

**Abstract**—The variability in the supply of pink shrimp (*Farfantepenaeus duorarum*) postlarvae and the transport mechanisms of planktonic stages were investigated with field data and simulations of transport. Postlarvae entering the nursery grounds of Florida Bay were collected for three consecutive years at channels that connect the Bay with the Gulf of Mexico, and in channels of the Middle Florida Keys that connect the southeastern margin of the Bay with the Atlantic Ocean. The influx of postlarvae in the Middle Florida Keys was low in magnitude and varied seasonally and among years. In contrast, the greater postlarval influx occurred at the northwestern border of the Bay, where there was a strong seasonal pattern with peaks in influx from July through September each year. Planktonic stages need to travel up to 150 km eastward between spawning grounds (northeast of Dry Tortugas) and nursery grounds (western Florida Bay) in about 30 days, the estimated time of planktonic development for this species. A Lagrangian trajectory model was developed to estimate the drift of planktonic stages across the SW Florida shelf. The model simulated the maximal distance traveled by planktonic stages under various assumptions of behavior. Simulation results indicated that larvae traveling with the instantaneous current and exhibiting a diel behavior travel up to 65 km and 75% of the larvae travel only 30 km. However, the eastward distance traveled increased substantially when a larval response to tides was added to the behavioral variable (distance increased to 200 km and 85% of larvae traveled 150 km). The question is, when during larval development, and where on the shallow SW Florida shelf, does the tidal response become incorporated into the behavior of pink shrimp.

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## Variability in supply and cross-shelf transport of pink shrimp (*Farfantepenaeus duorarum*) postlarvae into western Florida Bay

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Patterns of recruitment of coastal species are highly variable, mainly because of the complex interaction of biotic and abiotic factors across the different life history stages. These factors include but are not limited to reproductive dynamics, larval dispersal and behavior, physiological tolerances, and the hydrometeorological regime in which their life stages develop (e.g., Shanks, 1995; Cowen, 2002). The commercially valuable tropical penaeid shrimps that use different habitats during their life cycle (offshore spawning grounds and estuarine nursery habitats) have to cope with a large suite of physical processes and stimuli (Rothlisberg et al., 1995, 1996). The pink shrimp (*Farfantepenaeus duorarum*) of Dry Tortugas is one of the most economically and ecologically important species in southwest Florida. The pink shrimp supports an important year-round fishery of about 4000 metric tons in an area of 10,000 km<sup>2</sup> between Dry Tortugas and Key West (Iversen et al., 1960; Klima et al., 1986). The

Tortugas fishery is directly dependent on young shrimp that migrate from inshore nursery areas onto the offshore fishing grounds (Sheridan, 1996; Browder et al., 2002). Recruitment shows no relationship to spawning size; therefore harvest fluctuations are apparently due to environmental conditions rather than fishing operations (Nance and Patella, 1989). To effectively manage this species, it is necessary to have accurate information on the processes linking nursery and spawning ground populations.

Pink shrimp population dynamics are affected by physical processes and environmental conditions occurring in the southwestern (SW) Florida Shelf of the Gulf of Mexico, the Atlantic coastal zone, and the Florida Bay. Early research on gonad development (Cummings, 1961), distribution of larval stages (Jones et al., 1970), and analysis of length frequency distributions of fishery stock data (Iversen et al., 1960; Roberts, 1986) indicated that the center of spawn-

ing is northeast of the Dry Tortugas. If gravid females spawn northeast of the Dry Tortugas, larvae need to travel up to 150 km to reach the main nursery ground in western Florida Bay. Females spawn on the continental shelf at about 30 m of depth, where larvae develop, passing through several changes in feeding habitats, behavior, and physical stages (nauplii, zoeae, mysids) (Dobkin, 1961; Ewald, 1965; Jones et al., 1970). Postlarvae undergo between three and eight additional planktonic stages before settlement. Larvae develop rapidly, needing only about 30 days to become postlarvae ready to settle to the bottom (Ewald, 1965; Dobkin, 1961). Planktonic stages (larvae and postlarvae) approach the coast and postlarvae enter the nursery grounds of Florida Bay at about 9–10 mm total length (Tabb et al., 1962; Allen et al., 1980; Criales et al., 2000). Larval development and ocean hydrodynamics must be tightly linked to successfully bring these planktonic stages to their coastal nursery grounds.

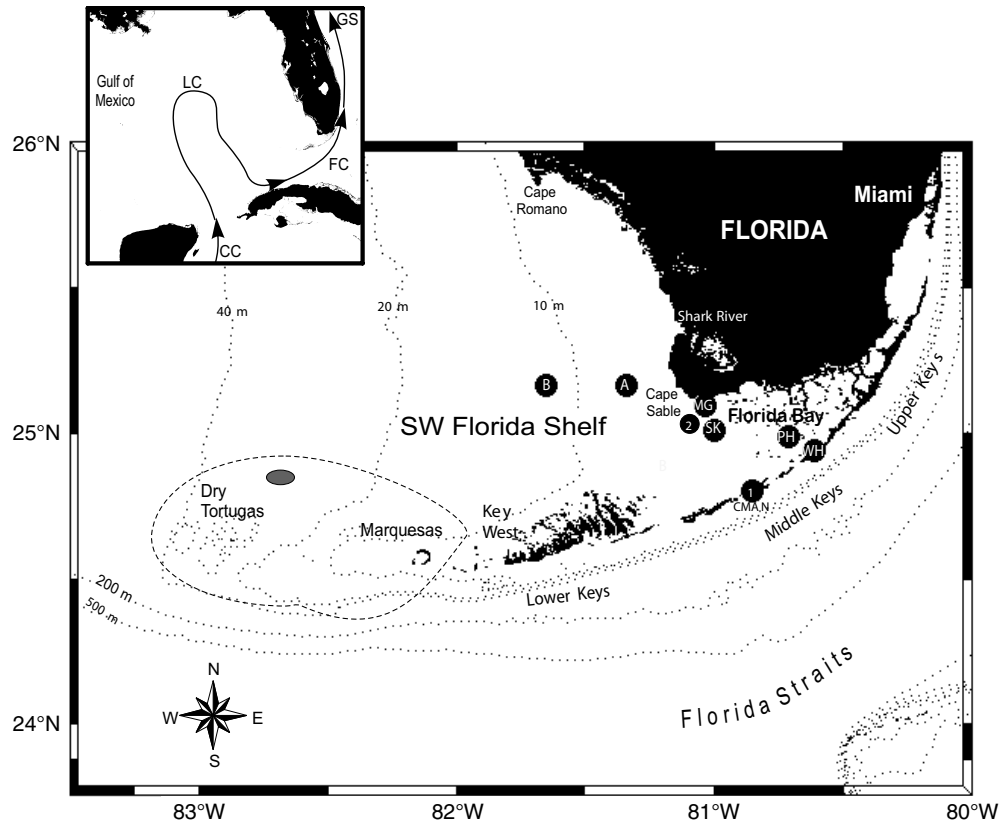
Mechanisms of transport used by planktonic stages of penaeid shrimps are highly variable, depending on the species, different environmental conditions, oceanic physical processes, and complexity of larval behaviors (e.g., Dall, 1990; Rothlisberg et al., 1995, 1996; Wenner et al., 2005). Physical oceanographic processes significantly affect the transport of planktonic stages from spawning to nursery grounds (Yeung and Lee, 2002; Criales et al., 2003). Two main immigration routes have been hypothesized for pink shrimp postlarvae entering Florida Bay: 1) postlarvae may drift south-southeast downstream with the Florida Current and enter Florida Bay through the tidal channels of the Lower and Middle Florida Keys (Rehrer et al., 1967; Munro et al., 1968), and 2) postlarvae may move northeast across the SW Florida shelf and enter the Bay at its northwestern boundary (Jones et al., 1970; Criales and Lee, 1995). The most widely recognized pathway for postlarvae to reach Florida Bay up-to-now has been by transport up the Atlantic side through the tidal channels of the Middle Florida Keys (Munro et al., 1968; Criales and McGowan, 1994; Criales et al., 2003). The favorable Ekman transport generated by the southeastern winds along the west-east oriented coast, and coastal counter-current flow generated by cyclonic eddies provide favorable onshore transport mechanisms along the Florida Keys coast (Criales and Lee, 1995; Lee and Williams, 1999). In contrast, larval transport across the broad, shallow SW Florida Shelf has not been well studied and questions exist about the feasibility of this pathway. Subtidal frequency flows are weak in the SW Florida shelf and mainly in the alongshore (north-south) direction as a direct response to wind events (Koczy et al., 1960; Weisberg et al., 1996; Lee et al., 2001). Tidal currents are strong mainly in the cross-shelf direction (Wang, 1998; Smith, 2000). Freshwater discharges from the Everglades affect a broad area of the SW Florida shelf (Lee et al., 2001; Jurado, 2003). Isopleths less than 32 are typically confined to the region between Cape Sable and Cape Romano, and from 32 to 36 extend from near Cape Romano to the vicinity of Dry Tortugas

in a highly variable annual pattern (Lee et al., 2001; Johns and Szymanski<sup>1</sup>).

For tropical penaeid shrimps that undergo larval development offshore, but whose nursery grounds are inshore, migratory behavior is a key factor for their advection to nursery grounds (Dall et al., 1990; Shanks, 1995). The simplest migratory behavior is vertical movement, and three types of vertical migrations are known to mediate horizontal transport of larvae: ontogenic, diel, and tidal (for reviews see Sponaugle et al., 2002). For some Australian penaeid species (banana prawn [*Fenneropenaeus merguensis*], grooved tiger prawn [*Penaeus semisulcatus*], and eastern king prawn [*Melicertus plebejus*]) it has been shown that early planktonic stages (protozoeae and mysids) perform diel vertical migration cued by light and that later in development (as postlarvae) the migration is cued by tides (Rothlisberg, 1982; Rothlisberg et al., 1983, 1995) and there is no cross-shelf displacement of larvae during the 15 days of diel behavior. Previous studies of pink shrimp in South Florida have clearly indicated ontogenic behavior for pink shrimp; postlarvae have a higher degree of mobility than earlier protozoeae and mysids (Temple and Fischer, 1965; Eldred et al., 1965; Jones et al., 1970; Criales and Lee, 1995). On the other hand, diel behavior is not so well determined. Although protozoeae, mysids and postlarvae were more abundant at the surface during the night than during the day, day and night differences have not been statistically significant in any of these previous studies. The effect of diel, tidal, or ontogenic combinations of behavior on cross-shelf transport from South Florida spawning grounds to western Florida Bay nursery grounds has not previously been explored. The postlarvae of many penaeid shrimps, including pink shrimp, are known to synchronize vertical migration with the tides at the entrance to estuarine nursery grounds (for reviews see Garcia and Le Reste 1981, Dall et al., 1990). This process is known as selective tidal stream transport (STST) (Forward and Tankersley, 2001). Penaeid postlarvae ascend in the water column during the flood and sit on the bottom during the ebb to maximize up-estuary movement (e.g., Rothlisberg et al., 1995). This behavior has been shown for pink shrimp postlarvae inside Florida Bay (Tabb et al., 1962; Roessler and Rehrer, 1971), but not along the border of the bay with the Gulf of Mexico. When during the life cycle and where on the shelf this tidal behavior begins and what the environmental cues are—these questions remain unanswered.

The purpose of our research was 1) to determine patterns of supply of pink shrimp postlarvae into Florida Bay through two distinct regions, 2) to define the most important transport route for planktonic stages from the Dry Tortugas into Florida Bay, 3) to examine alternative behavioral responses of larvae and postlarvae, and 4) to propose a recruitment mechanism for

<sup>1</sup> Johns, E., and D. Szymanski. 2003. Mixing it up in Florida Bay. Florida Bay News, summer 2003:1–3.



**Figure 1**

Map of the study area (with bathymetry) showing the channel net sampling stations at the northwestern and southeastern borders of the nursery grounds of Florida Bay, ADCP moorings, and CMAN and COMP stations. The Tortugas fishing grounds (area enclosed by dashed line) includes the center of spawning for *Farfantepenaeus duorarum* (filled ellipse). Northwestern stations: MG=Middle Ground and SK=Sandy Key; Florida Key stations: WH=Whale Harbor and PH=Panhandle; A and B=onshore and offshore ADCP moorings respectively; 1=Long Key CMAN station; 2=NW Florida Bay COMP station. Small map at the left corner indicates major currents in the Gulf of Mexico and off the coast of Florida. CC=Caribbean Current; LC=Loop Current; FC=Florida Current; GS=Gulf Stream.

pink shrimp across the SW Florida shelf that combines the effect of hydrodynamics with larval behavior. Four modes of behavior-related transport were simulated under hydrodynamic conditions occurring on the SW Florida shelf in order that the resulting distances traveled under each condition might be contrasted.

### Material and methods

Pink shrimp postlarvae were collected in two regions of Florida Bay to evaluate postulated hypotheses of eastern and western gateways and pathways of larval transport into the bay. The two study sites consisted of two large channels connecting northwestern Florida Bay with the SW Florida shelf of the Gulf of Mexico (Sandy Key Channel [SK], and Middle Ground [MG]); and of more confined tidal channels in the Middle Florida Keys that connect the Bay with the Atlantic Ocean (Whale Harbor [WH],

and Panhandle Key [PH]) (Fig. 1). Adjacent mud banks that are occasionally exposed at low tide and over-topped at higher tide stages define these channels. The averaged depth, tidal flow, and cross sectional area of the four channels are summarized in Table 1 to show the different levels of water flow through these pathways. Channels depths are similar, but western channels (Middle Ground and Sandy Key) have higher tidal flows and larger cross sectional areas than the Florida Keys channels (Table 1). Tidal fluctuations are primarily semidiurnal at all stations and have weaker diurnal constituents (Smith, 1998, 2000). Acoustic Doppler velocity meters (ADVMS) that measure continuous velocity and depth (tide and stage) and associated CTD instruments that measure conductivity and temperature were installed at each channel in January 2002. A boat-mounted acoustic Doppler current profiler (ADCP) was used to calculate total discharge across the cross-section of the channel during monthly sampling (Hittle et al., 2001).

Postlarvae were collected monthly in each channel during two nights around the new moon from January 2000 to December 2002. At the PH station sampling began in June 2000 after the original site (Captain Key channel) was abandoned because it had insufficient water flow for effective sampling. Two moored subsurface channel nets (net 1 and net 2) of 0.75-m<sup>2</sup> opening, 1-mm mesh size, and 500- $\mu$ m mesh in the codend were suspended with floats at 0.5 m depth. Nets were deployed each night before dusk and removed shortly after dawn each day. General Oceanic flowmeters (2030R16, Low Speed Rotor, Miami, FL) were mounted in the mouth of the nets and the volume of water filtered through the nets was calculated for each net. *Farfantepenaeus duorarum* postlarvae were sorted, identified, and preserved in 90% ethanol. The raw catch in each sample was standardized to numbers of postlarvae per 1000 m<sup>3</sup> of water filtered. The average number of postlarvae over the two sampling nights was used as the mean monthly concentration for each net. The average of monthly postlarval concentration for each region (northwestern Florida Bay vs. Florida Keys) was compared by using a nonparametric two-way analysis of variance (ANOVA) (Anderson, 2001).

Three 12-hour experiments were conducted in summer 2002 in the SK channel to document the behavioral response of pink shrimp postlarvae to ebb and flood tides. Consecutive pairs of night (i.e. dark) flood and dark-ebb plankton samples were taken hourly from 19:00 to 07:00 h from 9 to 10 July (new moon), 23 to 24 July (full moon), and 8 to 9 August (new moon). In addition, plankton samples were taken for 10 consecutive hours daily on 8 August to verify the response of postlarvae to light. The nonparametric Kruskal-Wallis test and analysis of variance (ANOVA) were used to determine differences in concentration of postlarvae between dark-ebb and dark-flood periods.

To evaluate the possible effect of environmental variables on larval supply to Florida Bay and the pattern of seasonality in postlarval concentrations, available time series of winds and sea surface temperature (SST) on the coastal shelf were examined in relation to our time series of monthly measured larval concentrations. In particular we were looking for a pattern that might help to determine the reason for the marked summer peak in the concentration of postlarvae at the western border of Florida Bay. Time series of hourly winds and sea surface temperature (SST) for the 3-year sampling period were obtained from the Coastal Marine Automated Network (CMAN) station at Long Key, and from the Coastal Ocean Monitoring and Prediction System (COMP) station in NW Florida Bay (Fig. 1). Temperature and wind time series from the Long Key CMAN station and the NW Florida Bay COMP station were highly correlated with each other ( $r^2=0.9$ ;  $P<0.01$ ). The longer Long Key time series were used for coastal SST and wind analysis. Wind speed and direction over the Keys, as measured at CMAN sites, are highly coherent (Peng et al., 1999) and useful for explaining currents on the SW shelf (Lee and Williams 1999). Monthly av-

**Table 1**

Mean cross section depth, peak tidal flow, and cross section area of the four channels sampled for pink shrimp (*Farfantepenaeus duorarum*) postlarvae at the north-western border of Florida Bay, Middle Ground (MG) and Sandy Key (SK), and at the southeastern edge in the Middle Florida Keys, Whale Harbor (WH), and Panhandle Key (PH). Area was calculated at zero (m) of mean sea level.

Station	Depth (m)	Peak tidal flow (m <sup>3</sup> /sec)	Cross area (m <sup>2</sup> )
MG	3.0	1420	2723
SK	3.1	570	1345
WH	3.3	280	407
PH	2.0	30	74

erages of wind vectors and SST were calculated from hourly CMAN time series data (years 2000 to 2002) to examine the effect of winds and SST on the monthly postlarval collections.

Time series of current data from two established stations with moored ADCPs and temperature and salinity sensors were used to drive our transport model. Initially, these data were examined to determine whether prevailing currents alone could explain the transport of larvae from the Tortugas spawning grounds to Florida Bay nursery grounds. These stations also were a source of salinity data used in one set of simulations. These stations were located on the inner SW shelf of the Gulf of Mexico, about 30 km from our MG station (Lee et al., 2001) (Fig. 1). This array monitored coastal currents as part of the Florida Bay Circulation and Exchange Study (Lee et al., 2001). The ADCP moorings were located at depths of 6.4 m (mooring A=onshore) and 11.6 m (mooring B=offshore) and recorded data every 30 minutes for a 3-year period (A=21 September 1997 to 15 October 2000; B=22 September 1997 to 17 October 2000). The two ADCP moorings were about 30 km apart. Lee et al. (2001) reported insignificant differences between currents in the vertical for cross-shelf transport in the shallow SW Florida shelf. Wind and current vectors were resolved into cross-shelf ( $u$ =east [+], west [-]) and alongshore ( $v$ =north [+], south [-] constituents). The east-west and north-south displacement of current and wind constituents (half-hour current data and the hourly wind data) was the product of each current and wind constituent by the respective time interval. Correlation analysis was conducted on currents and wind time series.

A harmonic analysis was conducted on the three-year ADCP raw data to define tidal constituents and current magnitude. Period ( $P_i$ ) and tidal excursion ( $T_i$ ) were calculated for each constituent from amplitudes ( $A_i$ ) and frequencies of the constituents as follows:

$$T_i = A_i P_i / \pi.$$

A simple Lagrangian trajectory model was developed to estimate the drift of planktonic stages. The model used the observed currents at ADCP moorings A and B to calculate trajectories. Because of the lack of information on spatial current variations and the difficulty of extrapolating vertical current profiles from one depth and bottom relief to other conditions, a simple two-dimensional (horizontal) simulation model was used. For the computations we selected the highest bin from the ADCP that had good data throughout the tidal cycle at each station. This bin typically was 1 m below the mean water level at that location and was the highest bin not affected by instrument sidelobe interference. Because instantaneous bottom currents were closely aligned in direction with surface currents and because magnitudes were only 25% lower, the tidal currents were barotropic and we used, therefore, the surface currents to estimate the largest possible distance traveled.

The larval transport was calculated with the equation

$$dx_i/dt = u_i,$$

where  $x_i$  = position vector of the larvae;  
 $t$  = time; and  
 $u_i$  = the local current velocity.

An Euler (forward in time) integration rule was used to numerically solve this equation. Because only two ADCPs (A and B) provided the current data for this large region, no attempt was made to extrapolate a current field from them. Simulations were run by using current meters A and B independently and by assuming that the current field was spatially homogeneous. The trajectories therefore were two-dimensional in the horizontal plane and the result was identical to a progressive vector diagram. Comparison between the two sets of trajectories (A and B) provided an estimate of the possible variability. The model was used to explore the potential transport of planktonic stages under various assumptions of behavior controlled by environmental cues: 1) a behavioral response to salinity and light, 2) a diel behavior, 3) a diel and tidal behavior throughout the planktonic phase, and 4) an ontogenic change that began with diel behavior and added a tidal behavior at the 15<sup>th</sup> day. All four hypotheses of larval behavior in relation to transport were simulated in order that their effects on distance traveled could be compared and contrasted. In all simulations, we assumed that larvae traveled only at night. We also assumed that the source of the pink shrimp larvae was located immediately northeast of the Dry Tortugas about 150 km from western Florida Bay (Cummings, 1961; Jones et al., 1970; Roberts, 1986). The program simulated distances traveled by particles for a period of 30 days (e.g., days 1–30, 31–60, 61–90, etc.), a period that corresponds to the estimated developmental period for pink shrimp from the time of hatching to the postlarval stage when larvae are ready for settlement (Dobkin, 1961; Ewald, 1965).

## Results

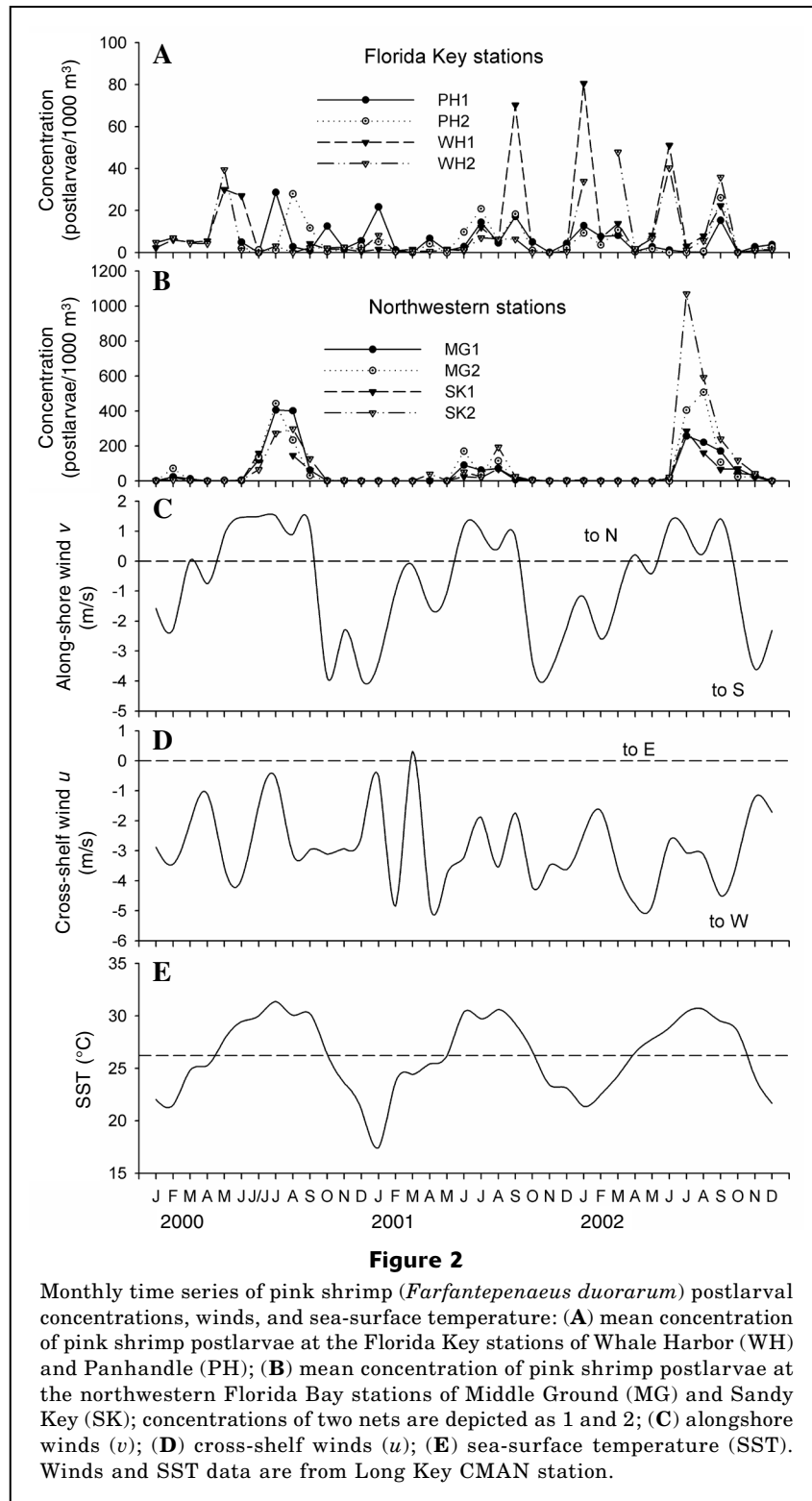
### Patterns of postlarval supply, SST, and winds

The monthly influx of postlarvae through the Middle Florida Keys channels (WH and PH) exhibited a highly variable temporal pattern from year to year. Postlarvae were observed every month through the three years (Fig. 2A). Peaks of postlarvae through the Middle Keys channels occurred in May, July, August, and October 2000; in January, July, and October 2001; and in January, March, June, and September 2002. In contrast, the monthly influx of postlarvae through the northwestern stations (SK and MG) showed a strong seasonal pattern with one distinct high peak centered in summer from July through September for each year of the 3-year period (Fig. 2B). The number of postlarvae entering through northwestern Florida Bay was much higher than through the Keys stations. The mean concentration of postlarvae per station over the 3-year period indicated that concentrations of postlarvae entering northwestern Florida Bay through SK and MG channels were about eight times greater than through the Florida Keys channels of WH and PH (Fig. 3). Results from a two-way ANOVA indicated that there was a significant effect of site (northwestern stations vs. Florida Key stations) and month on the supply of postlarvae entering Florida Bay (Table 2).

Winds showed a seasonal pattern; the spring and summer were dominated by weak southeasterly winds and the fall and winter, by strong northerly winds (Fig. 2, C–D). The monthly average alongshore showed a weak northward constituent in spring–summer of each year (Fig. 2C). The monthly average cross-shelf winds were consistently negative (toward the west) and showed no seasonality (Fig. 2D). The average temperature over the three-year time series was 26.1°C, and winter temperatures in 2000–01 were lower than in 2001–02 (Fig. 2E). In summer, during the period of peak postlarval immigration through the northwestern stations (MG and SK), the alongshore wind constituent was mainly northward, the cross-shelf wind was westward, and the SST was above average during the three-year period (Fig. 2, A–E). Postlarval concentrations at the northwestern stations were correlated with SST and alongshore winds (Fig. 2, B–E; Table 3). Postlarval concentrations at the Florida Keys stations (WH and PH) were not correlated with either winds or SST.

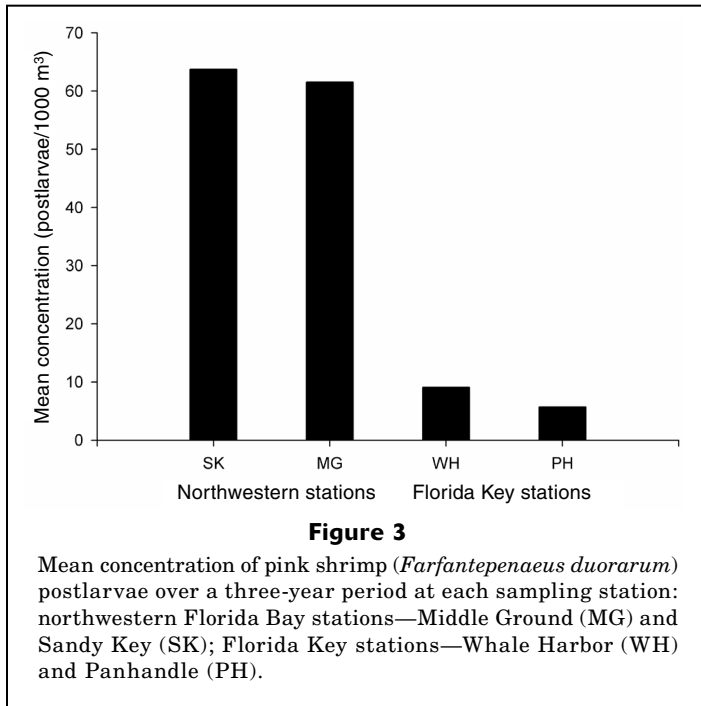
### Subtidal and tidal currents at the SW Florida shelf

Advective displacement derived from two ADCP velocity records indicated that the net current is primarily in the alongshore direction (Fig. 4, A and B). The alongshore flow from onshore mooring A was northward, had a total mean velocity of 0.0062 m/sec, and a total water displacement of  $589.3 \times 10^3$  m over the three years (Fig. 4A). The cross-shelf flow was westward, had a mean velocity of  $-0.0005$  m/sec, and a total water displacement of  $-289.7 \times 10^3$  m. The alongshore flow from offshore moor-



ing B was southward, had a mean velocity of  $-0.0038$  m/sec and a total water displacement of  $-364.7 \times 10^3$  m (Fig. 4B). The cross-shelf flow was eastward, had a mean speed of  $0.0015$  m/sec, and a total water displacement of

$145.5 \times 10^3$  m and a resultant southeastward current. The alongshore winds measured at Long Key were southward and had a total water displacement of  $16.1 \times 10^3$  m, and the cross-shelf winds were westward and had a total

**Table 2**

Results of a nonparametric two-way ANOVA of the effect of site and month on pink shrimp (*Farfantepenaeus duorarum*) postlarvae entering Florida Bay.  $P < 0.05$  is indicated with an asterisk. SS=sum of squares; MS=mean of squares.

Factor	df	SS	MS	F	P
Month	80	756.7	9.5	5.6	0.007*
Site	1	65.9	65.9	39.3	0.002*
Month × site	1	1191.5	1191.5	711.3	0.007*
Error	461	772.2	1.7		

**Table 3**

Correlation coefficients of pink shrimp (*Farfantepenaeus duorarum*) postlarval concentrations with sea surface temperature (SST), cross-shelf wind (U), and alongshore wind (V) at the four sampling stations of MG= Middle Ground, SK= Sandy Key, WH= Whale Harbor and PH= Panhandle. Environmental data are from Long Key CMAN station. Significant correlations ( $P < 0.05$ ) are indicated with an asterisk.

	SST	U	V
MG	0.82*	-0.025	0.67*
SK	0.73*	0.11	0.57*
WH	0.15	0.16	0.36
PH	-0.17	0.14	-0.09

water displacement of  $-86.3 \times 10^3$  m (Fig. 4C). The subtidal currents in this region are very weak as also observed by other investigators (Koczy et al., 1960; Rehrer et al., 1967). Correlation coefficients between winds and currents in the alongshore direction ( $v$ ) were significant for both onshore and offshore currents time series (Table 4). Correlation coefficients between winds and currents in the cross-shelf direction were higher in the onshore than in the offshore data series. This analysis indicated that prevailing currents, overall, were not favorable to passive transport of larvae from the Tortugas to western Florida Bay.

A harmonic analysis of the 3-year ADCP data showed that semidiurnal tidal constituents ( $M_2$ ,  $S_2$ ,  $K_2$ , and  $N_2$ , see Table 5 for explanation of abbreviations) are dominant on the SW Florida shelf.  $M_2$  was the strongest tidal constituent and its east-west constituent explained 95% of the total current variance. The east-west amplitude of the  $M_2$  constituent was 0.32 m/s for both moorings, and the north-south was 0.07 m/s for mooring A and 0.04 m/s for mooring B. The east-west amplitude (0.32 m/s) was much stronger than the long-term averaged subtidal cross-shelf constituent at both stations (0.001 m/s). The east-west tidal excursion of the  $M_2$  constituent was similar for both moorings, but a few meters larger on the offshore station (Table 5). This result indicates that it is reasonable to consider that there are similar tidal excursions on the SW shelf up to 50 km.

#### Ebb versus flood catches

Concentration of postlarvae collected hourly over a complete dark portion of a tidal cycle showed clearly that dark-ebb catches were negligible (<10%) by comparison with dark-flood catches (>90%) (Fig. 5, A–C). Hourly concentrations of postlarvae collected on the dark flood were 92.7% from 9 to 10 July, 90.2% from 23 to 24 July, and 86.9% from 8 to 9 August 2002. A nonparametric Kruskal-Wallis test showed significant differences in catches of postlarvae between dark-ebb and dark-flood periods (Kruskal-Wallis:  $H=15.5$ ,  $n=36$ ,  $P < 0.001$ ; (ANOVA:  $F=18.6$ ;  $P < 0.001$ ). Samples taken during the day on 8 August confirmed the hypothesis that postlarvae are present mostly at night in the water column (Table 6). A total of 18 postlarvae (31.5 postlarvae/1000 m<sup>3</sup>) were captured during 10 consecutive daylight hours, against 2657 (3702.5 postlarvae/1000 m<sup>3</sup>) captured during 10 consecutive hours of darkness. Although concentrations of postlarvae tend to increase with the tidal current, these differences were not significant (Kruskal-Wallis:  $H=10.3$ ,  $n=36$ ,  $P=0.5$ ). From 9 to 10 July, no postlarvae were captured during the hours of highest current speed (2:00 to 3:00 h), which coincided with high rain and winds (Fig. 5A). It is not clear whether these factors caused a change of behavior in the postlarvae or a malfunction of the net. From 23 to 24 July, concentration of postlarvae on the dark flood followed the cur-

rent speed; highest catches occurred at the maximum speed and lowest catches at the minimum speed (Fig. 5B). From 8 to 9 August, the highest peak of postlarvae occurred at the end of the dark-flood period when the current had decreased in speed (Fig. 5C).

### Transport simulations

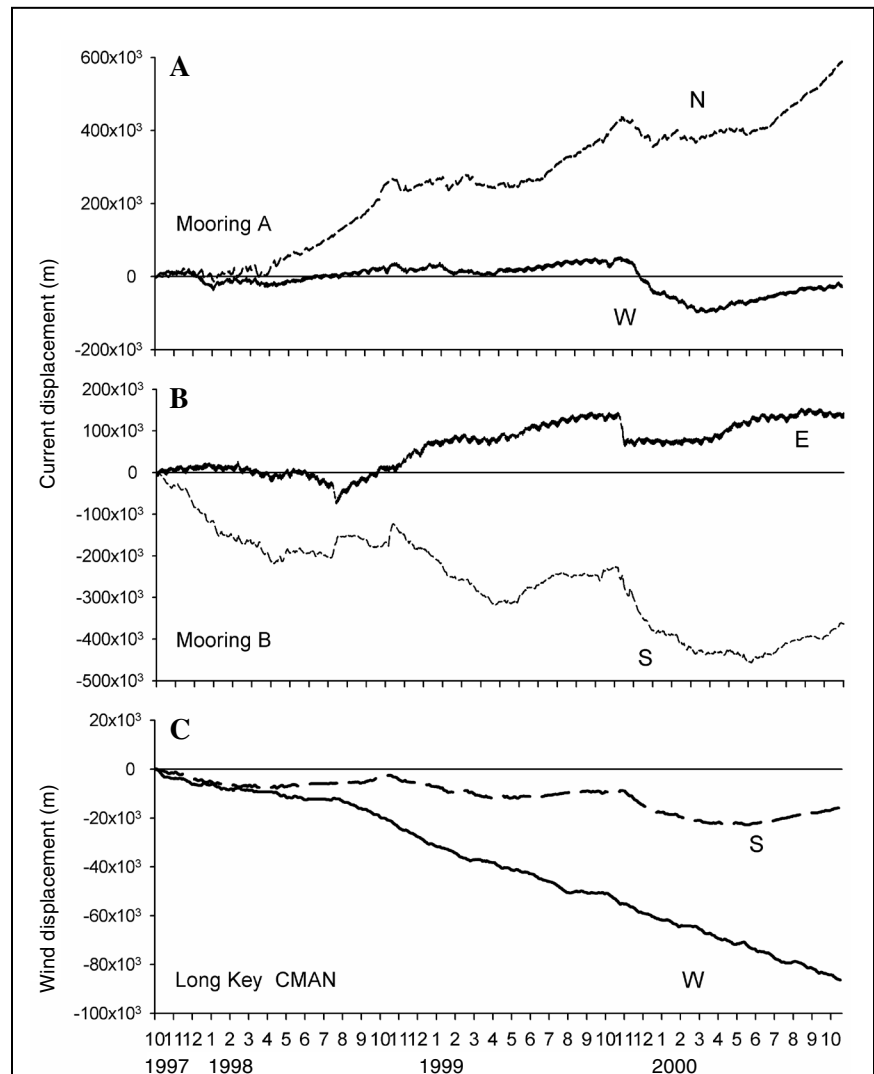
Results of channel net sampling showed that the greatest postlarval influx occurred at the northwestern border of the bay, where there was a strong seasonal pattern with maxima from July through September each year. Postlarval concentrations at the northwestern stations were correlated with the alongshore winds and with surface temperature but did not correlate with the cross-shelf winds. However, postlarvae need to travel up to 150 km across the shelf to reach their nursery grounds.

Cross-shelf transport mechanisms were explored by using a Lagrangian trajectory model that simulated the maximum distance traveled by planktonic stages moving at night for a 30-day period. Four scenarios of transport were modeled under different assumptions of behavior:

**Scenario 1** With the assumption that planktonic stages (larvae and postlarvae) of pink shrimp respond to light and salinity changes (Hughes 1969a, 1969b), the first simulation postulates that larvae and postlarvae move horizontally with a vertical migratory behavior cued by changes in salinity. Larvae and postlarvae swim to the surface at night when an increase in salinity is detected and remain near the bottom when the salinity decreases.

**Onshore mooring** The maximum distance traveled in the cross-shelf direction was 98 km eastward and 70% of larvae traveled up to 30 km (Fig. 6A). The average eastward distance in all simulations was 22 km. The maximum displacement occurred in fall-winter. Alongshore distances were as much as 25 km northward (70% of larvae) and 15 km southward (30%) (Fig. 6, A and B).

**Offshore mooring** The maximum distances traveled in the cross-shelf direction was 100 km (84% of larvae traveled 40 km). Alongshore distances were as much as 15 km northward (70%) and 20 km southward (30%) (Fig. 6, C and D).



**Figure 4**

Time series of current and wind displacement, October 1997–October 2000. Current data are from two ADCPs located at the SW Florida shelf, and wind data are from Long Key CMAN station; (A) onshore ADCP mooring A, (B) offshore ADCP mooring B; see ADCP locations in Figure 1. (C) Wind displacement. Alongshore constituents are represented by interrupted lines (N=north [+], S=south [-]) and cross-shelf by continuous lines (E=east [+], W=west [-]).

**Scenario 2** The second simulation assumes that planktonic stages travel at night using the instantaneous current.

**Onshore mooring** Distances traveled in the cross-shelf direction reached a maximum of 68 km and 75% of larvae traveled only 30 km eastward (Fig. 6A). The average eastward distance in all simulations was 15 km. The maximum displacement occurred in spring-summer (May to September 1998) during the first year and in fall-winter (October 1999 to February 2000) during the second and third year. Distances recorded in the alongshore direction were as far as 40 km northward (48% of larvae) and 30 km southward (52%) (Fig. 6, A and B).



**Offshore mooring** Maximum distance traveled in the cross-shelf direction reached 60 km eastward and 80% of larvae traveled less than 30 km. Distances recorded in the alongshore direction were as far as 40 km northward (51%) and 40 km southward (49%) (Fig. 6, C and D).

**Scenario 3** Under the assumption that pink shrimp larvae and postlarvae migrate vertically in a tidal cycle, the third simulation postulates that larvae and postlarvae swim in the water column near the surface at night during the flood tide and remain near the bottom during the ebb tide. In this simulation it is assumed that planktonic stages move by using the eastward cur-

rent (flood tide) during the postulated 30 days of larval development.

**Onshore mooring** The maximum distance traveled in the cross-shelf direction was 200 km eastward and 86% of the larvae exceeded 150 km. The average eastward distance in all simulations was 132 km. The maximum larval displacement occurred from December 1999 through March 2000. Distance traveled in the alongshore direction was 45 km northward (70%) and 5 km southward (30%) (Fig. 6, A and B).

**Offshore mooring** The maximum larval displacement in the cross-shelf direction was 200 km eastward and 85% of the larvae reached 150 km. The maximum eastward displacement occurred in fall and in winter. Distance traveled in the alongshore direction was as much as 40 km northward (82%) and 5 km southward (18%). The maximum distance traveled was recorded in March–April and June 2000 (Fig. 6, C and D).

**Table 4**

Correlation coefficients of wind and current components. *U* and *V* are the east-west and north-south components respectively. Nearshore currents are from onshore (A) and offshore (B) ADCP moorings over the SW Florida shelf. Wind data are from Long Key CMAN station. Significant correlations ( $P < 0.05$ ) are indicated with an asterisk.

	Mooring A		Mooring B	
	onshore		offshore	
	<i>U</i> -current	<i>V</i> -current	<i>U</i> -current	<i>V</i> -current
<i>U</i> -wind	-0.25*	-0.22*	-0.10	-0.06
<i>V</i> -wind	0.26*	0.55*	0.12	0.60*

**Scenario 4** In this simulation, it is assumed that there is a change in behavior for pink shrimp larvae—an assumption similar to the one taken in simulations for some Australian penaeid species (Rothlisberg, 1982; Rothlisberg et al., 1995, 1996). Early larval stages (protozoa and mysids) migrate vertically in a diel cycle and there is no cross-shelf displacement during the first 15 days of development. Later in development, postlarvae migrate by using tidally induced behavior superimposed on the diel behavior for the remaining 15 days of planktonic development, and the eastward current (flood tide).

**Onshore mooring** The maximum displacement of larvae in the cross-shelf direction was 100 km eastward

**Table 5**

Harmonic analysis results conducted on three years of ADCP data (September 1997–October 2000). Moorings were located at the SW Florida shelf: A (onshore) and B (offshore) moorings. *U* and *V* are the east-west and north-south tidal constituents, respectively. Explained variance of constituent *U* was 95% and of *V* was 50% (for A), and 96% and 29% (for B), respectively. M2=semidiurnal lunar; S2= semidiurnal solar; N2=semidiurnal larger lunar elliptic; K1=diurnal lunisolar; M1=diurnal smaller lunar elliptic; O1=diurnal principal lunar; K2=semidiurnal lunisolar.

	Tidal constituent	Period (h)	Tidal constituent <i>U</i>		Tidal constituent <i>V</i>	
			Amplitude (m/sec)	Tidal excursion (m)	Amplitude (m/sec)	Tidal excursion (m)
A	M2	12.42	0.321	4561.7	0.070	993.5
	N2	12.66	0.056	810.8	0.013	191.5
	S2	12.00	0.100	1368.2	0.017	239.3
	K1	23.93	0.049	1332.9	0.015	408.7
	M1	24.84	0.005	139.5	0.001	31.3
	O1	25.82	0.039	1139.1	0.010	289.9
	K2	11.97	0.025	345.6	0.010	135.8
B	M2	12.42	0.323	4593.0	0.038	539.4
	N2	12.66	0.057	828.3	0.007	105.9
	S2	12.00	0.105	1439.7	0.009	129.3
	K1	23.93	0.052	1434.4	0.008	213.9
	M1	24.84	0.003	93.9	0.002	54.1
	O1	25.82	0.043	1278.1	0.002	68.0
	K2	11.97	0.023	319.5	0.005	63.1

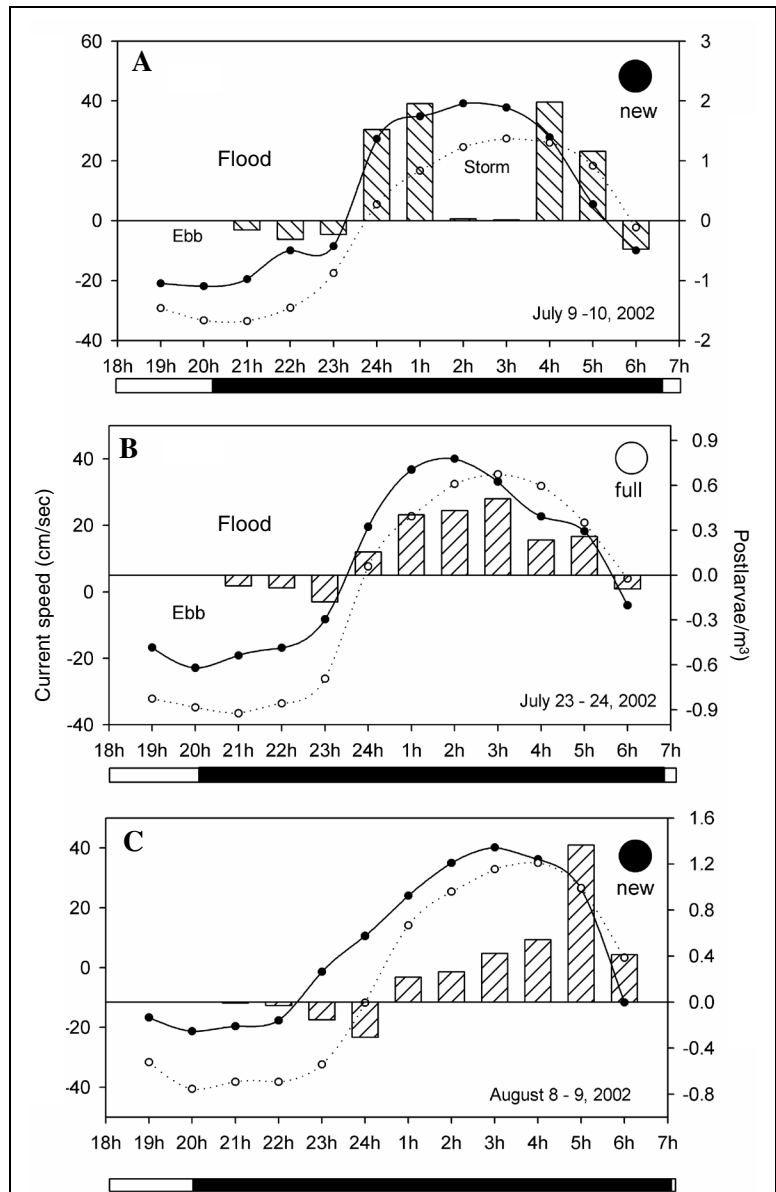
and 86% of larvae reached 80 km. The average eastward distance traveled in simulations was 66 km. The maximum distances traveled in the alongshore direction was 25 km northward (70% of larvae) and 10 km southward (30%). The maximum distance traveled was recorded in March–April and June 2000 (Fig. 6, A and B).

**Offshore mooring** The maximum displacement of larvae in the cross-shelf direction was 90 km eastward and 85% of larvae reached 80 km. Distance traveled in the alongshore direction reached 20 km northward (86% of larvae) and 5 km southward (14%) (Fig. 6, C and D).

## Discussion

The monthly influx of pink shrimp postlarvae entering Florida Bay through its northwestern border showed a strong seasonal pattern of annual high peaks in summer over the 3-year period. Postlarval concentrations were correlated with alongshore winds and sea surface temperature. Alongshore winds were seasonal, with a weak northward constituent in spring–summer of each year changing to a strong southward in fall and winter. This seasonal pattern agrees with the general circulation described for the SW Florida shelf, highly dependent on synoptic-scale winds, coupled with a strong seasonality and strong tidal currents (e.g., Weisberg et al., 1996; Wang, 1998; Smith, 2000; Lee et al., 2001). Although tidal currents seem to be the main vehicle of eastward transport for planktonic stages, alongshore winds may be fundamental for moving larvae northward along the SW Florida shelf by avoiding a drift with the Florida Current or with the cyclonic circulation of the gyres that form southwest of the Dry Tortugas (Lee et al., 1994; Fratantoni et al., 1998). Under these circumstances larvae may reach Florida Bay by the shortest route in summer using tidal currents and winds across the shallow SW Florida shelf and entering Florida Bay by its northwestern border. The summer seasonality of postlarval immigration may also be amplified by the seasonality of spawning because higher temperatures induce higher spawning activity (Cripe, 1994) and consequently more recruits to enter the Bay during favorable onshore conditions.

Another alternative explanation for the summer larval immigration is that larvae may take advantage of a distinct annual tidal cycle produced in summer every year as a result of the interaction of the periods of the diel vertical migration and the tidal constituent ( $S_2$ ,



**Figure 5**

Hourly concentration of pink shrimp (*Farfantepenaeus duorarum*) postlarvae at Sandy Key station (SK) during a complete dark (night) tidal cycle conducted during (A) new moon, 9–10 July 2002, (B) full moon, 23–24 July 2002, and (C) new moon, 8–9 August 2002. Right y-axis indicates concentration of postlarvae/ $m^3$ ; left y-axis is tidal current speed (cm/sec) measured by acoustic Doppler velocity meter (filled circle and solid line) and by flowmeter (empty circles and interrupted line). Positive values in the y-axes indicate transport into Florida Bay (flood), and negative values transport out of the Bay (ebb). Horizontal bars on the bottom indicate hours of darkness versus light.

$K_1$ ) with the annual cycle of the length of the night (Crales et al., 2005). Larvae moving vertically in the water column with a diel behavior can be transported up to 70 km onshore in summer because the eastward current of the tidal constituents matches the diel cycle over extended intervals in the shorter summer nights

**Table 6**

Data from ebb-flood experiment conducted at Sandy Key (SK) station during 20 consecutive hours. E=ebb, F=flood, L=light, D=dark. VWF = volume of water filtered.

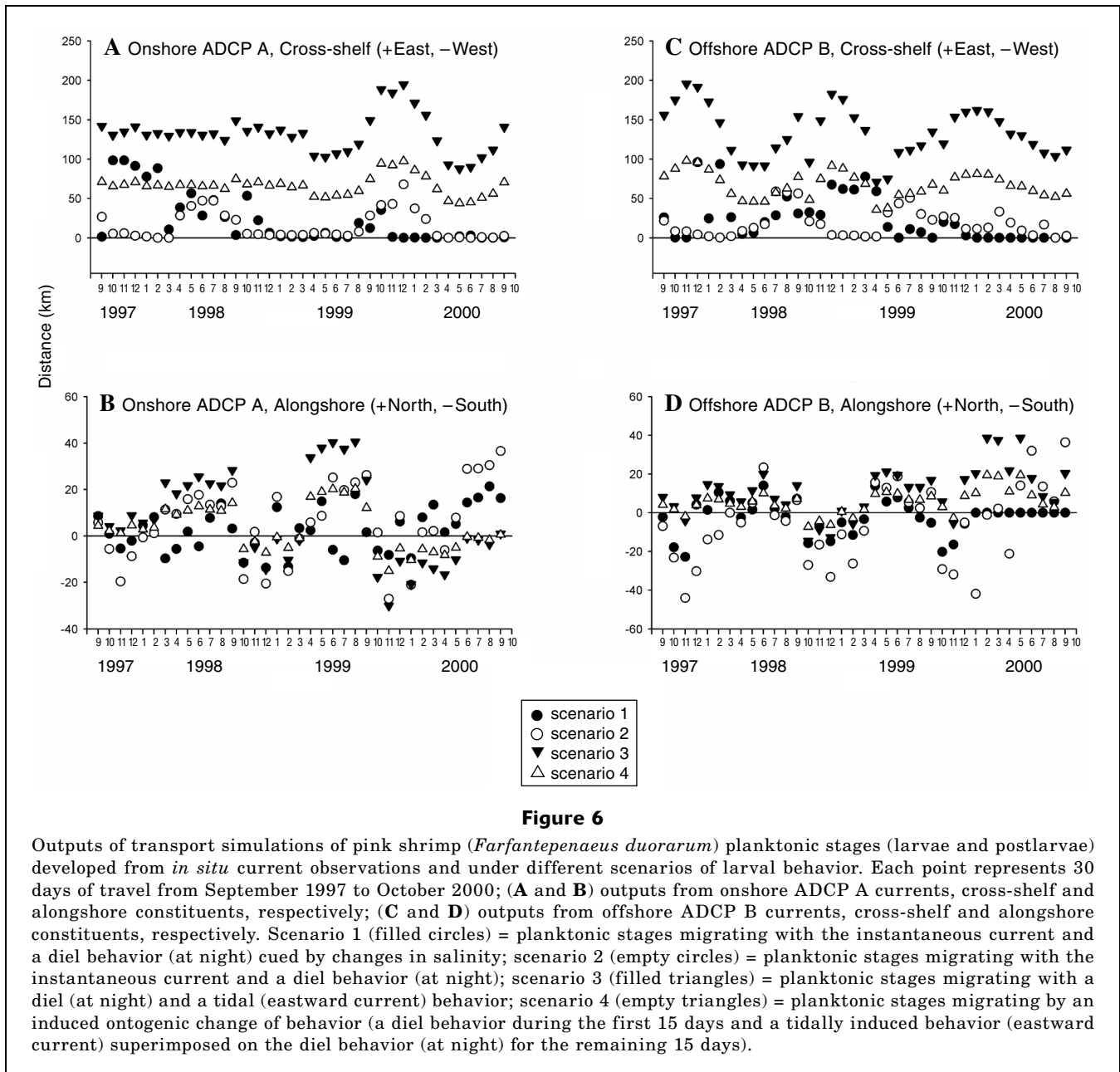
Date	Collection time	Tide stage	Light vs. dark	VWF (m <sup>3</sup> )	Number of postlarvae	Concentrations (postlarval m <sup>3</sup> )
08/08/2002	11:00	E	L	395.8	7	17.7
08/08/2002	12:00	E	L	535.3	2	3.7
08/08/2002	13:00	F	L	1360.1	0	0.0
08/08/2002	14:00	F	L	1262.3	0	0.0
08/08/2002	15:00	F	L	971.3	8	8.2
08/08/2002	16:00	F	L	531.2	1	1.9
08/08/2002	17:00	F	L	0.0	0	0.0
08/08/2002	18:00	F	L	0.0	0	0.0
08/08/2002	19:00	E	L	450.6	0	0.0
08/08/2002	20:00	E	L	575.6	0	0.0
08/08/2002	21:00	E	D	530.9	5	9.4
08/08/2002	22:00	E	D	477.6	14	29.3
08/08/2002	23:00	E	D	60.7	7	115.4
08/09/2002	0:00	E	D	263.3	87	330.4
08/09/2002	1:00	F	D	648.6	141	217.4
08/09/2002	2:00	F	D	944.3	247	261.6
08/09/2002	3:00	F	D	1164.1	491	421.8
08/09/2002	4:00	F	D	977.5	529	541.2
08/09/2002	5:00	F	D	737.8	1006	1363.6
08/09/2002	6:00	F	D	315.1	130	412.5

(Criales et al., 2005). Therefore, pink shrimp and other fish and invertebrate species that use tidal currents for transport with a daily vertical behavior may take advantage of this annual tidal cycle to improve their chances of reaching coastal nursery habitats.

The monthly influx of postlarvae through the Middle Florida Keys channels exhibited a highly variable seasonal pattern from year to year and from station to station. This section of the Keys coastal waters is frequented by coastal cyclonic eddies that originate at the Dry Tortugas and move downstream at 5–17 km/day along the edge of the shelf at intervals of 1 to 3 months (Fratantoni et al., 1998; Yeung et al., 2001). For planktonic stages, these eddies may serve as a delivery mechanism from offshore spawning grounds to the southeastern border of Florida Bay, allowing an onshore transport by the coastal countercurrent flow generated by the cyclonic circulation (Lee et al., 2001; Yeung et al., 2001; Criales et al., 2003). Episodic, mesoscale events associated with boundary current fronts and eddies may cause high variability in transport (Lee et al., 1994; Limouzy-Paris et al., 1997; Yeung and Lee, 2002). This variability was reflected in the influx of pink shrimp postlarvae through Middle Keys channels (Criales et al., 2003). The influx of postlarvae at WH and PH channels in the present study was also highly variable and there was no correlation with winds or sea surface temperature. Therefore, we hypothesized that

the high variability in postlarval influx detected at the Florida Keys channels reflects the temporal and spatial variability associated with the passage of coastal eddies.

Simulations of transport based on current observations indicated that passive larvae could not consistently be advected the estimated 150 km eastward across the shelf between spawning and nursery grounds in 30 days. This is true primarily because of the weak eastern current and the reversing nature of tides. In contrast, planktonic stages (larvae and postlarvae) moving at night with the eastward current (flood tide) can consistently travel 100 to 200 km in 30 days. Hypothetically, 85% of the larvae can be transported far enough from the known spawning grounds of Dry Tortugas to the nursery grounds in western Florida Bay in 30 days. Previous works conducted inside Florida Bay (Tabb et al., 1962; Roessler and Rehrer, 1971) and our own data obtained along the western border of Florida Bay demonstrated the ability of pink shrimp postlarvae to respond to the dark flood tide and to distinguish between day and night. Over 90% of postlarvae were caught in the dark flood period and only a few postlarvae were caught during daylight hours. This behavior needs to be investigated for early larval stages to define the exact age at which larvae begin reacting to change in tides and to environmental cues that trigger the vertical movement in relation to tidal stage. For other penaeid



species (*Fenneropenaeus merguensis*, *Penaeus plebejus*, and *Penaeus semisulcatus*) in the Gulf of Carpentaria, Australia, an ontogenic change in behavior has been documented for planktonic stages (Rothlisberg, 1982; Rothlisberg et al., 1995, 1996; Condie et al., 1999). Results of these studies showed that during the first two weeks of planktonic development, larvae migrate vertically in a diel cycle; later in development, the vertical migration is tidally induced. Under those conditions there was little or no systematic cross-shelf displacement of larvae during the first two weeks; afterward, cross-shelf displacement occurred rapidly (Rothlisberg et al., 1995; 1996). Simulation of transport for pink shrimp larvae using this ontogenic change of behavior

indicated that planktonic stages can be transported up to 100 km eastward and 85% of larvae reach 80 km. If this behavior applies to pink shrimp, the location of the spawning grounds needs to be reconsidered in favor of areas closer to Florida Bay. Alternatively, the behavior of early planktonic stages may have been underestimated. Results of this research indicated once again the extreme importance of defining larval behavior and including behavior in dispersal models.

The cue(s) that penaeid postlarvae use to migrate in the water column during the flood tide and to return to the bottom on the ebb tide are not completely understood and could be species specific. Hughes (1969a, 1972) demonstrated in laboratory experiments that

pink shrimp postlarvae react to changes in salinity by changing swimming direction. Postlarvae were more active in the water column with increases in salinity, and this finding implies a shoreward displacement with the flood tide. Similar responses to salinity changes have been found for postlarvae of *Farfantepenaeus californiensis*, *Farfantepenaeus brevisrostris*, *Litopenaeus stylirostris*, and *Litopenaeus vannamei* from the Mexican Pacific (Mair, 1980). The importance of a salinity cue for transport has been questioned for other penaeid species that inhabit hypersaline estuaries (southeast African, western Australia) in which penaeid postlarvae would need to move against a salinity gradient (Penn, 1975; Forbes and Benfield, 1986; Rothlisberg et al., 1995). Our simulations of transport guided by salinity changes indicated that planktonic stages could travel distances in the range of only 30 km in 30 days. This result may indicate that salinity is not the only environmental factor controlling long cross-shelf migrations of pink shrimp. However, Hughes (1969a, 1969b) in early experiments suggested that a salinity cue could apply to postlarvae near the nursery grounds. Changes in water pressure have been proposed as the only environmental factor that triggers the vertical migration of postlarval shrimps in the Gulf of Carpentaria, Australia (Penn, 1975; Forbes and Benfield, 1986; Rothlisberg et al., 1995). Laboratory experiments and numerical models have shown that tiger shrimps (*Penaeus semisulcatus* and *Penaeus esculentus*) larvae switch behavior when the change in water pressure with tides becomes a significant fraction of the total pressure (Rothlisberg et al., 1996; Condie et al., 1999; Vance and Pendrey<sup>2</sup>). This behavior only occurred in larvae above a certain size. However, it still remains to be determined whether, in a natural ecological context, the rates of relative changes of pressure are consistent with the tidal cycle periodicity and are detectable at absolute amounts in order to permit a behavioral response.

By means of simulations of transport, we have identified a potential STST mechanism for planktonic pink shrimp to migrate the estimated 150 km in 30 days from spawning to nursery grounds over the Florida shelf. Organisms inhabiting coastal ecosystems dominated by tides have the potential to control their cross-shelf movement through STST (Shanks, 1995). The extent of the transport depends on the speed of the tidal current and the time that organisms spend in the water column. Success in reaching the nursery grounds depends upon the stage in larval or postlarval develop-

ment when the tidal behavior is added. A dependence on tidal currents for the entire larval transport period was postulated for *Melicertus latisulcatus* in Western Australia (Penn, 1975). The shrimp *Lucifer faxoni* is the only species for which a STST mechanism across the shelf has been shown (Woodmansee, 1966). Strong tidal currents and several coastal sources of fresh water define the spawning grounds of the wide and shallow SW Florida shelf (Lee et al., 2001; Jurado, 2003). Under these conditions, parts of the SW Florida shelf may behave as an estuary in which planktonic pink shrimp may easily recognize tides by means of endogenous behavior or environmental variables.

From this study we determined that the greatest influx of postlarval pink shrimp occurred at the northwestern border of Florida Bay in summer. Postlarvae entering Florida Bay through the channels of the Middle Florida Keys occurred at a much lower magnitude and there were only sporadic peaks and no apparent seasonality in influx. The transport mechanism of planktonic stages of pink shrimp across the SW Florida shelf seems to depend heavily on semidiurnal tides and larval behavior, and much less on seasonal winds. The response of postlarvae to the tidal currents was clearly observed at the western margin of Florida Bay. Such behavior needs to be explored in early stages to define the age at which larvae begin to respond to tides, the location on the Florida shelf at which this response occurs, and the specific environmental cues linked to such behavior. With this information, more realistic simulations of transport can be made with a complete hydrodynamic model that would incorporate spatial and vertical variations in currents. Depending on the resulting transport, the location of spawning grounds may be better defined, leading to better protection of this valuable fishery resource. Information on recruitment variability and key environmental factors affecting larval transport are essential to accurately interpret stock assessments, maintain the ecological integrity of both spawning grounds and nursery grounds, and to effectively manage the pink shrimp fishery.

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<sup>2</sup> Vance D. J., and R. C. Pendrey. 2001. Vertical migration behaviour of postlarval penaeid prawns: a laboratory study of the effect of tide, water depth and day/night. In The definition of effective spawning stocks of commercial tiger prawns in the Northern prawn fishery and king prawns in the eastern king prawn fishery-behaviour of postlarval prawns, p. 28–52. Fisheries Research and Development Corporation (FRDC) Final Report (Project 97/108), 68 p. CSIRO Marine Research Laboratories, P.O. Box 120, Cleveland, Qld. 4163, Australia.

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