Endogenous swimming rhythms of juvenile blue crabs, *Callinectes sapidus*, as related to horizontal transport

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Abstract

The blue crab *Callinectes sapidus* settles and metamorphoses in areas of aquatic vegetation in estuaries. Crabs in the first–fifth instar stages (J1–5) then emigrate from these areas by walking on the bottom or pelagic dispersal throughout estuaries. The present study was designed to characterize the timing of this migration pattern relative to the light–dark and tidal cycles. Field sampling in Pamlico Sound, NC, USA indicated that J4–5 juveniles were most abundant in the water column during the night. J4–5 juveniles were collected from Pamlico Sound in an area near Oregon Inlet that has semi-diurnal tides, a Mid-Sound area where tides are weak, and on the West side where regular tides do not occur. Crabs from all three sites had a circadian rhythm in which they swam up in the water column during the time of darkness in the field. Peak swimming consistently occurred at about 0300 h, but was not related to the timing of the tidal cycle. Similar results were obtained for juvenile crabs from an adjacent estuary having semi-diurnal tides. Dispersal at night reduces predation by visual predators, and allows early juvenile blue crabs to disperse planktonically from initial settlement sites.
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1. Introduction

Within the life cycle of the blue crab *Callinectes sapidus* females release their larvae near the inlet to estuaries (e.g., Tankersley et al., 1998). Larvae are transported seaward where they pass through seven zoeal stages in coastal/offshore areas and then molt to the megalopa stage (Costlow and Bookhout, 1959). Wind events transport megalopae to the vicinity of estuary inlets (reviewed by Epifanio, 1995; Epifanio and Garvine, 2001) and they undergo flood-tide transport (Forward and Tankersley, 2001) for movement into and up estuaries. Megalopae settle and metamorphose in nursery areas of aquatic vegetation, such as seagrass beds (Orth and van Montfrans, 1987; Olmi et al., 1990; Etherington and Eggleston, 2000) and tidal marshes (Weinstein and Brooks, 1983; Orth and van Montfrans, 1987; Morgan et al., 1996; Etherington and Eggleston, 2000). Past studies indicate that juvenile blue crabs remain in these habitats until reaching the fifth to seventh instar (J5−7) when they begin to migrate throughout estuaries (Hines et al., 1987; Orth and van Montfrans, 1987; Pile et al., 1996). While these crabs may emigrate from benthic habitats by walking, recent research suggests that early-staged juveniles may move into the water column and undergo horizontal transport (i.e., 'secondary dispersal'; Blackmon and Eggleston, 2001; Etherington and Eggleston, in press; Etherington et al., in press). However, the cues or underlying behavior associated with such secondary dispersal remain unknown.

Horizontal movement of pelagic juveniles could be associated with tidal currents in regions influenced by the tides, or wind-generated currents in non-tidal areas. One area where juvenile crab dispersal takes place under a gradient of environmental conditions is the Albemarle–Pamlico Estuarine System (APES; North Carolina, USA), which is the largest lagoonal estuarine system in the United States (Fig. 1). The eastern boundary of the APES is delineated by a barrier island chain that restricts oceanic exchange to three main inlets, Oregon, Hatteras, and Ocracoke, respectively. As such, tidal exchange is limited to these inlet regions, with the relative magnitude of the principal M_2 semi-diurnal tidal component becoming negligible within a few kilometers of the inlets (Pietrafesa et al., 1986; Reyns, unpublished data). This, in addition to the shallow depth of the system (mean depth ~ 4.5 m), allows the circulation within the APES to set up with the onset of persistent winds (Pietrafesa et al., 1986). The APES is, therefore, a predominantly wind-driven estuarine system.

Since J4−5 blue crab juveniles disperse throughout the APES (Etherington and Eggleston, 2000, in press), the present study was undertaken to determine (1) if the pelagic abundance of J4−5 juveniles at different locations within Pamlico Sound is related to the diel cycle, (2) whether juvenile blue crabs have biological rhythms in vertical swimming behavior that could explain field distribution patterns and (3) whether these rhythms change when juveniles move from tidal to non-tidal areas. The observed rhythms were compared to those for juveniles of the same stage collected in an estuary (Newport River Estuary, North Carolina, USA; Fig. 1) with pronounced semi-diurnal tides (e.g., Tankersley et al., 2002).

Blue crabs have stage-dependent biological rhythms. Stage I zoeae lack a biological rhythm in vertical migration (Forward, unpublished data). However, megalopae have a circadian rhythm in vertical migration in which they swim to the surface during the time of day and descend at the time of night (Tankersley and Forward, 1994; Forward et al., 1997).
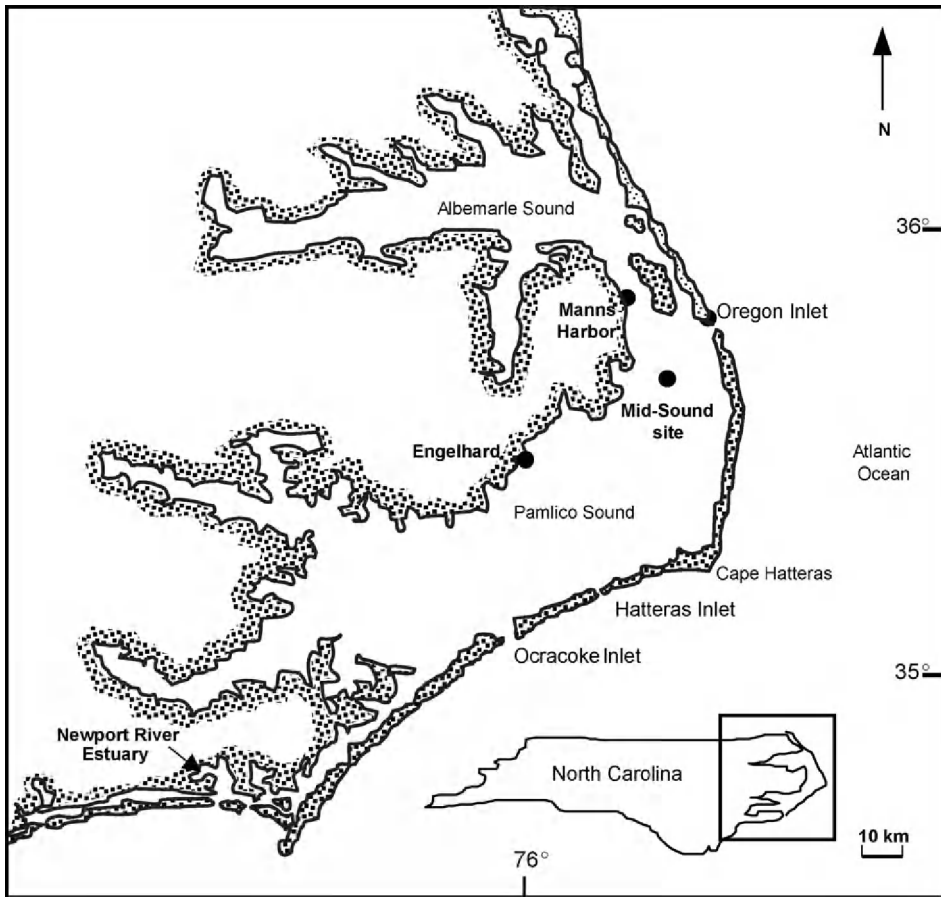
Fig. 1. The Albemarle–Pamlico Estuarine System (APES) in North Carolina, USA. Sites sampled within Pamlico Sound for juvenile blue crabs used in the rhythm experiments are denoted by filled circles and were located near Oregon Inlet, Mid-Sound site and on the West side of the Pamlico Sound at Manns Harbor and Engelhard. A comparison experiment was conducted with crabs collected in the Newport River Estuary.

Nothing is known about rhythms in juveniles but ovigerous females have circatidal rhythms in activity, egg maintenance and vertical migration that underlie their spawning migration (Forward et al., 2003a). The present study found that juvenile blue crabs had a circadian rhythm in vertical swimming regardless of where they reside within an estuary.

2. Materials and methods

2.1. Day/night distributions of juvenile blue crabs

The field study examined the spatiotemporal vertical distribution of juvenile blue crabs, *C. sapidus* Rathbun, during day–night cruises at 17 evenly spaced stations along four

transects crossing Pamlico Sound (average 35°28′ N; 75°45′ W; Fig. 1). All 17 stations were sampled during the day and then re-sampled during the night. Sampling all 17 stations took about 8 h. At each station, a neuston net (surface measure) and benthic sled (near-bottom measure) were simultaneously towed for approximately 5 min to cover a distance of 100 m. Both nets had mouth dimensions of 1×0.5 m, were fitted with 505-µm mesh, and equipped with General Oceanics flow meters to quantify the concentration of juvenile blue crabs (#/100 m^3). Samples were preserved in 75% ethanol, and the spine-to-spine carapace width (CW) of juvenile blue crabs was measured to classify individual crabs by instar stage (Pile et al., 1996). A total of six day–night cruises were conducted during September–October of 2000 and 2001. Data analyses focused on juvenile blue crabs measuring 6.0–9.1 mm CW. These crabs fall into the 4th and 5th juvenile instar size classes (following Pile et al., 1996) and are herein denoted as J4–5 juveniles. The response variable from the field study, the concentration of juvenile blue crabs, was calculated as the number of J4–5 crabs/100 m^3 of water. A four-factor ANOVA model was used to test if the concentration of juvenile J4–5 crabs varied by cruise, station, depth (surface vs. bottom net), and time of day (day vs. night).

2.2. Biological rhythms experiments

Juvenile blue crabs were collected from Pamlico Sound, during the middle of the blue crab recruitment season, from September to October, 2002 (Etherington and Eggleston, 2000). Because of the relatively large size of Pamlico Sound, collections were restricted to the northern basin of the sound (Fig. 1). Minimizing the spatial scale of the study area allowed us to focus our collection to three separate regions that experience different hydrodynamic forcing: (1) near Oregon Inlet; semi-diurnal tides, (2) Mid-Sound site; 35°34.97′ N, 75°38.52′ W; minimal tides, and (3) West-side at Engelhard and Manns Harbor; non-tidal. The average tidal amplitude at Oregon Inlet is 61 cm (Pietrafesa et al., 1986). Estimates of average tidal amplitude at the Mid-Sound and West-side sites were 8 and 0 cm, respectively.

Juvenile blue crabs were collected from randomly selected 1.674 m^2 areas of shallow (<1.5 m), nearshore benthic habitats near Oregon Inlet (seagrass, *Zostera marina* and *Halodule wrightii*) and West-side (detrital habitat) sites using a suction dredge apparatus with a 790-µm mesh collection bag (described by Orth and van Montfrans, 1987). A 1 m beam trawl with a 1-mm mesh net was used to collect juvenile crabs at the deeper Mid-Sound site (mud and shell hash habitat). Following collection, samples were immediately sorted, the carapace width (CW) of individual juvenile blue crabs was measured, and crabs were categorized by instar size-class following Pile et al. (1996). Following collection in the field, J4–5 juvenile blue crabs were placed into aerated estuarine water from the collection sites. Crabs were maintained outdoors in ambient light–dark conditions until transported to the Duke University Marine Laboratory, Beaufort, NC, USA for experimentation. Experiments began about 24–36 h following field collections.

Additional collections of J4–5 juveniles were made during November, 2002 in the Newport River Estuary near Beaufort, NC, USA (34°43′ N; 76°40′ W; Fig. 1). This area experiences semi-diurnal tides with maximum amplitudes of about 1.15 m above mean low water. Experiments with crabs collected in this estuary began the evening of collection.
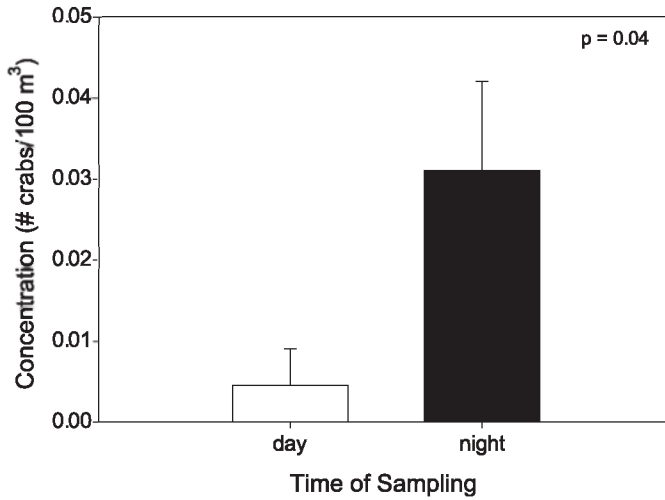
Fig. 2. Mean (+ standard error) concentrations of J4–5 juvenile blue crabs (*C. sapidus*) collected during the day and at night, throughout Pamlico Sound. $N = 403$ plankton tows.

Crabs were placed individually in rectangular Plexiglas columns ($24 \times 5 \times 7.5$ cm) that had a 4-cm diameter Plexiglas tube in the center. The entire column was filled with estuarine water adjusted to the salinity of the collection water and a single crab was placed inside each
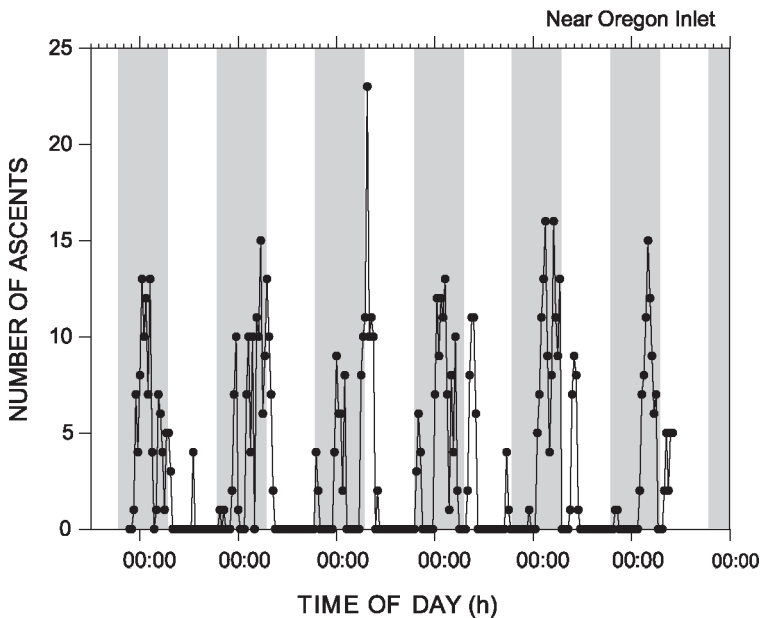

Fig. 3. *C. sapidus*. Actograph of the number of vertical swimming bouts in constant conditions at 0.5 h intervals for a representative J5 juvenile collected near Oregon Inlet of Pamlico Sound on October 21, 2002. The light–dark cycle in the field is shown by the white and grey bars. The free running period length was 24.4 h.

tube. The square sides of the column allowed optical viewing while the circular tube prevented crabs from clinging to the walls of the column. All experiments took place in a windowless room at about 25 °C. At about the time of normal sunset, room lights were extinguished and crab behavior monitored in apparent darkness for at least 6 days with a video system. The background light for viewing the crabs was filtered to near infra-red (780 nm). Previous studies have determined that blue crabs are insensitive to light in this region (e.g., Cronin and Forward, 1988). Cameras (Cohu model 4815-3000) were aligned to view multiple tubes and behavior recorded with time lapse video recorders (Panasonic model AGRT 600A). Although crabs were not fed during experiments, there was no mortality. Crabs that molted during the observation period were not included in the analysis.

Crabs were either quiescent on the bottom or made frequent swimming excursions up into the water column. Tapes were analyzed for the number of excursions above the bottom 1/3 of the column (8 cm) in each 0.5 h interval. This depth was selected because it was observed that when juveniles ascended above this distance from the bottom, they usually ascended to the surface. Time series were analyzed for periodicity (Tankersley and Forward, 1994) using a combination of autocorrelation and maximum entropy spectral analysis (MESA) following the procedures and algorithms described by Dowse and Ringo (1989). Rhythmicity was determined by plotting the autocorrelation coefficients calculated at 0.5-h lag intervals (= sampling interval) as a function of lag
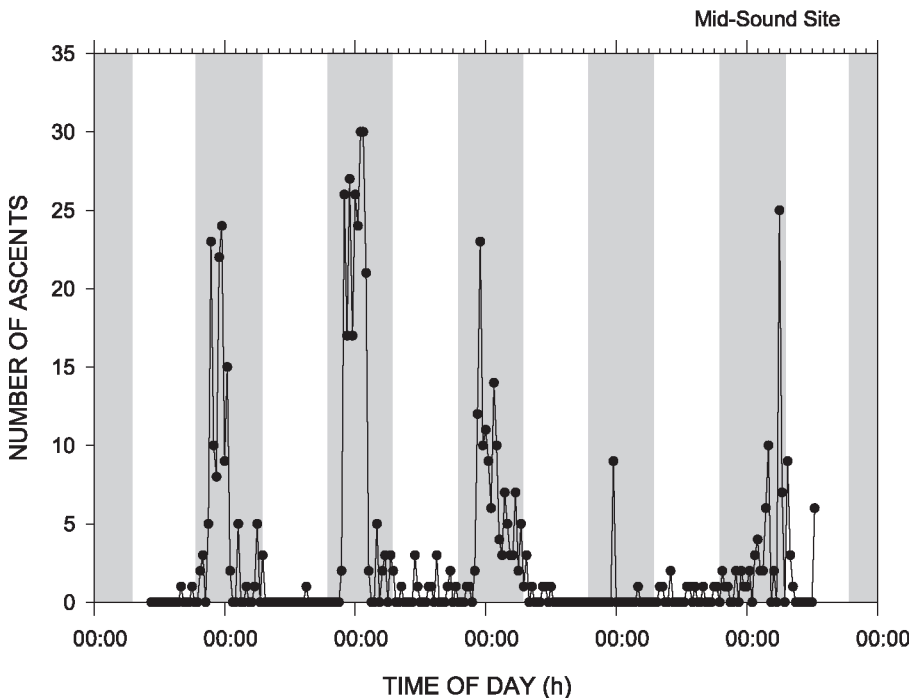

Fig. 4. *C. sapidus*. Actograph of the number of vertical swimming bouts in constant conditions at 0.5 h intervals for a representative J5 juvenile collected at the Mid-Sound site of Pamlico Sound on October 28, 2002. The light–dark cycle in the field is shown by the white and grey bars. The free running period length was 24.4 h.

(correlogram; Broom, 1979). Peaks in the autocorrelation plots exceeding $\pm 2/\sqrt{N}$ (N = sample size) were considered to indicate statistically significant rhythmicity at $p < 0.05$ (i.e., 95% confidence intervals; Chatfield, 1989). Period lengths were confirmed with MESA, which fitted the data to an autoregressive (AR) stochastic model and used Fourier analysis of the AR coefficients to detect cyclical behavior and rhythmicity (Levine et al., 2002). Only those peaks in the MESA plots that corresponded to peaks (i.e., exceeding the 95% confidence intervals) in the autocorrelation plots were considered to be significant. Period lengths were averaged from the MESA calculations for replicate crabs and the time of active vertical swimming related to the ambient light–dark (L–D) cycle and tidal cycle.

3. Results

3.1. Day/night abundance

The initial four-way ANOVA model of planktonic concentrations of J4–5 crabs determined that all factors (cruise, station, depth (surface vs. bottom) and their inter-
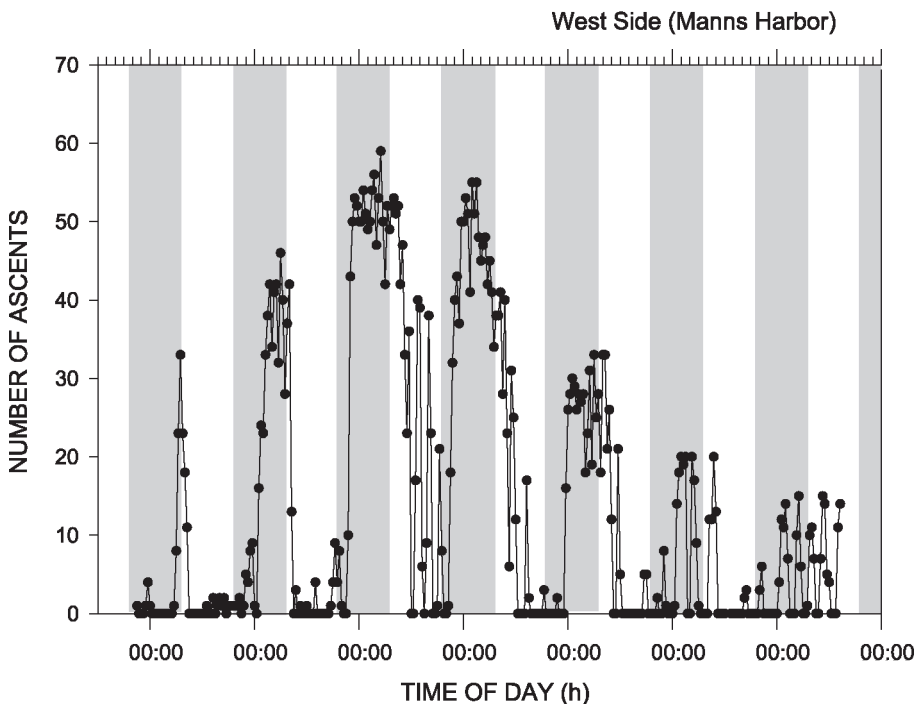

Fig. 5. *C. sapidus*. Actograph of the number of vertical swimming bouts in constant conditions at 0.5 h intervals for a representative J5 juvenile collected on the West side of Pamlico Sound at Manns Harbor on October 10, 2002. The light–dark cycle in the field is shown by the white and grey bars. The free running period length was 22.4 h.

actions, except for time of day, were insignificant ($p > 0.05$). Therefore, a reduced ANOVA model using only time of day as a factor was used. The concentration of J4–5 crabs from all sites was significantly greater in the water column at night than during the day ($df = 1,401$, $F = 4.18$, $p = 0.0415$; Fig. 2).

3.2. Biological rhythms

In total, biological rhythms in vertical swimming were measured in 34 J4–5 crabs. Almost all of the crabs (32/34 = 94%) displayed a circadian rhythm in which they swam vertically during the time of night in the field. A representative figure of the rhythm and the mean period length for the crabs from each collection location will be presented.

In *Pamlico Sound near Oregon Inlet*, eight out of nine crabs showed a circadian rhythm (Fig. 3) in vertical swimming. The average free running period length was 25.5 h (S.D. = 1.5 h; $n = 8$). Crabs had times of active vertical swimming at the time of night separated by times of inactivity during the time of day in the field. All seven of the juvenile crabs collected from the *Mid-Sound site* showed a circadian rhythm (Fig. 4). The
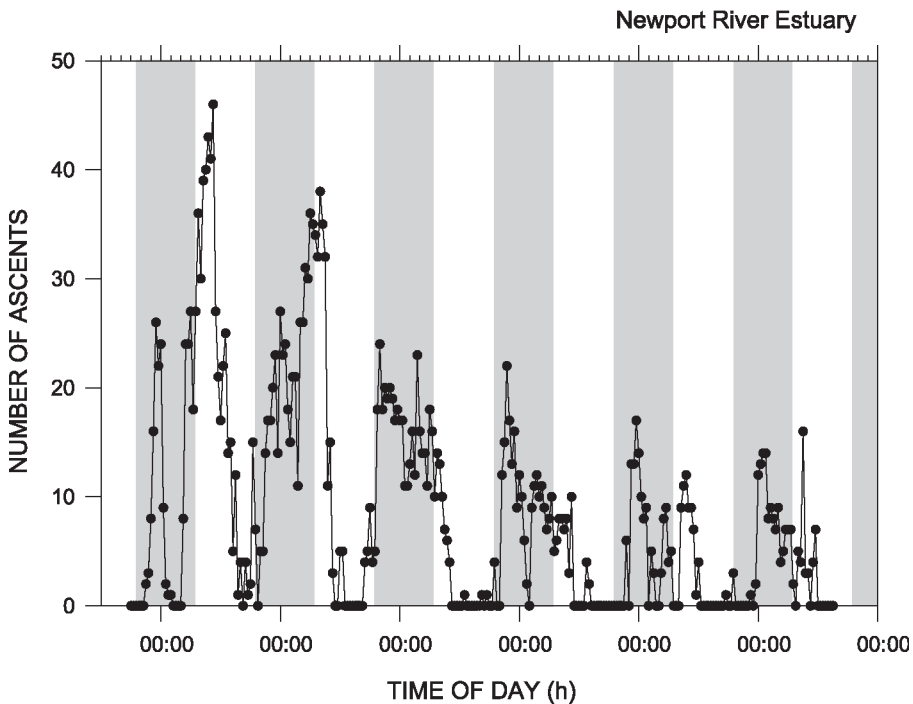

Fig. 6. *C. sapidus*. Actograph of the number of vertical swimming bouts in constant conditions at 0.5 h intervals for a representative J5 juvenile collected in the Newport River Estuary on November 4, 2002. The light–dark cycle in the field is shown by the white and grey bars. The free running period length was 24.4 h.

average free running period was 24.1 h (S.D. = 0.6 h; $n = 7$) and swimming corresponded to the time of night in the field. Crabs were collected from two sites (Manns Harbor and Engelhard) on the *West side of the Pamlico Sound*. Since results were the same between these sites, the results were combined. Almost all of the crabs (13/14 = 93%) showed a circadian rhythm, in which swimming occurred at the time of night (Fig. 5). The mean period length was 24.4 h (S.D. = 1.5 h; $n = 13$).

Although six J4–5 juvenile crabs were collected from the *Newport River Estuary*, two molted during the observation period. The remaining four crabs had a circadian rhythm in swimming activity (Fig. 6) that was similar to that of crabs from Pamlico Sound. The crabs were active at the time of night and the average free running period length was 23.1 h (S.D. = 2.3 h; $n = 4$).
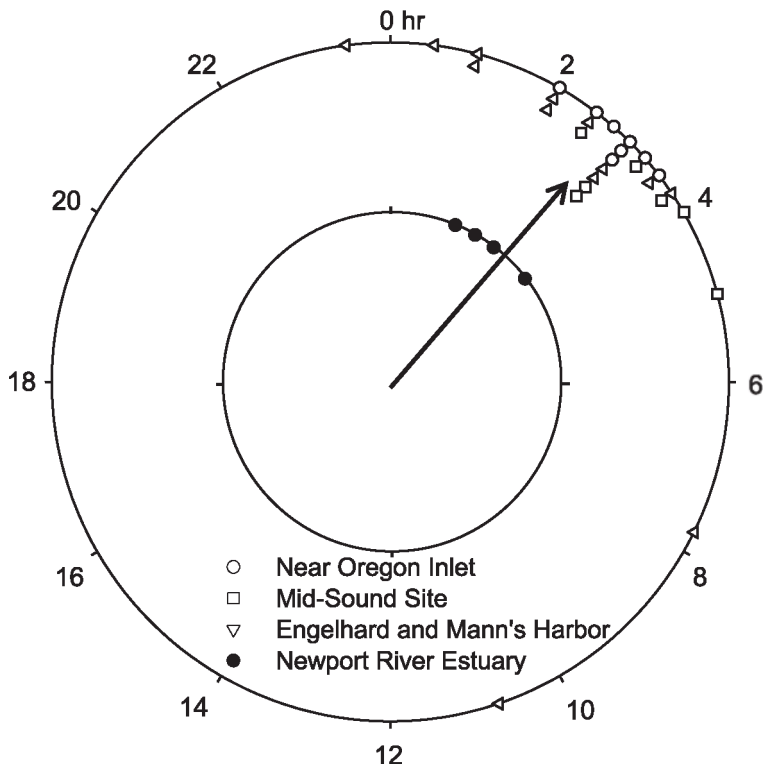

Fig. 7. *C. sapidus*. Phase relationship between time of maximum activity for J4–5 crabs from Pamlico Sound and the Newport River Estuary and time of day in the field. A time of 0 h corresponds to maximum crab activity at midnight, whereas a time of 12 h corresponds to maximum activity at noon that day. Crabs from all Pamlico sites are plotted ($n = 28$), with circles representing crabs from near the Oregon Inlet ($n = 8$), squares representing crabs from Mid-Sound site ($n = 7$), and triangles representing crabs from West side at Engelhard and Manns Harbor ($n = 13$). Filled circles represent crabs from the Newport River Estuary ($n = 4$). The mean vector for the distribution is represented by an arrow at 2.8 h ($r = 0.86$, $p < 0.001$, Rayleigh test).

Further analysis related the times of maximum swimming activity by crabs from Pamlico Sound and the Newport River Estuary to the actual time of day and tides at Oregon Inlet and the Newport River Estuary. Since the free-running period for each crab could change the relationship between the timing of peak swimming and the L–D and tidal cycles, the time of the first peak in swimming after 12 h in constant conditions was determined and related to the time of darkness and tide in the field. Running averages were used to smooth the data and the time of the maximum number of ascents/0.5 h was considered the time of peak swimming activity. The time of maximum crab activity during the 24-h day was determined for each crab that had a significant rhythm (autocorrelation analysis). The timing of peak activity was very consistent between crabs from different locations in Pamlico Sound and the Newport River Estuary and occurred around 3 h after midnight (Fig. 7; $\bar{a} = 2.89$ h, $r = 0.86$, $p < 0.001$, Rayleigh test).

In contrast, the same analysis related the times of peak activity of crabs from Pamlico Sound and the Newport River Estuary to tidal times at Oregon Inlet and in the Newport River Estuary. There was no relationship between crabs from all areas and the timing of the tidal cycle (Fig. 8; $p = 0.95$, Rayleigh test). More specifically, crabs collected from a tidal region near Oregon Inlet were most active during ebb tide,
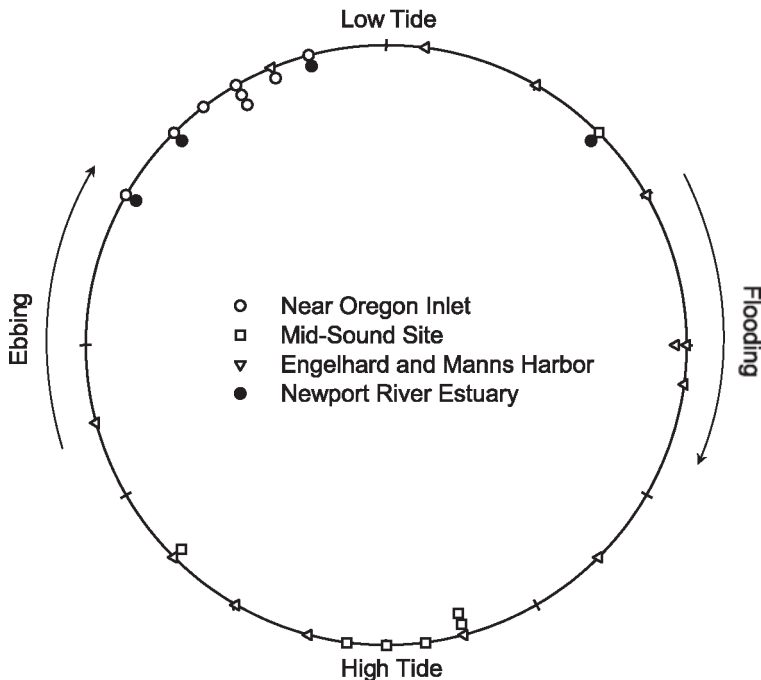

Fig. 8. *C. sapidus*. Relationship between times of maximum activity for J4–5 crabs collected from Pamlico Sound to the time of flood and ebb tide at Oregon Inlet. Symbols are the same as for Fig. 7. No mean vector is shown as the distribution is uniform ($p = 0.95$, Rayleigh test).

whereas crabs from the Newport River Estuary had peaks during both ebb and flood tides (Fig. 8).

4. Discussion

Blue crabs, *C. sapidus*, metamorphose in areas of aquatic vegetation in estuaries (e.g., Orth and van Montfrans, 1987; Etherington and Eggleston, 2000). Although studies in the Chesapeake Bay indicate that juveniles remain in nursery areas until the fifth to seventh instar (J5–7; Hines et al., 1987; Orth and van Montfrans, 1987; Pile et al., 1996), Etherington and Eggleston (2000, in press) suggested that juvenile blue crabs leave seagrass beds and begin migrating though the Albemarle–Pamlico Estuarine System (APES; Fig. 1) before the fifth instar (J5). The present study found that J4–5 juveniles were more abundant in the water column at night (Fig. 2), indicating that pelagic dispersal takes place at night in the APES. This finding corresponds to results from other field and laboratory experiments that have examined the secondary dispersal of early juvenile blue crabs, where crab activity increased at night (Blackmon and Eggleston, 2001; Etherington et al., in press).

Even though juvenile blue crabs can swim, the difference between potential swimming speeds and current speeds (e.g., Forward et al., 2003b) suggests dispersal from nursery areas depends upon current flow at the time juveniles are in the water column. In tidal areas of estuaries, crabs can enter the water column during flood tide (flood-tide transport) for movement up-estuary or enter the water column when the tide is ebbing (ebb-tide transport) for movement seaward (Forward and Tankersley, 2001). Within the APES, blue crabs could use tidal currents near inlets but in most of the sound, circulation is dependent upon winds (Pietrafesa et al., 1986). Indeed, Etherington and Eggleston (in press) have demonstrated that spatiotemporal patterns of juvenile blue crab distribution within the APES are correlated to various parameters associated with the wind (e.g., wind speed, magnitude, and direction). Since J4–5 juveniles are abundant in the water column during the night in this area (Fig. 2), the present study considered whether a biological rhythm in vertical swimming underlies this diel pattern and whether the rhythm was related to the light–dark or tidal cycle.

Rhythms were determined for juvenile crabs collected from an area near Oregon Inlet having semi-diurnal tides, a Mid-Sound site where tides are weak, and at the Western side of the sound where there are no regular tides. Crabs from all three locations had an endogenous rhythm, in which vertical swimming occurred during the night phase in the field. The average period lengths for crabs from the Inlet, Mid-Sound and West side were 25.5, 24.4 and 24.1 h, respectively. Although these periods suggest crabs only had a circadian rhythm, it is possible that swimming was occurring during a particular phase of the tide at night. The latter suggestion is incorrect for three reasons. First, the time of peak swimming by crabs from different areas was not consistently related to a specific nocturnal tidal phase (Fig. 8). Second, crabs from the Oregon Inlet area were exposed to the strongest tidal cycle but peak swimming occurred at the time of ebb tide in the field, which would have exported crabs from the estuary. Third, in instances where blue crabs (Forward et al., 2003a) and other crab

larvae (Tankersley and Forward, 1994; Zeng and Naylor, 1996a,b,c) have rhythms in vertical migration related to tides, there are two peaks during the lunar day (24.8 h). The most comparable situation relates to female blue crabs. During their spawning migration, females are observed to swim at the surface of the estuary only during ebb tides at night (Tankersley et al., 1998). However, when ovigerous blue crabs are placed under constant conditions in the laboratory, they have a circatidal rhythm in which peaks in vertical swimming correspond to consecutive ebb tides during both the day and night in the field. The free running period lengths ranged from 12.1 to 12.9 h (Forward et al., 2003a).

Alternatively, the timing of peak swimming by early juvenile blue crabs in this study consistently occurred at about 0300 h for crabs collected from Pamlico Sound and the Newport River Estuary (Fig. 7). Since a similar endogenous rhythm in vertical swimming was observed for J4–5 juveniles collected from different locations (Figs. 3–6), it is concluded that juveniles have a circadian rhythm in vertical swimming, in which they swim in the water column at the time of night. This pattern is similar to that for nocturnal diel vertical migration, in which zooplankton ascend in the water column near the time of sunset and descend near the time of sunrise (e.g., Forward, 1988). The functional significance is also probably similar in that zooplankton and juvenile crabs are at shallow depths in the water column at times of low light to avoid visual predators (Zaret and Suffern, 1976; Stich and Lampert, 1981). Since juvenile crabs do not swim continuously in the water column, but rather undergo a series of ascents and descents (Figs. 3–6), dispersal at night will occur through a series of hops into the water column.

Within the blue crab life cycle, there is an ontogeny of biological rhythms at different developmental stages. Stage I zoea lack a biological rhythm in vertical migration and just swim to the surface of the water column (R. Forward, unpublished data). This behavior is useful for transport seaward from estuaries to coastal/offshore developmental areas. Megalopae have a circadian rhythm in vertical migration, in which they ascend during the time of the day phase and descend at the time of the night phase (Tankersley and Forward, 1994; Forward et al., 1997). This rhythm may underlie reverse diel vertical migration observed in coastal areas. Megalopae are at the surface during the day and a proportion descends at night (McConaugha, 1988).

A circadian rhythm is also observed in J4–5 juvenile blue crabs (Figs. 3–6) but the phasing is different from that of megalopae. Juveniles ascend in the water column at times of the night phase and descend at times of the day phase. This pattern would lead to dispersal in estuaries during darkness to avoid visual predators. A circadian rhythm would function in both tidal and non-tidal areas of estuaries but has the potential problem that juveniles could enter the water column during ebb tide and be exported from the estuary. The change in timing of the swimming phase of the circadian rhythm between megalopae and J4–5 juveniles leads to the question of whether earlier blue crab stages, which remain in areas of aquatic vegetation, have an endogenous rhythm and if so, what is its phasing. Finally, ovigerous females have a circatidal rhythm in vertical swimming that underlies ebb-tide transport during their spawning migration (Forward et al., 2003a). The changes in these endogenous rhythms are clearly related to the complex life cycle of the blue crab, and likely are adaptations

to habitat-specific physical and biological factors affecting the different developmental stages.

Acknowledgements

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