relationship (Thurman 2002, 2003).

Vertical swimming by newly hatched zoeae for ETT from estuaries is likely to be associated with the distance between adult habitats and the sea (López-Duarte and Tankersley 2007*a*). Larvae that are released at the time of high tide near inlets or on adjacent coasts (euhaline habitats) should be transported by ebbing currents rapidly away from the adult habitat to the sea. In such species, selection for vertical swimming for ETT should be relatively weak. Assuming swimming is costly (Young 1995), these species should show weak or no ETT swimming behavior. In contrast, selection should be stronger for vertical swimming for ETT in species that release larvae inside estuaries in oligohaline and mesohaline habitats. Thus, STST behaviors exhibited by fiddler crab zoeae for emigration from estuaries and by postlarvae for immigration to adult habitats may be adaptations that, coupled with adult osmotic tolerance, have allowed fiddler crabs to diversify and occupy the full range of estuarine habitats. The objectives of the present study were to determine if the circatidal vertical swimming exhibited by *U. pugilator* (*Celuca*) and *U. minax* (*Minuca*) zoeae for ETT is common among members of the genus *Uca* and to determine whether the location of the adult habitat relative to coastal development areas (euhaline, mesohaline, or oligohaline: salinities of 30–35, 5–18, and 0.5–5, respectively) or phylogeny better predicted the presence and strength of circatidal swimming rhythms in zoeae. This study constitutes the first broad intraspecific test of the hypothesis that larval vertical swimming rhythms have evolved to promote larval emigration from estuaries to the coastal ocean.

Methods

Collection of ovigerous crabs—Ovigerous fiddler crabs (*Uca* spp.) with late-stage embryos within 2 d of hatching (De Vries et al. 1983; Brown and Loveland 1985) were collected by hand between May 2005 and November 2007 from 10 locations along the Atlantic and Gulf Coasts of the United States and the Pacific and Caribbean coasts of Panama (Fig. 2). The goal was to sample *Uca* spp. populations from a range of phylogenetic groupings and adult habitats. Habitats were classified as oligohaline (OH), mesohaline (MH), and euhaline (EH). Each species was assigned to one, or sometimes two, of the three habitat types based upon known distributions, habitat preferences,
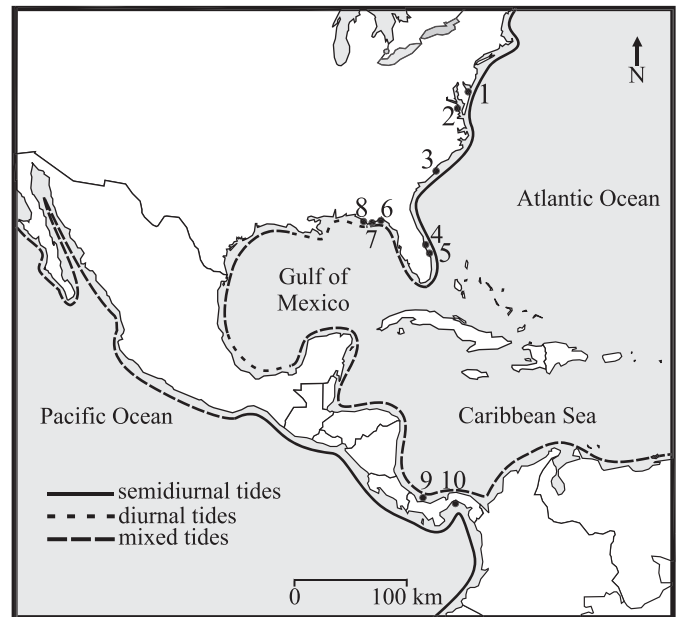

Fig. 2. Locations of collection sites for ovigerous fiddler crabs along the Atlantic and Gulf Coasts of the United States (1. Delaware Bay; 2. Chesapeake Bay; 3. Winyah Bay Estuary; 4. Sebastian Beach; 5. Ft. Pierce; 6. Wakulla Beach; 7. Turkey Point; 8. St. Joe Bay) and the Caribbean and Pacific coasts of Panama (9. Isla Colon and 10. Panama City). Dashed and solid lines along the coastlines indicate the distribution of the tidal regimes (semidiurnal, diurnal, and mixed).

and salinity tolerances of the adults (Crane 1975; Thurman 2003, 2005). Assignment of species to subgenera was based upon morphological (Rosenberg 2001) and molecular (Sturmbauer et al. 1996) studies. Fifteen species from four different subgenera (*Boboruca*, *Minuca*, *Celuca*, and *Uca*) were included in the study (Fig. 1; Table 1). Every effort was made to collect sympatric species and to sample the same species from areas with different tidal patterns.

Collection sites along the Atlantic Coast included locations in Delaware Bay (Lewes, Delaware), Chesapeake Bay (Point Lookout State Park, Maryland), Winyah Bay (Georgetown, South Carolina), and Indian River Lagoon (Coon Island and Jim's Isle, Ft. Pierce, Florida). Along the Gulf of Mexico, crabs were collected in St. Joe Bay, (Port St. Joe, Florida), St. James Island (Turkey Point, Florida), and Goose Creek Bay (Wakulla Beach, Florida). In Panama, crabs were collected along the Caribbean coast in the archipelago of Bocas del Toro (Smithsonian Marine Field Station, Isla Colon, Panama), and on the Pacific coast in Bahia de Panama (Smithsonian Punta Culebra Nature Center, Old Rodman Naval Base, and Diablo Heights, Panama City, Panama) (Fig. 2; Table 1).

Collection sites included areas with different tidal patterns and amplitudes (for complete description, *see* López-Duarte and Tankersley 2007*b*; Table 1). Locations along the Atlantic Coast of North America experience semidiurnal tides (tidal amplitude ~ 1 m). Both mixed and diurnal tidal regimes occur within the Gulf of Mexico (tidal amplitude ~ 0.5 m). In Panama, the Caribbean and Pacific

Table 1. Collection sites and associated tidal regimes, salinity conditions, and habitat preferences (OH, oligohaline; MH, mesohaline; EH, euhaline) for the 15 *Uca* spp. and two outgroup species (*Cardisoma guanhumi* and *Armases cinereum*) examined in the study. Adult habitat and salinity preferences are based on Crane (1975) and Thurman (2002, 2003, 2005). *See* Fig. 2 for map of collection locations.

Subgenus and species	Habitat	(Location) Collection site	Tidal regime	Latitude (°N)	Longitude (°W)
Boboruca					
U. thayeri	EH to MH	(9) Isla Colon, Panama	Mixed–semidiurnal	09°21′04.5″	82°15′25.2″
		(5) Ft. Pierce, Florida	Semidiurnal	27°28′40.4″	80°18′46.9″
Celuca					
U. beebei	EH	(10) Rodman Flats, Panama City, Panama	Semidiurnal	08°56′55.4″	79°34′23.7″
U. leptodactyla	EH	(5) Ft. Pierce, Florida	Semidiurnal	27°28′28.8″	80°17′50.7″
U. panamensis	EH	(10) Punta Culebra, Panama City, Panama	Semidiurnal	08°54′42.8″	79°31′45.2″
U. panacea	EH to MH	(7) Turkey Point, Florida	Mixed–semidiurnal	29°54′58.1″	84°30′37.7″
		(8) Port St. Joe, Florida	Diurnal	29°48′10.9″	85°18′06.4″
U. terpsichores	EH	(10) Rodman Flats, Panama City, Panama	Semidiurnal	08°56′55.4″	79°34′23.7″
Minuca					
U. burgersi	EH	(9) Isla Colon, Panama	Mixed–semidiurnal	09°21′04.5″	82°15′25.2″
U. ecuadoriensis	MH to OH	(10) Diablo Heights, Panama City, Panama	Semidiurnal	08°57′55.2″	79°34′12.9″
U. herradurensis	MH to OH	(10) Diablo Heights, Panama City, Panama	Semidiurnal	08°57′55.2″	79°34′12.9″
U. longisignalis	MH to OH	(8) Port St. Joe, Florida	Diurnal	29°48′10.9″	85°18′06.4″
		(6) Wakulla Beach, Florida	Mixed–semidiurnal	30°06′17.8″	84°15′41.6″
U. minax	OH	(2) Cape Lookout, Maryland	Semidiurnal	38°03′32.7″	76°19′50.3″
U. pugnax	MH	(1) Lewes, Delaware	Semidiurnal	38°47′18.3″	75°09′54.2″
		(3) Winyah Bay, South Carolina	Semidiurnal	33°21′01.5″	79°11′27.4″
U. rapax	EH	(9) Isla Colon, Panama	Mixed–semidiurnal	09°21′04.5″	82°15′25.2″
		(5) Ft. Pierce, Florida	Semidiurnal	27°28′40.5″	80°18′46.9″
U. vocator	EH	(9) Isla Colon, Panama	Mixed–semidiurnal	09°21′04.5″	82°15′25.2″
Uca					
U. stylifera	EH	(10) Rodman Flats, Panama City, Panama	Semidiurnal	08°56′55.4″	79°34′23.7″
Outgroups					
Cardisoma guanhumi	EH	(9) Isla Colon, Panama	Semidiurnal	09°21′04.5″	82°15′25.2″
		(4) Sebastian Beach, Florida	Semidiurnal	27°52′28.8″	80°27′19.9″
Armases cinereum	OH to MH	(3) Winyah Bay, South Carolina	Semidiurnal	33°21′01.5″	79°11′27.4″

coasts experience mixed (tidal amplitude ~ 0.3 m) and semidiurnal (tidal amplitude ~ 5 m) tides, respectively.

To determine whether ebb-phased circatidal rhythms in swimming are present in other brachyuran crabs and are linked to the location of the adult habitat relative to offshore development areas, ovigerous *Cardisoma guanhumi* (Family Gecarcinidae) and *Armases* (=*Sesarma*) *cinereum* (Family Grapsidae) were also collected at sites along the Atlantic Coast of North America and the Caribbean coast of Panama and treated as "outgroups" in the analysis (Table 1). Adult *C. guanhumi* inhabit terrestrial and semiterrestrial burrows in mangrove forests and other low-lying tropical coastal habitats. Ovigerous females migrate up to 5–6 km across land to release larvae near the time of high tide (Gifford 1962). *A. cinereum* adults occupy the high intertidal zone of salt marshes and mangrove forests throughout estuaries and typically occur sympatrically with several fiddler crab species, including *U. pugilator* and *Uca pugnax* (Teal 1958). A vertical swimming rhythm that would promote ETT has been recently reported in this species (Morgan and Anastasia 2008).

Ovigerous females were maintained individually in laboratory glass aquaria containing ~ 1 liter of filtered (< 5 μm) seawater with a salinity of 34 and temperature of 24–26°C. Newly hatched zoeae from the same egg mass were transferred to filtered (< 5 μm) seawater at a salinity of 34 and allowed to feed ad libitum on rotifers (*Brachionus* sp.) for 1 h prior to being used in experiments.

Monitoring and analysis of larval activity—Larval swimming was monitored under constant conditions using a time-lapse video system (López-Duarte and Tankersley 2007*a,b*, 2009). Approximately 200–500 stage I larvae from one female were placed in a clear rectangular Lucite chamber (interior dimensions: 5 cm × 5 cm × 19 cm) filled with < 5-μm filtered seawater at salinity of 35. Full-strength seawater was used for all experiments regardless of the location of the collection site, since *Uca* larvae, even

those from low-salinity areas of estuaries, survive best at near-oceanic salinities (Morgan 1987; Brodie et al. 2007), and previous studies have indicated that the salinity has no effect on larval swimming behaviors (López-Duarte and Tankersley 2009). The top of the chamber was partially sealed with a clear plastic lid to prevent evaporation. Temperature was maintained at 24°C. Larval swimming was monitored continuously for 72 h using a video system consisting of a black-and-white video camera (Panasonic BP 334) attached to a video frame-grabber board (VCE-Pro, Imperx) running on a laptop computer (Inspiron 8200, Dell Corp.). The chamber was back-illuminated with constant far-red light (maximum transmission 775 nm), to which crab larvae are insensitive (Forward and Cronin 1979). Thus, recordings were made of larvae that were in perceived darkness. The camera's focal length, field of view, and depth of field were adjusted to record the number of larvae in the upper one third of the chamber. Imaging software (Video Capture Essentials Pro 2.6, Imperx) controlling the frame grabber captured and stored digitized (720 × 500 pixels) images of the upper portion of the chamber at 0.5-h intervals. Time series of swimming activity were constructed by counting the number of larvae swimming in each frame and plotting those numbers as a function of time. For each crab species and population sampled (Table 1), trials were repeated four times ($n = 4$) using larvae from single clutches of four different females.

Time series of larval activity were analyzed for rhythmicity using both visual inspection and Lomb-Scargle periodogram analysis of the actograms (Scargle 1982; Ruf 1999; Autosignal, SeaSolve Software). Larval swimming activity was classified as ''rhythmic-circatidal'' (RC) if actograms contained regular oscillations in activity that continued for at least three cycles and had a dominant period that was statistically significant and close to the length of the periods of one (for areas with semidiurnal and diurnal tides) or both of the dominant tidal constituents (for areas with mixed tides) at the collection site. Thus, crabs from areas with semidiurnal and diurnal tides were expected to have rhythms with free-running periods around 12.4 h (range: 11–13 h) and 24–24.8 h (range: 22–27 h), respectively (López-Duarte and Tankersley 2007b; Morgan and Anastasia 2008). Larvae from mixed tidal systems were expected to have rhythms that included cycles around 12.4 h (circatidal), 24–24.8 h (circadian or circalunidian), or both. Dominant periodic signals in the activity traces were determined by constructing periodograms, i.e., plots of normalized power values (magnitude-square of the Lomb spectrum) as a function of period (h). Peak values in the periodogram that exceeded the 95% confidence interval (calculated using Monte Carlo trials) were considered to be statistically significant at $\alpha = 0.05$ (Scargle 1982; Chatfield 1989). Time series that contained oscillations in activity lasting less than three cycles, regardless of whether they were corroborated by significant tide-related peaks in the periodograms (i.e., cycles with periods outside of the expected values for a circatidal rhythm), were classified as being ''weakly rhythmic'' (WR) rather than rhythmic-circatidal (RC). Activity traces that lacked any apparent oscillations in swimming activity were classified as ''ar-

rhythmic'' (AR), even if they contained spurious significant peaks in the periodograms at periods that were consistent with tidally related cycles in activity.

If a significant circatidal rhythm was determined to be present in the actograms for at least three of the four replicates for a crab species from the same location, then the zoeae were considered to possess a circatidal rhythm in swimming. Synchrony between larval activity and the expected tidal cycle at the collection site (Table 1) was determined using cross-correlation analysis (SPSS 17.0, SPSS). Predicted tidal heights relative to mean lower low water (MLLW) for all locations were obtained from Tides and Currents Pro 2.5 (Nautical Software). Plots of cross-correlations as a function of lag interval (1 lag = 0.5 h) were used to determine the phase relationship between larval swimming and tide stage. Thus, statistically significant peaks at positive or negative lags indicated that maximum swimming activity occurred that many hours after (+ lags) or before (− lags) the time of expected high tide. Cross-correlation values that exceeded the 95% confidence intervals ($\pm 2/\sqrt{N}$) were considered to be statistically significant (Chatfield 1989).

Results

When monitored under constant conditions, *Uca* stage I zoeae displayed three general patterns in swimming activity. The first pattern was a lack of an apparent rhythm in vertical swimming (arrhythmic; AR). Only species from coastal areas and euhaline (EH) regions of estuaries were arrhythmic (Table 2). Larvae either remained near the surface for the duration of the trial (e.g., Fig. 3A–C), or activity levels were initially high but declined precipitously after 24–36 h, so that relatively few larvae were swimming in the upper portion of the chamber at the end of the recording period (e.g., Fig. 3D,E). Although activity levels were low at the end of the trial, larval survival was > 75%. Species displaying this pattern included *Uca beebei*, *Uca burgersi*, *Uca leptodactyla*, *Uca panamensis*, *Uca rapax* (from Isla Colon, Panama), *Uca stylifera*, *Uca terpsichores*, *Uca thayeri* (from Isla Colon, Panama), *Uca vocator*, and the outgroup species *Cardisoma guanhumi* (Table 2; Figs. 3, 4A,B; *see* Web Appendix: http://www.aslo.org/lo/toc/vol_56/issue_5/1879a1.pdf).

The second pattern was a weak rhythm in vertical migratory behavior that lasted for less than three cycles (weakly rhythmic; WR). At the beginning of the trials, larvae would swim for periods toward the upper portion of the test chamber, but then the numbers of swimming larvae would decrease (e.g., Fig. 5). However, the magnitude of the relative change in abundance in the upper chamber of the column was often minimal (30–40%). After the initial oscillations (lasting 24–48 h), larvae either swam arrhythmically near the surface for the remainder of the trial (e.g., Fig. 5E), or they swam little, and their numbers near the surface declined (e.g., Fig. 5A–C). Periodogram analysis often failed to detect these weak, short-duration swimming rhythms (i.e., no peaks exceeded the 95% confidence interval). Species displaying this weakly rhythmic pattern were found predominantly in euhaline areas as adults and

Table 2. Classification of time series of swimming activity of fiddler crab zoeae from each sampling location (OH, oligohaline; MH, mesohaline; EH, euhaline). Far-right columns contain the number of replicate trials (out of 4) in which the activity pattern was classified as rhythmic-circatidal (RC), weakly rhythmic (WR), or arrhythmic (AR). Species in bold met the criteria for possessing an ebb-phased endogenous tidal rhythm in vertical swimming activity.

Species	Habitat	Collection site	Tidal regime	Activity pattern RC	WR	AR
U. beebei	EH	Rodman Flats, Panama City, Panama	Semidiurnal	—	1	3
U. burgersi	EH	Isla Colon, Panama	Mixed–semidiurnal	—	2	2
U. leptodactyla	EH	Ft. Pierce, Florida	Semidiurnal	—	3	1
U. panamensis	EH	Punta Culebra, Panama City, Panama	Semidiurnal	—	—	4
U. rapax	EH	Isla Colon, Panama	Mixed–semidiurnal	—	2	2
		Ft. Pierce, Florida	Semidiurnal	1	3	—
U. stylifera	EH	Rodman Flats, Panama City, Panama	Semidiurnal	—	2	2
U. terpsichores	EH	Rodman Flats, Panama City, Panama	Semidiurnal	—	3	1
U. vocator	EH	Isla Colon, Panama	Mixed–semidiurnal	—	1	3
U. thayeri	EH to MH	Isla Colon, Panama	Mixed–semidiurnal	—	1	3
		Ft. Pierce, Florida	Semidiurnal	1	3	—
U. panacea	EH to MH	Turkey Point, Florida	Mixed–semidiurnal	4	—	—
		Port St. Joe, Florida	Diurnal	3	1	—
U. pugnax	EH to MH	Lewes, Delaware	Semidiurnal	4	—	—
		Winyah Bay, South Carolina	Semidiurnal	4	—	—
U. ecuadoriensis	MH to OH	Diablo Heights, Panama City, Panama	Semidiurnal	4	—	—
U. herradurensis	MH to OH	Diablo Heights, Panama City, Panama	Semidiurnal	4	—	—
U. longisignalis	MH to OH	Port St. Joe, Florida	Diurnal	3	1	—
		Wakulla Beach, Florida	Mixed–semidiurnal	3	1	—
U. minax	OH	Cape Lookout, Maryland	Semidiurnal	4	—	—
Outgroups						
Cardisoma	EH	Isla Colon, Panama	Semidiurnal	—	1	3
guanhumi		Sebastian Beach, Florida	Semidiurnal	—	1	3
Armases cinereum	OH to MH	Winyah Bay, South Carolina	Semidiurnal	4	—	—

included *U. beebei, U. burgersi, U. leptodactyla, Uca longisignalis, Uca panacea* (from Port St. Joe, Florida), *U. rapax, U. stylifera, U. terpsichores, U. thayeri, U. vocator,* and *C. guanhumi* (Fig. 5; Table 2; *see* Web Appendix for summary).

All species that exhibited a pronounced endogenous tidal rhythm in swimming for at least three cycles (classified as RC) were collected from mesohaline and oligohaline areas of estuaries. They included *Uca ecuadoriensis, Uca herradurensis, U. longisignalis, U. minax, U. panacea, U. pugnax,* and the outgroup *Armases cinereum* (Figs. 4C, 6, 7; Table 2; *see* Web Appendix). Although larvae from one clutch of *U. thayeri* from Ft. Pierce were rhythmic-circatidal, larvae from the remaining three females expressed only weak rhythms (Table 2). In general, the swimming rhythms of zoeae of these species consisted of an active phase, in which most of the individuals swam in the upper portion of the experimental chamber for several hours, followed by an inactive phase, in which $< 30\%$ of the larvae were present in the top portion of the chamber (e.g., *U. pugnax*; Fig. 6A). The number of activity peaks per day varied according to the tidal pattern at the collection site. Larvae from semidiurnal regimes exhibited two activity peaks per day of approximately equal amplitude (Fig. 6). Periodogram analyses confirmed that the dominant period matched the period of the dominant semidiurnal tidal constituent ($M_2 = 12.42$ h; $\bar{X} \pm$ SE, 12.43 $\pm$ 0.05 h, $n = 24$, all species combined). Zoeae from mixed tidal regimes exhibited alternating cycles in activity that had slightly different amplitudes (Fig. 7A,B). Periodograms for these time series contained significant activity peaks at $\sim$ 12.4 h and 24–25 h ($\bar{X} \pm$ SE, 12.37 $\pm$ 0.13 h, $n = 7$; $\bar{X} \pm$ SE, 22.12 $\pm$ 0.55 h, $n = 5$), which correspond closely to the periods of the dominant tidal constituents of mixed tidal patterns (semidiurnal [$M_2 = 12.42$ h] and diurnal [$K_1 = 23.93$ h and $O_1 = 25.82$ h]). Zoeae of species collected from areas with diurnal tides exhibited one swimming cycle per day, which was confirmed by single significant peaks in the periodograms at $\sim$ 24.8 h (e.g., Fig. 7C,D; $\bar{X} \pm$ SE, 24.01 $\pm$ 0.23 h, $n = 6$). These larvae continued to swim for the duration of the trials with little dampening, suggesting that their swimming rhythms most likely continued for several cycles beyond the 72-h observation period. Dampening of the rhythm in later cycles was most likely a result of a decline of energy reserves, since $> 75\%$ of the larvae were still alive at the end of the recording time.

For trials with significant peaks in the periodogram analysis, the synchrony between rhythms observed in the time series and the expected tidal cycle at the corresponding collection site was determined using cross-correlation analysis. In species from areas with semidiurnal tides, maximum cross-correlation coefficients were found between 1- and 4-h lags after high tide ($\bar{X} \pm$ SE, 3.06 $\pm$ 0.20 h, $n = 24$), corresponding to the expected time of peak ebb-currents. The pattern was similar for larvae from areas with different tide patterns, with maximum cross-correlation coefficients at 3.43 $\pm$ 0.43 h ($\bar{X} \pm$ SE; $n = 7$) for

A) *Uca burgersi* (Isla Colon, Panama)

C) *Uca vocator* (Isla Colon, Panama)

18.29

D) *Uca beebei* (Rodman Flats, Panama City, Panama)

E) *Uca panamensis* (Punta Culebra, Panama City, Panama)

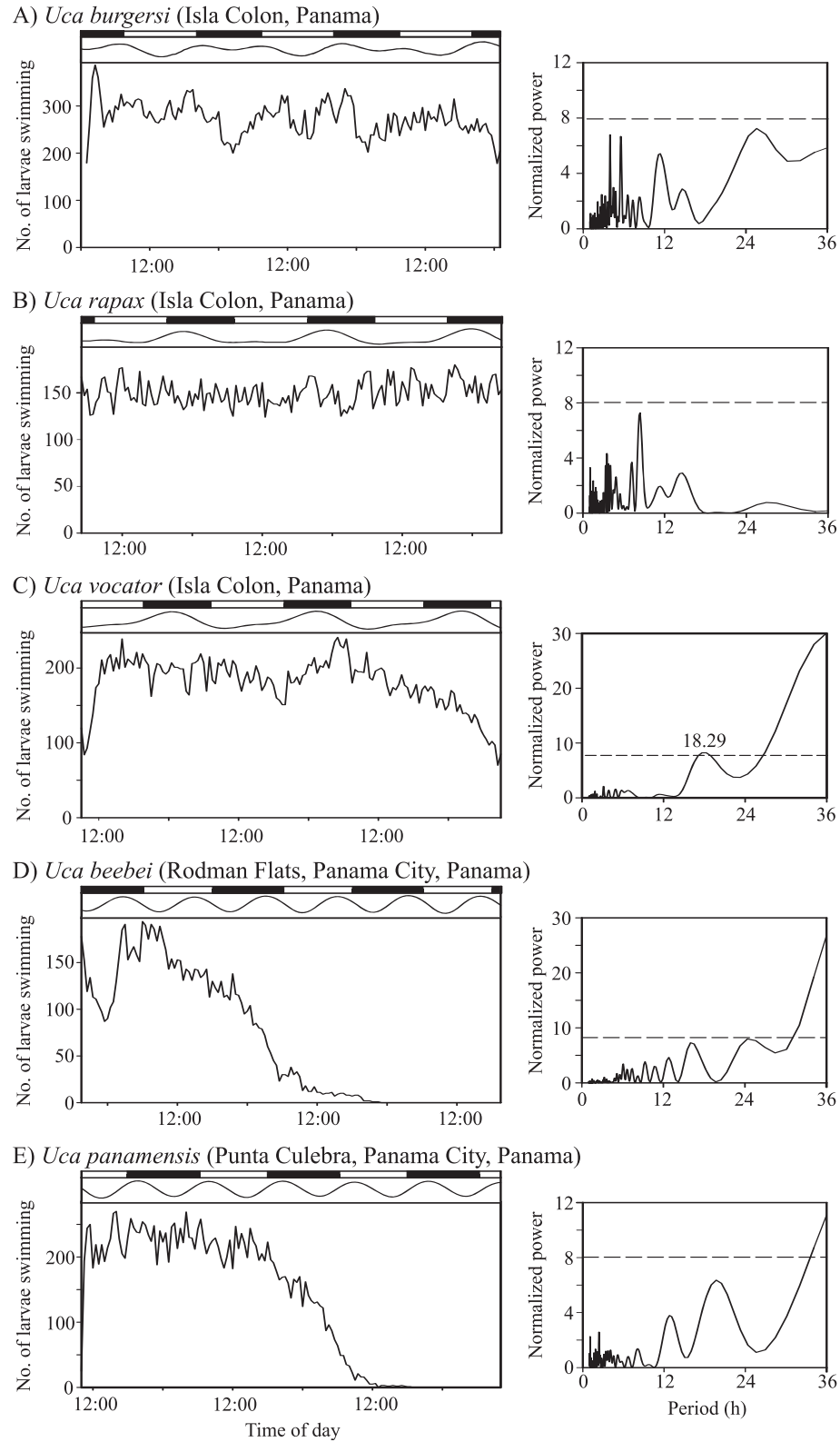B) *Uca rapax* (Isla Colon, Panama)

Time of day

Period (h)

Fig. 3. Representative actograms (left panels) and corresponding periodograms (right panels) for crab larvae that exhibited swimming behaviors classified as arrhythmic (AR). Groups of larvae from the same brood were monitored under constant conditions for 72 h. Expected tidal and day–night cycles are indicated above the actograms. Dashed horizontal lines in the periodograms indicate the 95% confidence intervals. Lengths (in h) of dominant periods in the periodograms are indicated above statistically significant ($p < 0.05$) peaks.
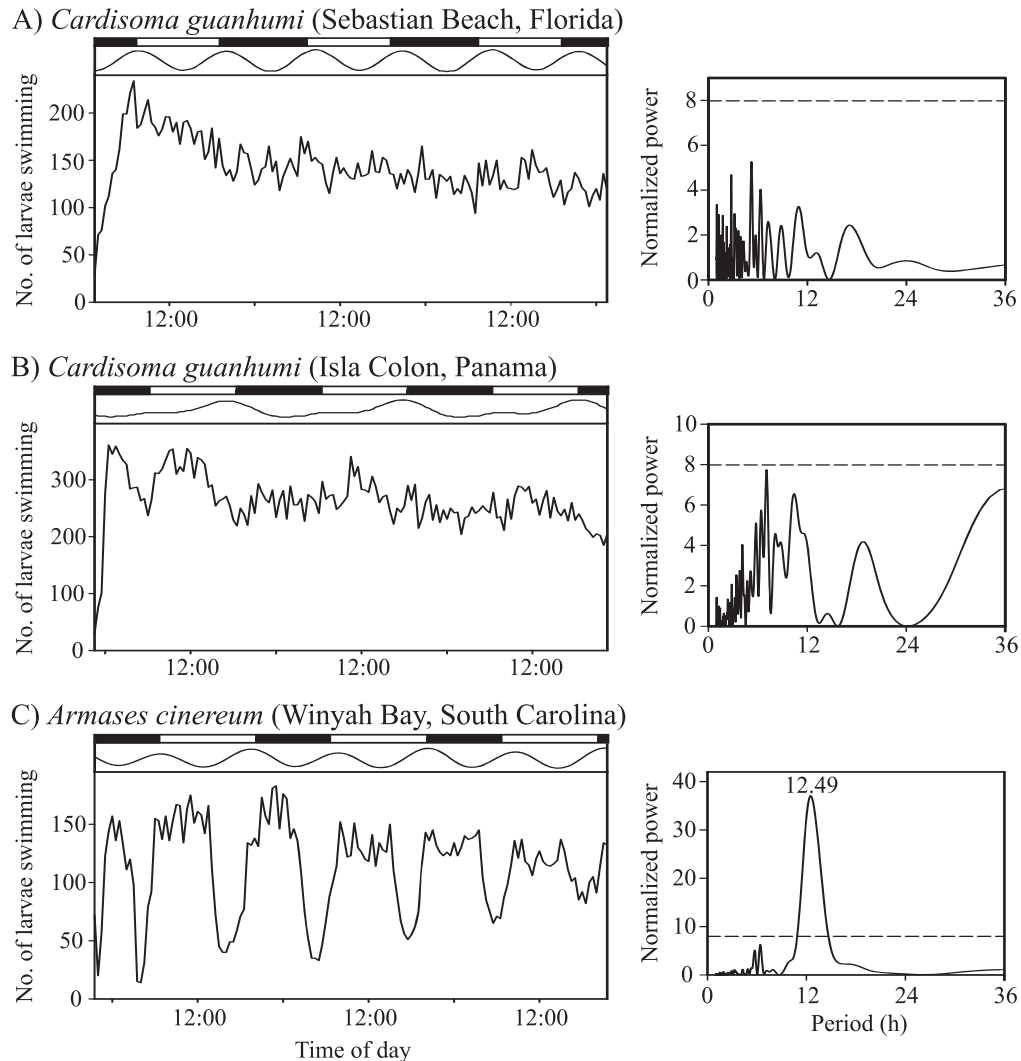
Fig. 4.   Representative actograms (left panels) and the corresponding periodograms (right panels) for *Cardisoma guanhumi* and *Armases cinereum* larvae collected from areas with semidiurnal tides. Time series for *C. guanhumi* and *A. cinereum* were classified as arrhythmic (AR) and rhythmic-circatidal (RC), respectively. Further details are in the legend for Fig. 3.

species from mixed tide areas, and 10.33 ± 1.74 h ($\bar{X} \pm$ SE; $n = 6$) for species from habitats with diurnal tides. In all cases, larvae were inactive during the flood phase of the tides at collection sites.

Discussion

Differences in the swimming activity of the 15 species of fiddler crabs in this study were primarily associated with differences in the location of adult habitats relative to the coastal ocean. Endogenous tidal rhythms in swimming were widespread among members of the "derived American clade" but were present only in those species that live as adults in mesohaline and oligohaline areas of estuaries (Table 2). Swimming rhythms exhibited by *U. ecuadoriensis*, *U. herradurensis*, *U. longisignalis*, *U. panacea*, and *U. pugnax* were similar in period and phase to those previously documented in larvae of *U. pugilator* (López-Duarte and Tankersley 2007*a,b*; Morgan and Anastasia 2008) and *U.*

minax (López-Duarte and Tankersley 2009). The periods of the circatidal rhythms of all these mid- and upper-estuarine species matched the periods of the dominant tidal constituents at the collection sites (~ 12.4 h in semidiurnal areas, ~ 12.4 h and ~ 24.8 h in mixed areas, and ~ 24.8 h in diurnal areas). Peaks in activity were synchronized with the expected time of ebb tide, indicating that the rhythms are appropriately timed to promote down-estuary transport (ETT) and export from the estuary.

Arrhythmic and weakly rhythmic patterns in swimming were observed in fiddler crab species that typically occur in coastal and lower-estuarine habitats (euhaline areas) as adults, including *U. beebei*, *U. burgersi*, *U. leptodactyla*, *U. panamensis*, *U. rapax*, *U. stylifera*, *U. terpsichores*, *U. thayeri*, and *U. vocator* (Table 2). The lack of consistent rhythmic swimming activity was confirmed by the absence of statistically significant peaks in the periodograms at periods that matched the tidal periods at the collection sites. In general, larvae of these species first moved toward

A) *Uca leptodactyla* (Ft. Pierce, Florida)

B) *Uca stylifera* (Rodman Flats, Panama)

C) *Uca terpsichores* (Rodman Flats, Panama)

D) *Uca rapax* (Ft. Pierce, Florida)
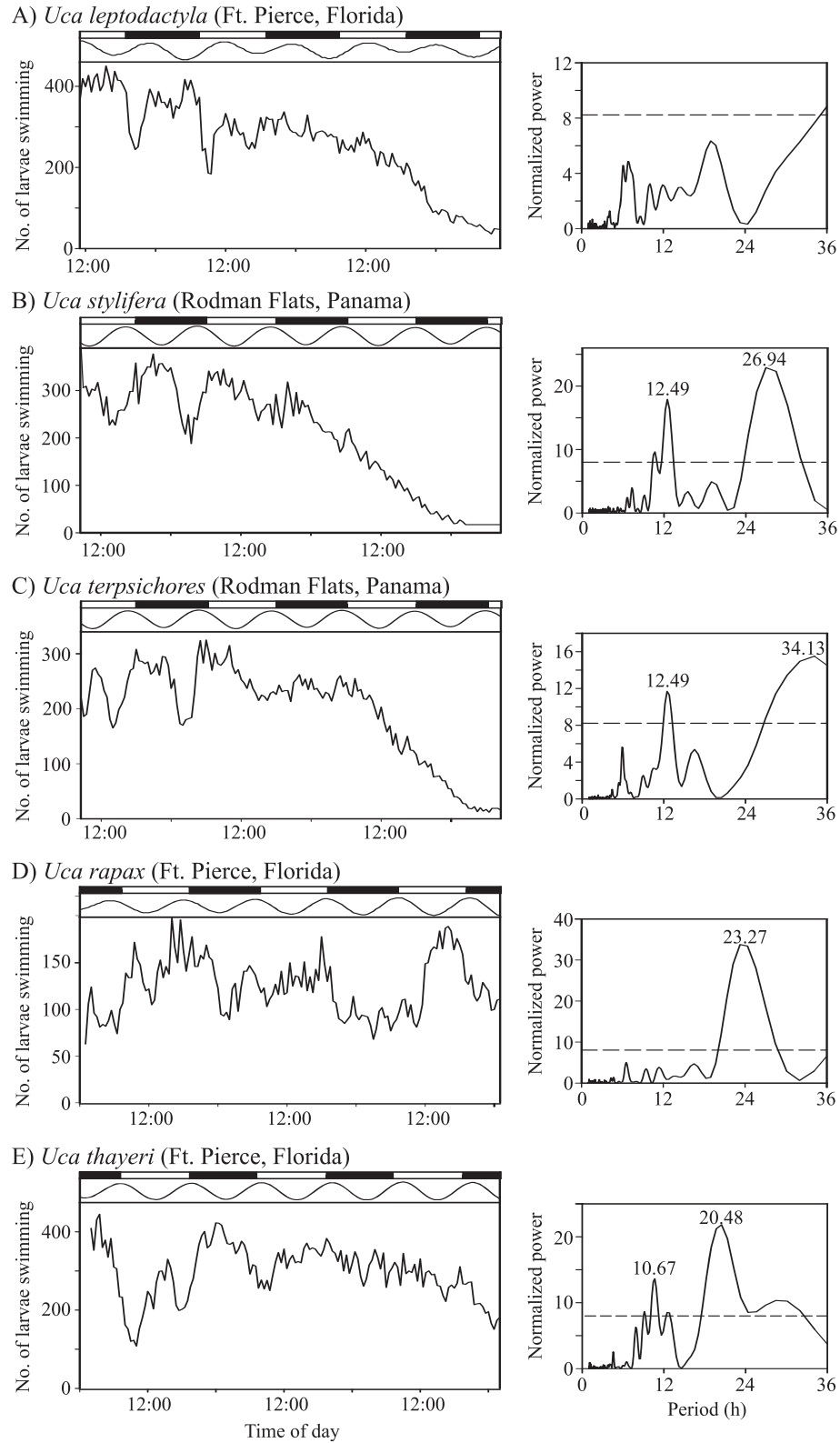
E) *Uca thayeri* (Ft. Pierce, Florida)

Fig. 5. Representative actograms (left panels) and corresponding periodograms (right panels) for crab larvae that exhibited swimming behaviors classified as weakly rhythmic (WR). Further details are in the legend for Fig. 3.
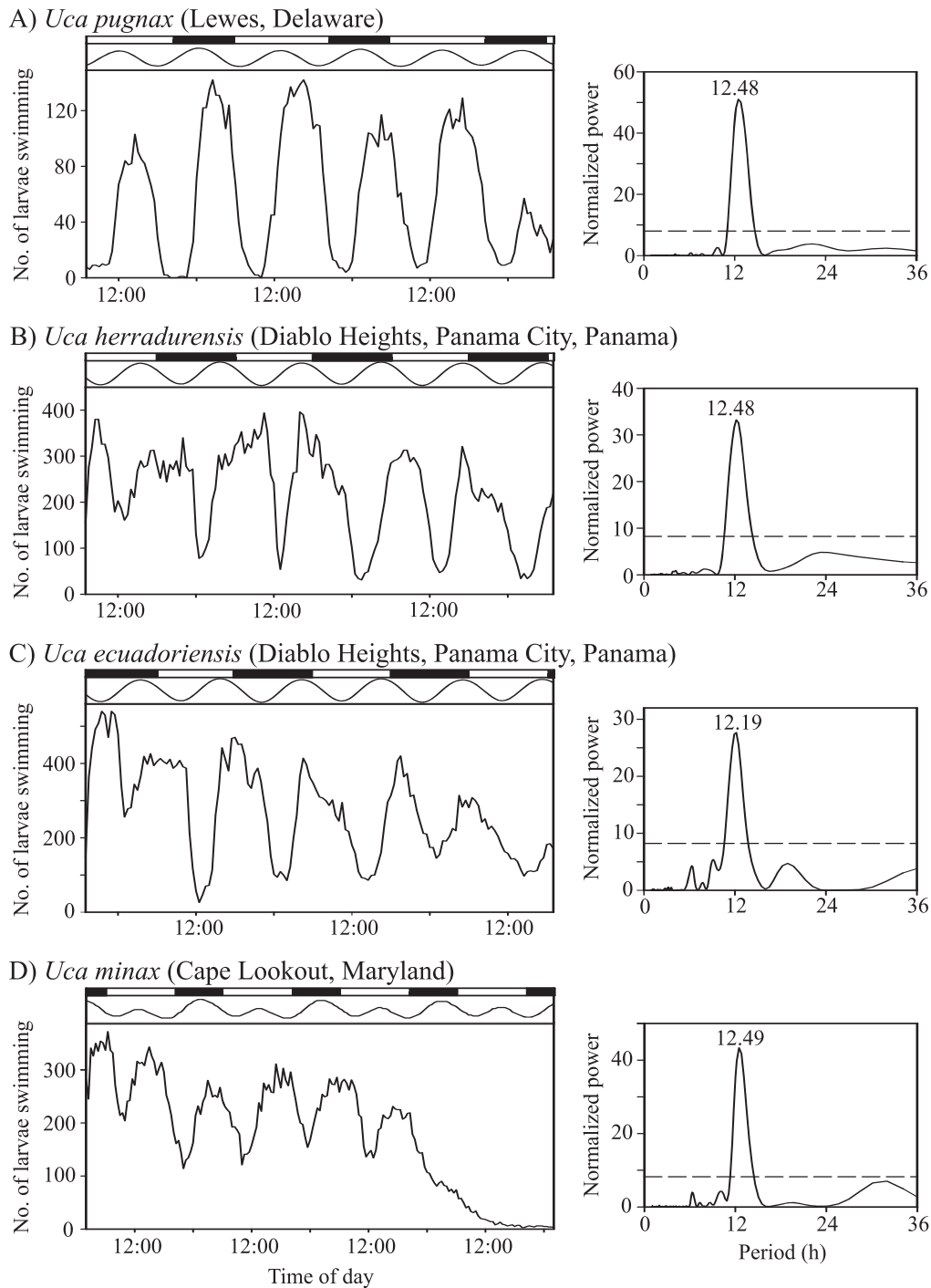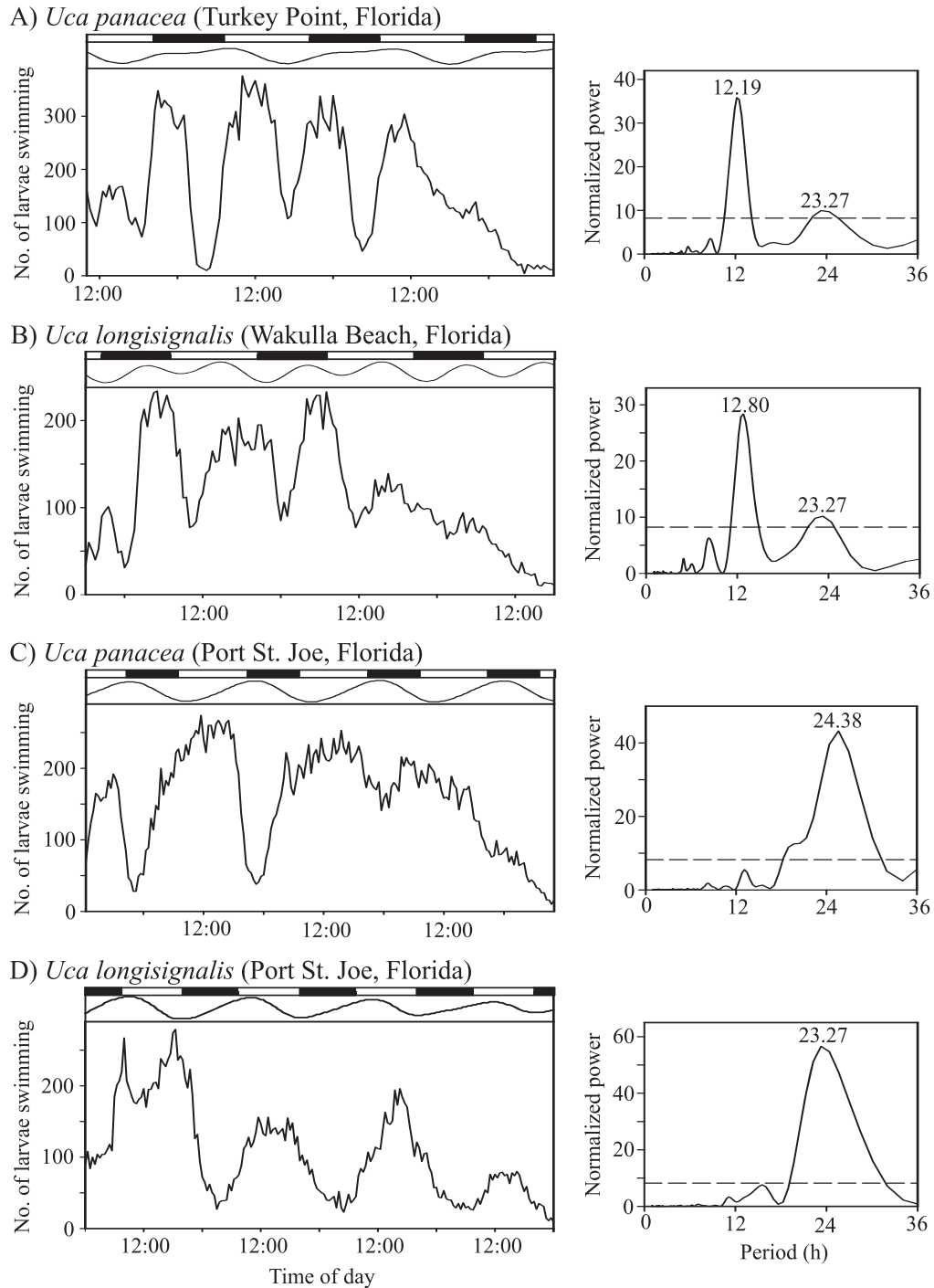
Fig. 6. Representative actograms (left panels) and corresponding periodograms (right panels) for crab larvae collected from areas with semidiurnal tides that exhibited swimming behaviors classified as rhythmic-circatidal (RC). Further details are in the legend for Fig. 3.

the surface and then down as activity gradually declined after 24–48 h. In some cases, weakly rhythmic larvae moved in and out of the upper portion of the chamber for a few cycles before activity declined.

Upward movement toward the surface following release is common in invertebrate larvae and is thought to facilitate the advection and dispersal of larvae away from adult

habitats by strong surface currents (reviewed by Young 1995; Queiroga and Blanton 2005). Moreover, results of the current study are consistent with those reported for zoeae of the blue crab *Callinectes sapidus* (López-Duarte and Tankersley 2007a). Although *C. sapidus* adults are distributed throughout estuaries like many *Uca* species, newly hatched zoeae do not use ETT for down-stream transport

Fig. 7. Representative actograms (left panels) and corresponding periodograms (right panels) for crab larvae collected from areas with either mixed semidiurnal (A–B) or diurnal (C–D)l tides that exhibited swimming behaviors classified as rhythmic-circatidal (RC). Further details are in the legend for Fig. 3.

and flushing from the estuary. Instead, prior to larval release, ovigerous blue crabs leave mating areas and migrate seaward using ETT to spawn near inlets and coastal waters (Tankersley et al. 1998; Carr et al. 2004). Release occurs near the time of high tide, and larvae remain near the surface and are transported seaward by surface currents (reviewed by Epifanio 2007; López-Duarte and

Tankersley 2007*a*). Thus, ovigerous females transport entire broods down-estuary, and their larvae reach development areas in a single tidal cycle (Carr et al. 2005).

Classification of the swimming activity of the zoeae for a given species was consistent for populations inhabiting areas with different tidal patterns and amplitudes (Table 2). Larvae of *U. panacea*, *U. pugnax*, *U. longisignalis*, *U.*

herradurensis, *U. ecuadoriensis*, and *U. minax* collected in different estuaries displayed circatidal rhythms in swimming that matched the period and phase of the local tides. These results are similar to those previously described for *U. pugilator* populations inhabiting areas with semidiurnal, diurnal, and mixed tides (Lopez-Duarte and Tankersley 2007*a*,*b*; Morgan and Anastasia 2008), and they provide additional support for the hypothesis that the timing system controlling the behavior is flexible. Moreover, circatidal rhythms were not always present in zoeae of sympatric species. *Uca pugilator* zoeae from Ft. Pierce, Florida, exhibit a strong circatidal rhythm (López-Duarte and Tankersley 2007*b*), whereas *U. thayeri*, *U. rapax*, and *U. leptodactyla* collected from the same area showed no signs of an endogenous rhythm in swimming (Table 2).

Swimming patterns of *Uca* zoeae were unrelated to the phylogenetic relationships among species based on both molecular (Levinton et al. 1996; Sturmbauer et al. 1996) and morphological (Rosenberg 2001) characters. All *Uca* species in the Americas are placed in one of four subgenera, *Boboruca*, *Celuca*, *Minuca*, and *Uca* (Levinton et al. 1996; Sturmbauer et al. 1996; Rosenberg 2001; Fig. 1). Representatives of all four groups were included in the present study (Fig. 1), and each subgenus contained species that lacked a rhythm in vertical swimming, as well as ones that possessed a well-defined circatidal rhythm that could underlie ETT (Table 2). In a similar study of the osmoregulatory capabilities of several species of *Uca* from locations along the Atlantic and Gulf of Mexico coasts, Thurman (2003) found that habitat and ecological distribution of the species had a greater effect on osmoregulatory ability than evolutionary relatedness. Similarly, salinity tolerance and habitat and substrate preferences are better predictors of interspecific differences in the circatidal swimming behaviors of *Uca* zoeae than phylogeny (Table 2). Furthermore, these results suggest that the ETT behavior of zoeae represents an adaptation that may have facilitated the invasion of estuaries by species that undergo development in offshore areas.

Larval emigration from estuarine habitats to coastal waters to undergo development is a widespread life-history trait of brachyuran crabs, and, with notable exceptions, it is typically accomplished in a few tidal cycles by stage I larvae (Christy and Stancyk 1982; Brookins and Epifanio 1985; Christy 2003). Transport to high-salinity areas is considered adaptive because it reduces predation by fish and physiological stresses due to low salinities and high temperatures encountered in shallow estuarine habitats (reviewed by Morgan 1987; Christy 2011). Although adult *Uca* spp. are euryhaline, fiddler crab larvae appear to lack the ability to tolerate brackish water conditions. Because adult fiddler crabs inhabiting low-salinity and near-freshwater areas of estuaries are unable to migrate to higher-salinity areas to spawn, larvae are released near adult habitats where salinities are typically too low for larvae to survive (Morgan 1987; Brodie et al. 2007). Rapid transport away from these areas is facilitated through the synchronous timing of larval release around the time of high tide (DeCoursey 1979; Forward 1987; Morgan and Christy 1995), taking advantage of the ebbing currents.

However, larvae released at significant distances from inlets are incapable of reaching coastal areas in a single tidal cycle (Sandifer 1973, 1975; Brodie et al. 2007). Relative distances to inlets vary with location, but a recent study suggests that *U. minax* larvae from populations within the Winyah Bay Estuary, South Carolina (> 50 km away from the inlet) would require approximately 1.5–2.5 d to be exported from the estuary using ebb-tide transport (Brodie et al. 2007).

Differences in expression of circatidal rhythms in larvae of coastal and estuarine fiddler crabs that promote their downstream transport appear to be widespread among other crab species that release larvae in similar habitats. Larvae of the two outgroup species included in this study also displayed markedly different activity patterns. As with fiddler crabs from euhaline areas, *Cardisoma guanhumi* zoeae lacked any obvious rhythmic pattern in swimming. In contrast, *Armases cinereum* occurs sympatrically with several estuarine fiddler crabs species (e.g., *U. pugilator* and *U. minax*), and their larvae exhibited a strong endogenous rhythm in swimming behavior that was similar to the one present in estuarine fiddler crabs (i.e., *U. ecuadoriensis*, *U. herradurensis*, *U. longisignalis*, *U. minax*, *U. pugilator*, *U. panacea*, and *U. pugnax*; Table 2). Circatidal rhythms may be a common behavioral trait of crabs and other invertebrates that live within estuaries as adults but leave the estuary to complete development in the sea.

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