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FIELD OBSERVATIONS ON SELECTIVE TIDAL-STREAM TRANSPORT FOR POSTLARVAL AND JUVENILE PINK SHRIMP IN FLORIDA BAY

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ABSTRACT

Postlarvae and juveniles of pink shrimp were collected in the summers of 2005 and 2006 at three stations in northwestern Florida Bay, the main nursery ground of this species in South Florida. Collections were made at one- or two-hour intervals during three full moon nights and two new moon nights at depth intervals in the water column. Results of the five collections were consistent with the assumption that postlarvae use a flood-tide transport (FTT) to advance into the estuary by ascending in the water column during the dark-flood tide and resting near the bottom during the ebb tide. Evidence of a FTT were higher numbers of postlarvae per hour collected during the flood tide vs. ebb tide and the large number of postlarvae collected with highest velocity flood tide currents. ANOVA indicated significant differences in the number of postlarvae collected between tidal stages and moon phases, but not among depths. Postlarvae were more abundant during new moon than full moon. We also found different patterns of postlarval distribution between the new and full moon. During the new moon, a large peak of postlarvae occurred coincident with highest current speeds, whereas, with one exception, during the full moon postlarvae were more abundant in the second half of the flood period near the slack tide. In contrast, juveniles exhibited a behavior and migratory pattern opposite to that of postlarvae. ANOVA indicated significant differences between the number of juveniles captured between tidal stages and among depths, but not between moon phases. Juveniles were found almost exclusively near the surface on the ebb tide. Significantly larger juveniles were captured on the dark-ebb rather than on the dark-flood tide during both moon phases, suggesting that older juveniles were leaving the Bay on the ebb tide.

KEY WORDS: Florida Bay, pink shrimp, selective tidal stream transport

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INTRODUCTION

Many estuarine fishes and invertebrates perform vertical migrations synchronized with the phases of the tide to achieve horizontal movement, or conversely to maintain themselves in specific areas. This general mechanism is known as Selective Tidal Stream Transport (STST), and more than one behavioral pattern has been associated with it (Shanks, 1995; Forward and Tankersley, 2001; Queiroga et al., 2006). A flood-tide transport (FTT) occurs when organisms use the flood phase for shoreward transport and in-migration to estuaries (Morgan et al., 1996; Queiroga and Blanton, 2005). An ebb-tide transport (ETT) or ebb-phased migration is used for seaward transport and out-migration from estuaries (Lopez-Duarte and Tankersley, 2007; Ogburn et al., 2007). One remarkable aspect of the STST within a species is the reversal in direction of migration at different life stages. The pink shrimp, *Farfantepenaeus duorarum* (Burkenroad, 1939), is one of a few species appearing to have this capability. Evidence of the FTT in south Florida pink shrimp is: 1) the vertical migrations of postlarvae and late myses larval stages synchronized with the semidiurnal tide on the inner Southwest Florida Shelf (SWF) (Criales et al., 2007), 2) the significantly higher number of postlarvae collected during the dark-flood tide at the western border of Florida Bay (Tabb et al., 1962; Roessler and Rehrer, 1971; Criales et al., 2006), and 3) a cumulative flood-tide transport observed in postlarvae reaching settlement locations (Criales et al., 2010). Juveniles, on the other hand, have been collected from the water column in large numbers in Florida Bay during the hours of dark-ebb tide (Yokel et al., 1969; Beardsley, 1970). Even though the importance of this STST mechanism is recognized, there is still a lack of fundamental understanding of how complex suites of behaviors enable organisms to complete migrations between adult and juvenile or larval habitats in diverse environments.

Florida Bay is a triangular-shaped estuary located at the southern tip of Florida consisting of a complex network of shallow basins separated by carbonate mud banks and mangrove islands (Lee et al., 2008) and connected by narrow channels. The mud-bank/shallow basin system has a mean water depth of 1.4 m and is largely covered by seagrasses (turtle grass, manatee grass, and shoal grass), the main habitat of juvenile pink shrimp in the Bay. Seagrasses and pink shrimp have similar spatial patterns across the Bay with the greatest abundances in western Florida Bay that decrease eastward into the interior of the Bay (Costello et al., 1986; Zieman et al., 1989).

Tides in Florida Bay are variable because of the interaction of Gulf of Mexico mixed semidiurnal tides and the primary semidiurnal tides of the North Atlantic Ocean entering through channels in the Florida Keys (Wang et al., 1994; Smith, 2000, 2005). In northwestern Florida Bay tidal currents are strong and the semidiurnal tide (M_2) reaches amplitudes of almost 40 cm (Smith, 1997; Wang et al., 1994). With distance into the bay tidal amplitude is reduced to about 1 cm, and water level is largely influenced by wind (Lee et al., 2008). Pink shrimp postlarval access to the interior of Florida Bay is largely limited by tidal flow (Criales et al., 2010).

Tropical penaeid shrimp have complex life cycles with an inshore estuarine-dependent nursery phase supporting an offshore spawning phase and fishery. Female pink shrimp in South Florida spawn in the vicinity of the Dry Tortugas about 150 km from the nursery ground of Florida Bay (Munro et al., 1968; Roberts, 1986). Larvae develop rapidly, needing only about 30 days from hatching to become postlarvae ready to settle and assume a benthic life stage (Ewald, 1965; Dobkin, 1961). Transport of larvae from spawning ground to nearshore nursery ground may occur in a process of at least two stages affected by tidal currents, winds, and larval behaviors that includes a diel vertical migration (DVM) and a tidal behavior (Criales et al., 2007, 2010). Postlarvae enter the nursery grounds of Florida Bay at about 9–10 mm total length (Allen et al., 1980). Pink shrimp reside in the bay for several months before returning as juveniles/sub adults to the spawning population and fishery (Costello and Allen, 1966). Florida Bay is the main nursery ground of pink shrimp and many other estuarine species, although other coastal ecosystems also serve as nursery grounds (Browder and Robblee, 2009).

The main objectives of this research were: 1) to confirm the tidal behaviors of postlarvae and juveniles in northwestern Florida Bay, 2) to investigate vertical patterns of postlarvae and juveniles during nocturnal migrations, and 3) to determine migration patterns of postlarvae during new and full moon in relation to the stage of the current.

Materials and Methods

The postlarvae and juveniles of pink shrimp were collected in northwestern Florida Bay during five nightly sampling during the summers of 2005 and 2006 at three stations: navigational Marker 6 (MK6), Conchie Channel (CH), and Joe Kemp Key (JK) (Fig. 1). The selected stations were those that had the largest observed concentrations of postlarvae during a 2-year study of pink shrimp postlarvae (Criales et al., 2010). Site MK6 was located in the main channel entering northwestern Florida Bay from the Southwest Florida Shelf. Sites CH and JK were located in relatively narrow channels confined by shallow seagrass-covered banks extending eastward from MK6. The mean depth of these stations was 2.5 m at MK6, 2.0 m at CH, and 1.5 m at JK. Tidal amplitude varied to about 30 cm at MK6, 15 cm at CH, and 10 cm at JK (Smith, 1997). Samples were collected with moored channel nets that swing in response to the ebb and flood of tidal currents. Moored channel nets had a 0.75-m^2 mouth, 1-mm mesh size, and 500-µm mesh in the cod-end. Channel nets were sampled from dusk to dawn on 1- or 2-h intervals. Channel nets were suspended from buoys to sample at different depth strata.

In July 2005 samples were collected during the new moon at JK every two hours in the subsurface stratum (weather conditions prevented collecting samples every one hour at two depth strata). During the full moon in August 2005, MK6 and JK were sampled simultaneously on one-hour intervals at two depths, subsurface and intermediate (Table 1). In August 2006, collections were made at CH during the new and full moon. Based on results from 2005, samples were collected every 2 h at four depths: surface, subsurface, intermediate, and near-bottom. Surface nets were centered at 0.3 m, subsurface at 0.65 m, intermediate at 1.2, and near-bottom at 1.8 m. The postlarvae and juveniles of the pink shrimp were sorted from the drift seagrass and algae collected in each net, concentrated in a 0.5 mm sieve, and preserved in 90% ethanol in separate labeled containers.

A General Oceanic flow meter (low speed rotor) was suspended in the mouth of each net, but reliable readings were obtained only at the subsurface. These values were used to calculate current speed for each sampling period. Current speed varies with depth across the bay (Lee et al., 2008), and we were unable to ensure the accuracy of our current-at-depth data; therefore, catches of postlarvae and juveniles were expressed in raw numbers by time interval (1- or 2-h) for analysis. The juvenile catch was analyzed only for 2006 because the number of juveniles collected in 2005 was low due to the lack of sampling in the surface stratum (Table 1). Non-parametric Kruskal-Wallis ANOVAs on ranks followed by Tukey-type multiple comparison tests were conducted to determine the effect of tidal stage, depth strata, and moon phase on postlarval and juvenile abundance (Sokal and Rolf, 1988).

Carapace length (CL) and total length (TL) were measured on 1598 postlarvae selected randomly from samples collected simultaneously at JK and MK on 18-19 August 2005. Carapace length was measured to the nearest 0.1 mm from the postorbital margin of the carapace to the mid-dorsal posterior margin of the carapace and TL was measured to the nearest 0.1 mm from the tip of the rostrum to the posterior border of the telson. Measurements were examined for normality and homogeneity of variance. The data for both stations satisfied the normality assumption (Shapiro-Wilk test, $P > 0.8$; Shapiro and Wilk, 1965). An ANOVA was carried out on the CL measurements to determine whether differences in size were related to depth or station. Measurements of CL and TL were also performed on 230 juveniles collected in the surface strata during the full moon on 9-10 August 2006 and on 140 juveniles collected during the new moon on 23-24 August 2006. An ANOVA was conducted on the CL measurements of juveniles to determine whether differences in size were related to tidal stage.

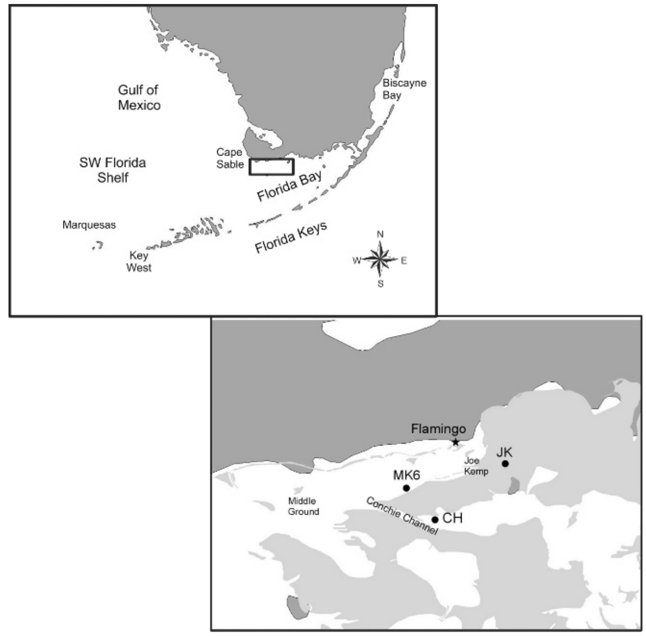

Fig. 1. Map of the study area showing sampling stations in northwestern Florida Bay, Florida, U.S.A.

Results

Postlarvae collected during the new moon of July 2005 at JK were present in the water column almost exclusively during the flood tide, with a large peak in abundance recorded at 0300 hours during highest current speed

Table 1. Summary of five nightly collections of pink shrimp postlarvae and juveniles conducted from dusk to dawn during new and full moon periods in northwestern Florida Bay. Mean depth of strata sampled were 0.30 m (su = surface), 0.65 m (s = subsurface), 1.2 m (i = intermediate) and 1.8 m (nb = near-bottom). No Pl = Total number of postlarvae; and No Ju = Total number of juveniles.

Collection	Station	Date	Hour	Moon	Sampling frequency	Depth strata	No Pl	No Ju
1	Joe Kemp (JK)	6-7 July 2005	17:00-07:00	new	every 2 h	s	5178	45
2	Marker 6 (MK6)	18-19 August 2005	21:00-07:00	full	every 1 h	s, i	9654	67
3	Joe Kemp (JK)	18-19 August 2005	20:00-07:00	full	every 1 h	s, i	2062	54
4	Conchie channel (CH)	9-10 August 2006	20:00-07:00	full	every 2 h	su, s, i, nb	1282	910
5	Conchie channel (CH)	23-24 August 2006	20:00-06:00	new	every 2 h	su, s, i, nb	24,429	665

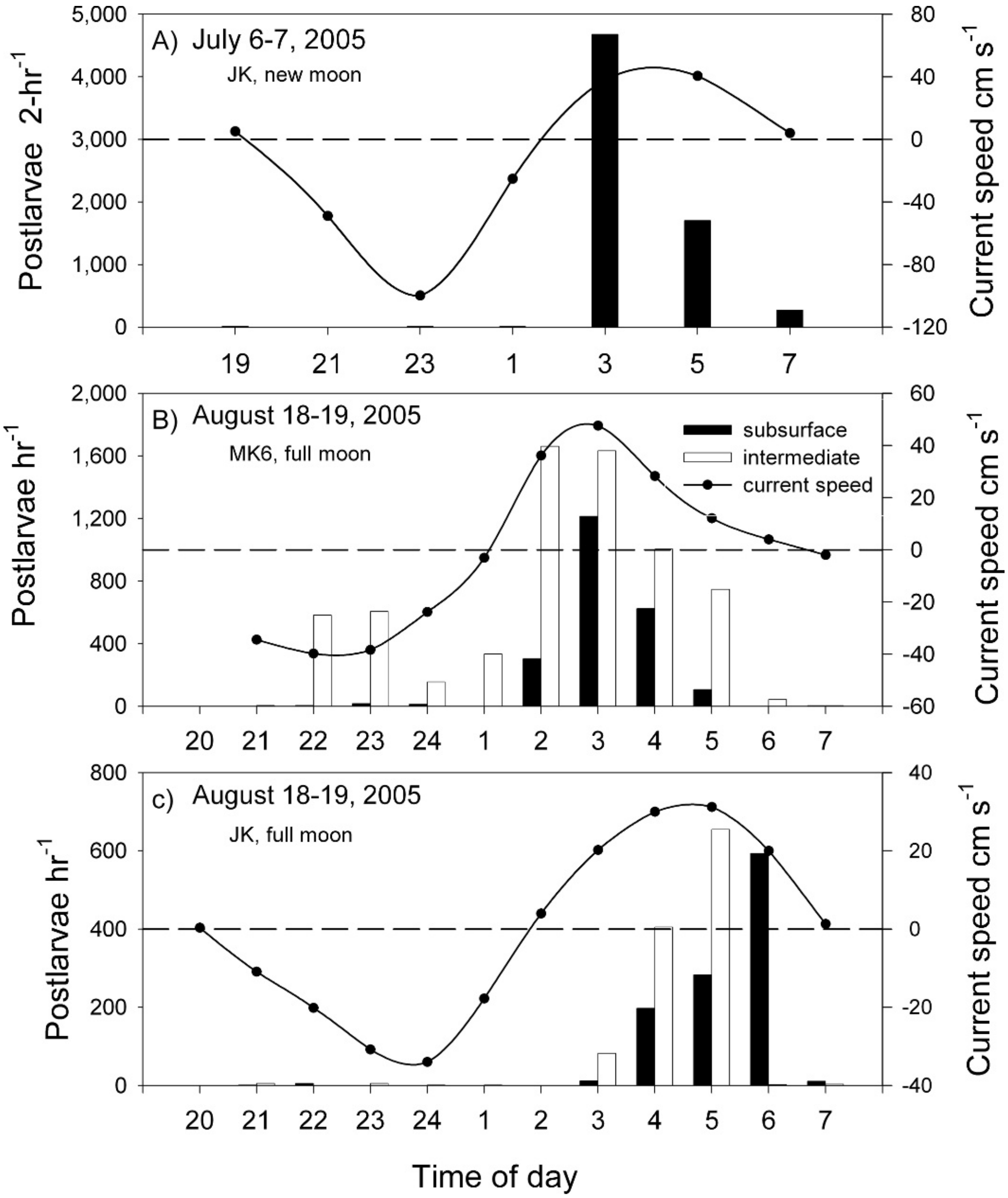

Fig. 2. Numbers of *Farfantepenaeus duorarum* postlarvae (bars) collected during nightly sampling in summer 2005: A, at Joe Kemp (JK) every 2 h in the subsurface stratum during the new moon on 6-7 July 2005; B-C, at Marker 6 (MK6) and Joe Kemp (JK), respectively, every 1 h in the subsurface and intermediate strata during the full moon on 18-19 August 2005. Current speed (lines) was calculated from flowmeter readings located in the subsurface net. Positive values on the y-axis indicate transport into Florida Bay (flood tide), and negative values indicate transport out of the Bay (ebb tide).

Table 2. Results of non-parametric Kruskal-Wallis ANOVAs of the effect of tidal phase and depth on pink shrimp postlarvae collected every 1 or 2 h from dusk to dawn in northwestern Florida Bay during summer 2005. The variables analyzed were tidal phase (ebb = e, flood = f), and depths (subsurface = s, intermediate = i). * denotes significant differences at $p \leq 0.05$, ** denotes significant differences at $p \leq 0.001$.

	Factor	H	*p*	*n*
New moon, 6–7 July 2005 Joe Kemp	Tide (e, f)	4.1	0.03*	8
	Depth (s)	–	–	–
Full moon, 18–19 August 2005 Joe Kemp	Tide (e, f)	4.45	0.03*	24
	Depth (s, i)	0.03	0.95	24
Full moon, 18–19 August 2005 Mark Mile 6	Tide (e, f)	5.56	0.01**	24
	Depth (s, i)	1.37	0.24	24

(Fig. 2A). The number of postlarvae decreased during the remainder of the night as current speed decreased. ANOVA results yielded significant differences between the number of postlarvae collected between flood and ebb tide (Table 2).

Stations MK6 and JK were sampled at two depths simultaneously during the full moon of August 2005. Time series at MK6 indicated that postlarval abundance peaked between 0200 and 0300 hours, during the period of highest current speed, in both depths sampled (Fig. 2B). Time series at JK showed a progressive increase in postlarval abundance during the flood tide period to reach a maximum between 0500 and 0600 hours, after current velocity had slowed (Fig. 2C). At JK (Fig. 2C) the number of postlarvae collected in the subsurface and intermediate strata was about the same (mean ± SD, 83.5 ± 6.2 and 88.2 ± 2.1 respectively). At MK6, more postlarvae were collected in the intermediate (670 ± 0.7) than in the subsurface (254 ± 0.7) strata. An ANOVA indicated a significant difference in the number of postlarvae collected between flood and ebb, but not between depths (Table 2).

The mean CL (± SE) of postlarvae collected simultaneously at MK6 and JK stations during the full moon indicated that postlarvae at JK were larger (1.91 ± 0.17) than at MK6 (1.86 ± 0.21) (Fig. 3) and differences were statistically significant (ANOVA Kruskal-Wallis test: $H = 8.02$, $N = 1596$, $P = 0.0046$). JK is about 7 km further into Florida Bay than MK6. Postlarvae collected from the intermediate strata were larger than those from the subsurface at both stations, but size difference by depth was not significant (ANOVA Kruskal-Wallis ANOVA, $H = 2.12$, $N = 1596$, $P = 0.1453$).

Sampling in August 2006 took place at CH during both the new and full moon in four depth strata (Figs. 4, 5). The time series of postlarval catches during the full moon indicated that a large number of postlarvae were captured during the flood tide at all four depths, but catch was distributed throughout flood tide period with no obvious peak coincident with highest current speed (Fig. 4A). The largest numbers of postlarvae were collected at 0500 hours, whereas peak current speed occurred at about 0300 hours. In contrast, time series of postlarvae captured during the new moon indicated that most postlarvae were captured during the flood tide at all four depths, with a large peak of

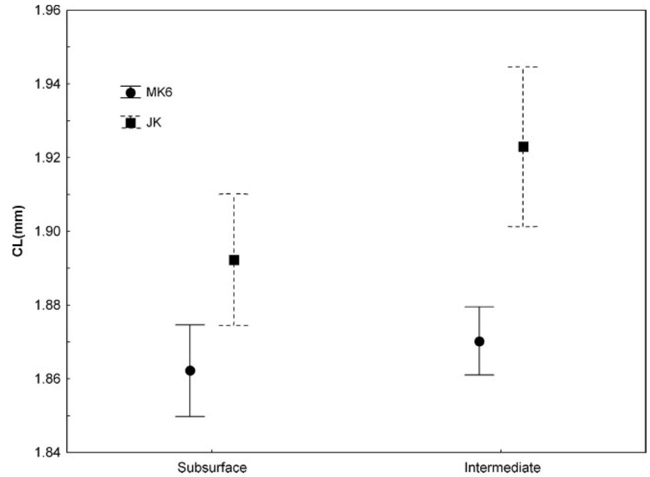

Fig. 3. Carapace length (CL, mean ± SE) of *Farfantepenaeus duorarum* postlarvae collected during full moon on 18-19 August 2005 at the Marker 6 (MK6) and Joe Kemp (JK) stations at two depths, subsurface and intermediate.

postlarvae occurring in the subsurface and intermediate strata at 0400 hours coincident with highest current speed (Fig. 4B).

Time series of juveniles showed a different pattern to that of postlarvae. During the full moon, a large peak of juveniles was recorded in the surface strata at 2300 hours coinciding with the peak of the ebb tidal current (Fig. 4C). The number of juveniles captured in the other depth strata was small (maximum 36 shrimp). During the new moon, a similar peak of juveniles was observed in surface waters at 0000 hours coinciding with peak ebb currents, but juveniles were also relatively abundant during the hours preceding peak ebb tide and early flood tide (Fig. 4D). The number of juveniles captured in depth strata other than surface was small during peak ebb tide.

The mean number (± SD) of postlarvae collected during the full and new moon of August 2006 indicated that postlarvae were collected in large numbers during the new moon in the subsurface strata, and that numbers decreased with depth (Fig. 5A). Fewest postlarvae were captured in the surface strata. The number of postlarvae collected during full moon was low for all depth strata. Postlarvae collected during the new moon were about 19 times (1200 ± 405) more abundant than those collected during the full moon (52 ± 12). An ANOVA indicated significant differences in the number of postlarvae captured between tidal stages and between moon phases but not among depths (Table 3).

In contrast, the majority of juveniles captured were taken at the surface during both the full and the new moon; relatively few juveniles were observed in the other depth strata (Fig. 5B). An ANOVA indicated significant differences in the number of juveniles captured between the two tidal stages and the four depths but not between moon phases, although, generally, more juveniles were captured during the full moon than during the new moon (Table 3). Numbers of juveniles caught in the surface stratum were significantly greater than at intermediate and near-bottom depths.

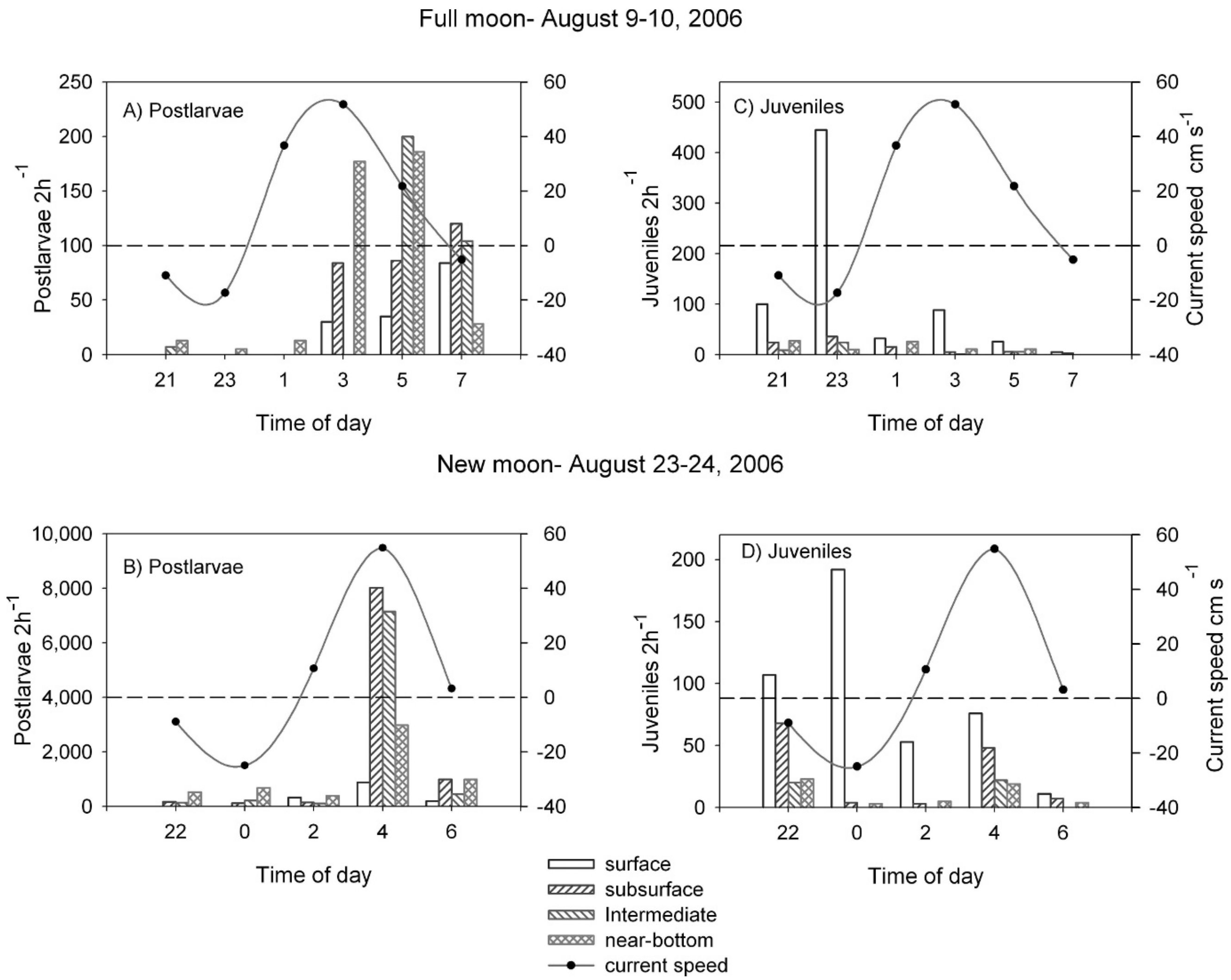

Fig. 4. Numbers of *Farfantepenaeus duorarum* postlarvae (A-B) and juveniles (C-D) (bars) collected during nightly sampling in summer 2006 at Conchie Channel (CH) every 2 h in four depth strata (surface, subsurface, intermediate and near-bottom) during the full moon on 9-10 August 2006 (A and C), and the new moon on 23-24 August 2006 (B and D). Current speed (lines) was calculated from flowmeter readings located in the subsurface net. Positive values on the y-axis indicate transport into Florida Bay (flood tide) and negative values transport out of the Bay (ebb tide).

ANOVA results indicated significant differences in the size of juveniles collected during the ebb and the flood during both the full moon ($H = 63.1$, $N = 229$, $P \leq 0.000$) and the new moon ($H = 21.7$, $N = 137$, $P \leq 0.002$). Large shrimp (CL > 8 mm) were captured during the ebb tide period, and smaller shrimp (CL < 8 mm) were captured during the flood tide period (Fig. 6). Differences in sizes between ebb and flood were more pronounced during the full moon than during the new moon.

The number of postlarvae per hour collected during the new moon at JK (6-7 July 2005) and CH (23-24 August 2006) showed a peak abundance coincident with highest current speeds (Figs. 2A, 4B). In contrast, sampling during the full moon at JK (18-19 August 2005) and CH (9-10 August 2006) indicated that postlarval catch increased during the second half of the flood period as current speed declined approaching slack tide; a large number of postlarvae were present during the late flood tide (Figs. 2C, 4A). The full moon pattern at MK6 more closely resembled the new moon pattern at JK in 2005 and CH in 2006, peaking coincident with the highest current speeds (Fig. 2B).

Discussion

Results of five nightly collections were consistent with postlarval pink shrimp using flood-tide transport (FTT) to advance into the Florida Bay nursery, ascending in the water column during the dark-flood tide and resting near the bottom during the ebb tide. Our previous work indicated that the postlarvae of pink shrimp were absent from the water column during the daytime (Criales et al., 2006), indicating a nocturnal activity period for *F. duorarum*. The strongest evidence of this FTT was that a significantly higher number of postlarvae per hour were collected during the dark-flood tide than during the dark-ebb tide in all five cases. Furthermore, most postlarvae were collected during hours of highest flood tide current

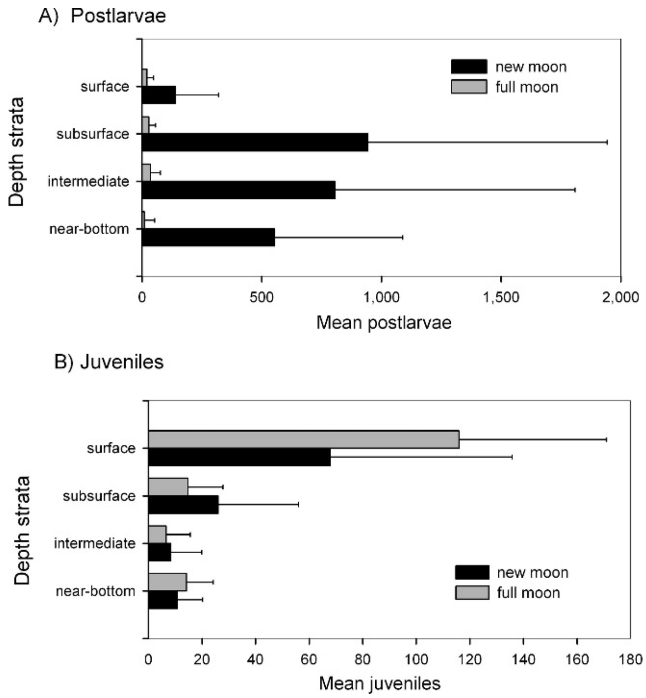

Fig. 5. Mean numbers (± SD) of *Farfantepenaeus duorarum* postlarvae (A) and juveniles (B) collected at four depth strata (surface, subsurface, intermediate, and near-bottom) at Conchie Channel (CH) during nightly sampling of the full moon on 9-10 August 2006 and the new moon on 23-24 August 2006.

speeds, when onshore transport would be greatest (Morgan et al., 1996; Christy and Morgan, 1996). Although more postlarvae were collected in subsurface and intermediate strata than in surface or near-bottom strata during the dark-flood tide, depth differences were not statistically significant. This suggests that the depth at which postlarvae migrate during FTT may reflect a balance of factors rather than just the behavioral element involved in this process. Assuming flood tide speeds at depth are sufficient to achieve in-migration to the nursery ground, other factors such as light, availability of food, predator avoidance, and perhaps proximity to settlement habitat may also influence the vertical position of postlarvae in the nighttime water column.

Table 3. Results of non-parametric Kruskal-Wallis ANOVAs of the effect of tidal phase, depth, and moon phase on pink shrimp postlarvae and juveniles collected every 2 h from dusk to dawn at Conchie Channel (CH) in northwestern Florida Bay during full moon (08–09 August 2006) and new moon (23–24 August 2006). The variables analyzed were tidal phases (ebb versus flood), depths (surface, subsurface, intermediate and near-bottom), and moon phases (new versus full). * denotes significant differences at $p \leq 0.05$, ** denotes significant differences at $p \leq 0.01$.

	Factor	H	*d.f.*	*p*
Postlarvae	Tide	4.61	1	0.02*
	Depth	4.39	3	0,22
	Moon	19.55	1	0.00**
Juveniles	Tide	5.05	1	0.02*
	Depth	17.39	3	0.00**
	Moon	0	1	0.93

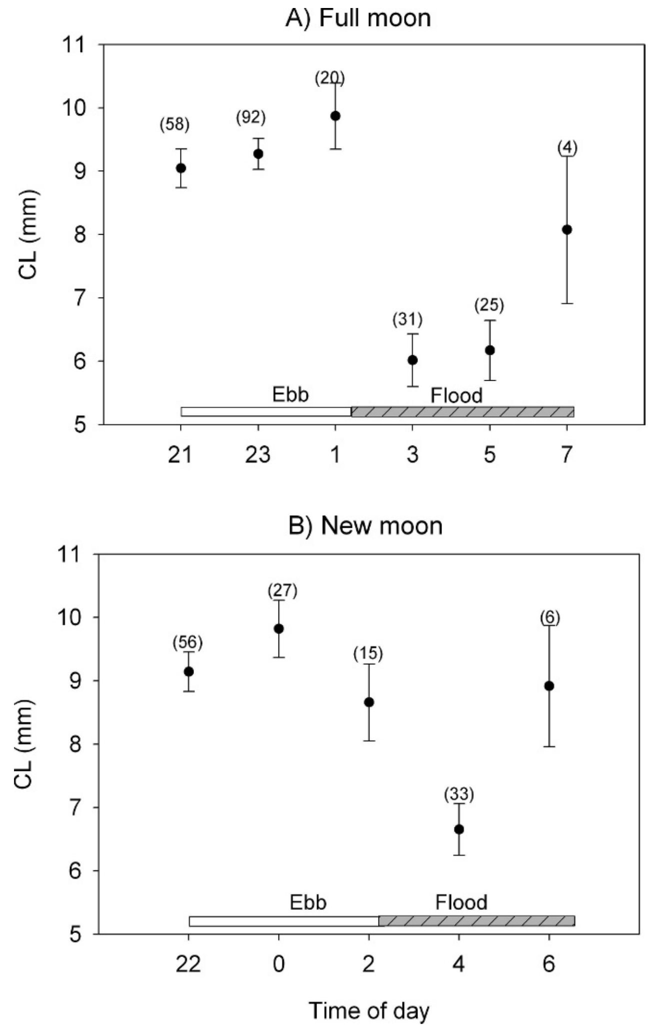

Fig. 6. Carapace length (CL, mean ± SE) of *Farfantepenaeus duorarum* juveniles in relation to the time of collection during nightly sampling of (A) the full moon on 9-10 August 2006 and (B) the new moon on 23-24 August 2006 at Conchie Channel (CH). The numbers in parenthesis are the number of shrimps measured; the bar on the bottom indicates the tidal stage (ebb and flood).

Juveniles exhibited a behavior and migratory pattern opposite to that of postlarvae; they were found mainly in the surface stratum on the ebb tide. We also found significantly larger juveniles on the surface during the dark-ebb than the dark-flood tide, suggesting that older shrimp were leaving this bay with the ebb-tide. Yokel et al. (1969) and Beardsley (1970) first observed the emigration of juveniles from Florida Bay by the Buttonwood Canal, a man-made waterway connecting Whitewater Bay with northwestern Florida Bay at Flamingo.

Postlarvae collected during two new-moon nights at JK and CH showed a peak abundance approximately coinciding with peaks in flood tide current speed. A similar pattern was previously reported during the new moon in the Buttonwood Canal (Tabb et al., 1961; Roessler and Rehrer, 1971) and near Sandy Key (Criales et al., 2006). In contrast, more postlarvae were collected during two full-moon nights at JK and CH during the second half of the dark-flood tide when current speed approached slack tide. These different new and full moon patterns may indicate differences between migration and settlement with respect to the sampling stations. Postlarvae collected at JK were larger than those from MK6, with a size close to settlement (Allen et al., 1980). Our previous research also suggested that postlarvae settle in shallow seagrass habitat near JK and CH (Criales et al., 2010). It is likely that postlarvae collected at JK during the full moon were settling rather than moving with the tides but this hypothesis needs to be tested.

Several studies have indicated that the vertical migration of organisms that perform flood and ebb migrations is controlled to a large degree by behavioral responses to exogenous environmental factors that change predictably with the tide, or by an endogenous clock with a tidal or circadian periodicity (Shanks, 1995; Forward and Tankersley, 2001; Forward et al., 2007; Lopez-Duarte and Tankersley, 2007). Hughes (1969) demonstrated in the laboratory that postlarval pink shrimp were active in the water column when salinity increased (as on the incoming tide) and dropped to the substrate when salinity decreased (as on the outgoing tide). Often, however, organisms with a tidal rhythm showed a similar change in behavior, increasing swimming activity in the water column on the increase of any variable(s) associated with changes of the tides (salinity, temperature, turbulence, or depth) and reducing activity with a decrease in this variable (Tankersley et al., 1995; Forward et al., 2003). Salinity alone may not control all activities involved in the FTT, especially when changes in salinity in Florida Bay are highly variable in magnitude (Lee et al., 2006) and frequency. Hypersaline conditions often occur during summer periods (Kelbe et al., 2006), when there is the greatest influx of postlarvae to western Florida Bay. Hypersaline conditions create a negative salinity gradient (increasing salinity with distance into the estuary) from the bay's western boundary to its interior (Criales et al., 2010), providing the wrong cue for postlarvae to enter the water column because salinity during flood tide may be lower than during ebb tide. Turbulence is another potential variable involved in the tidally related migration process of pink shrimp and has been identified as an environmental cue involved in the tidal transport of blue crab megalopae (Welch et al., 1999; Welch and Forward, 2001). Further research needs to be conducted under controlled laboratory conditions to evaluate the responses of pink shrimp postlarvae to salinity, turbulence, and pressure.

In this research, the two known tidal behaviors of pink shrimp (FTT and ETT) were observed in postlarvae and juveniles, respectively, collected at the same location in Florida Bay under the same environmental conditions, suggesting that an ontogenetic change in behavior has occurred after the postlarval phase. Precisely what triggers this behavioral reversal in pink shrimp and when exactly it occurs is unknown. Studies conducted on other species with similar behavior suggest that it may be associated with physiological changes (Forward and Tankersley, 2001) and behavioral plasticity (Morgan and Anastasia, 2008).

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