

Key factors influencing transport of white shrimp (*Litopenaeus setiferus*) post-larvae into the Ossabaw Sound system, Georgia, USA

E. L. WENNER,^{1,*} D. M. KNOTT,¹
C. A. BARANS,¹ S. WILDE,¹ J. O. BLANTON²
AND J. AMFT²

¹South Carolina Department of Natural Resources, Marine Resources Research Institute, Charleston, SC 29422, USA

²Skidaway Institute of Oceanography, Savannah, GA, USA

ABSTRACT

We examined conditions under which white shrimp (*Litopenaeus setiferus*) post-larvae enter an estuarine channel receiving high freshwater discharge and one receiving negligible discharge in the Ossabaw Sound system of Georgia, USA, during 1997 and 1998. We used surface nets to collect plankton over several 14-day periods, during which consecutive tows were made at night against the flooding current at stations in the inlet channels. During these sampling periods, additional intensive periods of around-the-clock surface and near-bottom (using a bottom sled) plankton tows were made. Data on oceanographic conditions were obtained from moored instrument arrays and shipboard sampling. We identified three key factors that influenced the densities of post-larval white shrimp in time and space within the Ossabaw inlet system. The first factor was a critical minimum temperature of coastal waters of 27–28°C. Once the threshold temperature was reached, lunar tidal stage became a key factor when the full duration of the flood tide coincided with darkness during peak ingress. This peak also coincided with an increase in water level within the system by more than 0.2 m, which induced an additional influx of water that reinforces the flood current over the ingress period. Our results suggest that the direction of subtidal currents (into or out of the system) becomes a significant factor in post-larval ingress when influx of water coincides with the time of favorable temperature conditions and nighttime flood tides.

Key words: estuaries, *Litopenaeus setiferus*, post-larvae, south-eastern USA, tidal transport, white shrimp

INTRODUCTION

The most valuable fishery of South Carolina and Georgia in the United States is directed at the penaeid white shrimp (*Litopenaeus setiferus*) resource. Coastal oceanographic and meteorological processes greatly influence early life-history stages of penaeid shrimp, which have a weakly swimming larval stage that must be transported from continental shelf waters, where the adults spawn, to estuarine nursery grounds (Weinstein, 1988; Rogers *et al.*, 1993; Epifanio, 1995; Rothlisberg *et al.*, 1995). There is evidence that the magnitude of the post-larval white shrimp stocks is related to subsequent adult harvests (DeLancey *et al.*, 1994). Although successful recruitment of planktonic larvae is a critical determinant of adult shrimp stock size, our ability to understand and predict inter-annual and spatial variations is limited. The interaction between the behavior of post-larval white shrimp and the hydrographic processes that transport them to their estuarine nursery grounds produces complex temporal patterns of ingress and three-dimensional larval distributions. Predicting the extent of the commercial and recreational harvest, based on estimates of larval and juvenile abundance, may be a critical part of managing the shrimp fishery for maximum yield.

Transport of penaeid post-larvae is a complex process in which more than one mechanism may be involved, simultaneously or in series. Suggested mechanisms include selective tidal transport cued by synchronized salinity changes (Hughes, 1969a,b), endogenous rhythms (Hughes, 1972) or hydrostatic pressure (Forbes and Benfield, 1986; Rothlisberg *et al.*, 1995). Another transport hypothesis suggested that changes in coastal water temperature and salinity associated with cold fronts act as environmental cues in combination with diel movements of the post-larvae to facilitate transport (Rogers *et al.*, 1993). The interaction of diel vertical migration with tidal and

*Correspondence. e-mail: wennere@mrd.dnr.state.sc.us

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wind-forced currents has also been suggested as a possible mode of recruitment (Rothlisberg *et al.*, 1983; Wenner *et al.*, 1998). Regardless of the mechanism, for successful recruitment it is necessary to have a pool of larvae available within a zone located within 5 km of the coast (Blanton *et al.*, 1999).

Analysis of cross-sections of hydrographic structure through the coastal frontal zone off North Edisto Inlet, South Carolina, revealed that upwelling-favorable winds reinforce an estuarine-like circulation that enhances cross-shelf water transport (Blanton, 1996). The movement of surface water offshore is indicated by shallow low-density lenses with a cross-shelf width of about 20 km, a result that has been verified in numerical simulations (Blanton *et al.*, 1989). This mechanism appears to be responsible for moving large quantities of coastal water seaward.

Based on our previous research, tidal circulation in the vicinity of an idealized inlet was modeled using a three-dimensional non-linear finite element model (Kapolnai *et al.*, 1996). In the presence of freshwater discharge, the principal route into the inlet was skewed toward a narrow band next to the northern shore. Moreover, strong convergence at fronts emanating from estuaries helped to retain particles such as larvae once they were entrained at the front. These findings suggest that larval ingress routes dominated by circulation processes may differ, depending on the presence or absence of buoyant discharges through the inlets. A more recent model study based on the North Edisto Inlet, SC (Blanton *et al.*, 1999) showed that when freshwater discharge is absent, passive particles (proxies for larvae) are withdrawn from the continental shelf in a narrow zone upwind of the inlet and adjacent to the coast. The withdrawal zone width is less than 5 km wide. That study pointed out that the source location of larvae depended more on the wind acting on the scale of inlet separation rather than on a larger scale such as the width of the continental shelf.

Shoreward currents capable of advecting larvae into the vicinity of south-eastern inlets occur during both upwelling and downwelling conditions. These onshore currents, however, are present during upwelling only near the bottom, while during downwelling they occur near the surface. Thus, whether or not larvae are carried shoreward during either upwelling or downwelling conditions depends critically on the vertical migratory behavior of the organism (Blanton *et al.*, 1995; Wenner *et al.*, 1998). Recent results from our work on white shrimp post-larvae in the North Edisto River of South Carolina verified the importance of vertical positioning in the water column. Downwelling winds with an onshore stress component were

associated with the largest ingress of white shrimp (Wenner *et al.*, 1998). In order to derive maximum benefit from the downwelling regime, post-larvae would have to spend most of their time near the surface to be advected into the withdrawal zone of the inlet. The onshore flow would be more efficiently generated in shallow water next to the coast by the onshore wind component rather than the southerly alongshore component along the Georgia coast.

Our North Edisto study showed that, in addition to wind-driven transport, density of white shrimp post-larvae changes with tidal stage (Wenner *et al.*, 1998). This suggests that post-larvae may be using diurnal tides experienced in estuaries of the south-eastern US to facilitate movements into the estuary. A number of field and laboratory studies have addressed the concept that penaeid shrimp undergo diel vertical migration (Renfro and Brusher, 1982; Matthews *et al.*, 1991; Rogers *et al.*, 1993) as a means to enhance recruitment to estuaries. One of the few studies that examined shrimp distribution in an estuary found that post-larvae of *Fenneropenaeus merguensis* change their vertical distribution from mid-depth to near bottom when surface salinities are drastically reduced due to run-off and when a salt wedge is present (Staples, 1980).

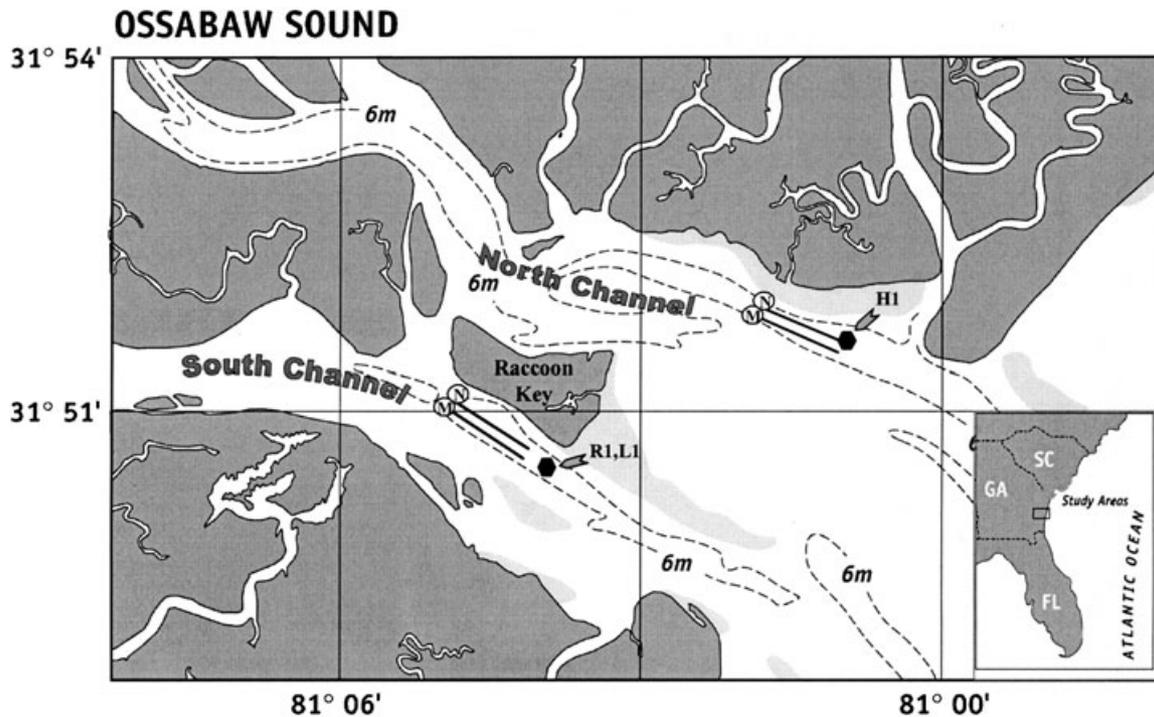
The present study addresses the importance of transport mechanisms through channels with different salinity and tidal current regimes in the Ossabaw Sound system of Georgia. Specifically, we examine and compare conditions under which white shrimp post-larvae enter an estuarine channel receiving high freshwater discharge and one receiving negligible discharge. The objectives of this study were to evaluate the role of vertical migration by white shrimp post-larvae during ingress; to describe hydrographic conditions that existed during ingress of white shrimp post-larvae; and to identify the combination of mechanisms that contributed to post-larval transport.

MATERIALS AND METHODS

Study area

The Ossabaw Sound system contains the mouths of the Ogeechee and Little Ogeechee Rivers, which will be referred to hereafter as the South Channel and the North Channel, respectively (Fig. 1). A mean annual freshwater discharge of $\sim 70 \text{ m}^3 \text{ s}^{-1}$ drains a coastal plain watershed of about 7000 km^2 into the South Channel, which is separated from the North Channel by Raccoon Key and a long linear shoal that extends seaward. At its mouth, the South Channel has a depth of 7–8 m at low water and a width of about 1.5 km.

Figure 1. Map of the sampling locations in Ossabaw Sound, GA. Symbols show the specific locations of plankton (N,M) and hydrographic (R1,L1,H1) data collection; a detailed explanation of station designations and data collected at each station are given in Table 1.



The Little Ogeechee River connects an urbanized watershed in Chatham County, GA, to the ocean through the North Channel, with only a small volume of localized freshwater discharge. Near its mouth, the North Channel has a depth of about 10 m and a breadth of nearly 2 km. Raccoon Key inhibits significant direct exchange of water between the two channels of Ossabaw Sound.

Oertel and Dunstan (1981) estimated the mean tide volume of the tidal prism in Ossabaw Sound to be $2.7 \times 10^8 \text{ m}^3$. Tidal currents typically range from ~ 50 to 75 cm s^{-1} (Dörjes and Howard, 1975). Ebb currents are usually stronger than flood in both channels of Ossabaw Sound.

Post-larval sampling

Post-larval ingress, as used here, describes the movement of shrimp post-larvae from the coastal ocean into the estuary. Our sampling scheme was divided into *extensive* and *intensive* phases. In each phase, surface plankton tows were collected over a 14-day period, during which time consecutive 5-min tows were made against the flooding current in the inlet channels at the approximate rate of 3 per hour. Samples were collected only during the night, excluding the

crepuscular period within an hour before sunrise or after sunset. The schedule for this extensive sampling phase was chosen because previous studies (Wenner *et al.*, 1998) suggested that greatest ingress occurs near the surface during nighttime flood tide incursions. The varying influences of the diel and tidal cycles, as well as vertical migration behavior, were thus minimized for this extensive evaluation of ingress. The number of samples collected each night ranged from 3 to 18 in each channel, depending upon the extent to which the flood tide coincided with nighttime.

Two stations (N and M) in the South Channel, approximately 6 km upriver from the inlet mouth, were sampled during 1997 and again, at virtually the same locations, during 1998 (Fig. 1). In the North Channel, which was sampled simultaneously with the South Channel in 1998, tows were made at two similarly designated stations (N and M), approximately 3.5 km landward from the mouth of the inlet (Fig. 1).

During the course of each 14-day extensive sampling period, additional intensive periods of around-the-clock surface and near-bottom plankton tows were made (Table 1). Samples were collected to examine the effects of diel and tidal periodicity on post-larval

Table 1. Site and station designations for biological and hydrographic sampling efforts in Ossabaw Sound, GA, along with the dates and locations of data collection.

Sampling description	Dates	Station	Location
1997 South Channel			
Plankton sampling	June 9–25	N	31°50.98'N, 81°04.57'W
Plankton sampling	June 9–25	M	31°50.88'N, 81°04.68'W
Hydrographic mooring [B: v, p, t, c; MW: t, c]	June 2–July 1	R1	31°50.55'N, 81°03.99'W
Wind measurements	June 1–July 6	NDBC-41008	31°24.13'N, 80°52.23'W
1998 South Channel			
Plankton sampling	June 5–20	N	31°51.00'N, 81°04.62'W
Plankton sampling	June 5–20	M	31°50.92'N, 81°04.72'W
Hydrographic mooring [B: v, p, t, c; MW: t, c; S: t, c]	May 18–June 24	L1	31°50.55'N, 81°04.05'W
Wind measurements	May 1–June 29	NDBC-41008	31°24.13'N, 80°52.23'W
1998 North Channel			
Plankton sampling	June 5–20	N	31°51.82'N, 81°01.35'W
Plankton sampling	June 5–20	M	31°51.73'N, 81°01.48'W
Hydrographic mooring [B: v, p, t, c; MW: t, c]	May 18–June 24	H1	31°51.64'N, 81°01.01'W
Wind measurements	May 1–June 29	NDBC-41008	31°24.13'N, 80°52.23'W

Codes for instrument deployments: B, bottom; MW, midwater; S, surface; v, current velocity; p, subsurface pressure; t, water temperature; c, conductivity.

ingress, and to determine the importance of vertical migration to ingress. In 1997, intensive neap-tide sampling was conducted at station M in the South Channel on June 12, one day before the first quarter moon, and again during spring tides on the full moon of June 20. Although the sampling design called for hourly sampling over a 25-h period, a mechanical failure on the sampling vessel ended that effort after 8 h on the June 12 intensive phase. During 1998, two 25-h cruises were successfully conducted at station M in both the South and North Channels. The first occurred on the full moon spring tides of June 10/11, and the second was on the neap tides of June 17/18. The amplitude difference in neap and spring tide for these particular dates was only ~15 cm in both channels.

Surface tows were made with a rectangular neuston frame (1 m wide, 0.5 m high), equipped with a 0.505 mm mesh conical nitex net and flowmeter, which was towed with the top of the frame slightly emergent, to collect surface plankton down to a depth of slightly less than 0.5 m. Post-larvae were also collected near the bottom of the water column during the intensive sampling phases using two bottom sleds constructed of stainless steel and aluminum. Plankton nets, identical to those used on the neuston frames, were attached to the sleds, and they were opened and closed at sampling depth by a motor controlled from the deck via an electrical cable. Sensors attached to

the sleds provided real-time readout (every 1.2 s) of information about the depth, pitch and roll of the frame, the status of the opening/closing device, and the flowmeter reading. Data from the sensors were recorded on a portable computer that integrated the flowmeter reading and the frame orientation (and resultant area of the mouth opening) to provide instantaneous and cumulative readings of the volume filtered through the net. This information was used to detect instances when the net failed to open or the frame was not towing the net properly. Preliminary testing of the bottom sled showed that it was most effective when pulled in the same direction as the tidal current, so bottom tows were made down current.

All plankton samples were carefully rinsed into the cod-end of the net and then through a 0.5 mm sieve to reduce the volume prior to preservation in the field with 5% buffered seawater formalin. In the laboratory, all penaeid post-larvae were sorted using Bogorov trays under 60× magnification. For bottom samples that contained substantial volumes of sandy sediments, Ludox medium was used to separate plankton from the sand. Post-larvae were counted and identified to species under a dissecting microscope, using keys and diagnostic characteristics described by Pearson (1939), Chuensri (1968), and Ringo and Zamora (1968). Some samples that contained large numbers of post-larvae were split and subsampled prior to estimating

the total number. After the shrimp post-larvae in each sample were counted or estimated, the total number for each species was divided by the volume of water filtered, and the resultant densities were standardized to the number per 100 m³. The total length (tip of rostrum to tip of telson) of up to 30 post-larvae were measured from each sample, using an ocular microscope in a dissecting microscope.

Oceanographic and meteorological data acquisition

Moored instruments

Oceanographic conditions were monitored and recorded every 6 min using instrument arrays deployed on moored stations located slightly seaward of the path of the net tows that sampled for post-larvae (Table 1). Moorings were deployed for 30 days in 1997 and for 37 days in 1998 in both the North and South Channels of Ossabaw Sound (Table 1). H1 (1997) and L1 (1998) were located in 8.5 m of water in the South Channel (Fig. 1). Temperature and conductivity were recorded at three depths by SEACATs (SeaBird Electronics, Inc., Bellevue, WA, USA). Salinity was computed from conductivity and temperature readings, using standard algorithms. A pressure sensor in the bottom instrument measured water depth, and an S4 current meter (InterOceans, Inc., San Diego, CA, USA) was attached to the mooring 1.0 m above the bottom. The instrument array at station H1, which was deployed in 12.3 m of water in the North Channel in 1998 (Fig. 1), was similar to that in the South Channel, except that it lacked the floating SEACAT instrument. Both moorings were deployed 1–2 weeks prior to plankton sampling and were removed at the conclusion of the study.

CTD casts

During the extensive phases of plankton sampling, a Model 25 Sealogger® CTD (SeaBird Electronics, Inc.) with a SeaTech fluorometer was deployed immediately prior to the start of each plankton tow to obtain a vertical profile of conductivity, temperature, fluorescence and depth. Salinity and density were computed from the conductivity, depth and temperature readings, using standard algorithms. The SeaTech fluorometers, which measure chlorophyll *a* fluorescence, were calibrated against phytoplankton cultures prior to the cruises. This showed that the instrument output was linear over their maximum range. Natural plankton samples were collected from the surface during selected vertical profiles, and portions were concentrated on filters and later extracted in acetone prior to measuring Chl *a* in the laboratory with a Turner Designs (Sunnyvale, CA,

USA) fluorometer. These data were used to derive calibration curves to convert *in situ* fluorescence from CTD vertical profiles into Chl *a* readings (in $\mu\text{g L}^{-1}$).

During the intensive phases (24-h sampling), hourly CTD casts were taken downstream of station M, where plankton tows were conducted in the South Channel during the spring intensive phase and in the North Channel during the following neap-tide phase. These series of fixed-position casts were made in lieu of casts otherwise taken from the vessel that towed the plankton nets, immediately prior to each tow.

Wind measurements

Hourly readings of wind speed and direction were obtained from NOAA's National Data Buoy Center, Station 41008 at Gray's Reef. This buoy is located approximately 50 km south-south-east of Ossabaw Sound, and meteorological data from this station are representative of local coastal wind conditions.

Data analyses

Measurements of current speed and direction in the inlet throat were rotated relative to the axis of the main inlet channels, so that values of the *x*-component represented the speed of the flood and ebb current. Ebb was defined as positive. For multiple regression analyses, a value called 'mean tidal current' was assigned to each plankton tow, to indicate the relative magnitude and direction of the predominant nighttime tidal current that coincided with each plankton sampling survey. This value was computed as the average of hourly current measurements taken over the duration of each nighttime period, including the ebbing portion of the tidal phase that occurred after dark.

Time series data from the moorings were analyzed in two forms. One form consisted of the 6-min samples, which allowed us to preserve the high-frequency variability that is dominated by the tide, while the second form preserved the variability induced by weather and other sub-tidal frequency events. Alongshore and offshore components of wind stress were defined by rotating the coordinate system 40° clockwise from north, to align it with the coastline. The resulting rotation makes the cross-shelf component align to within 5° of the orientation of the North and South Channels (Fig. 1). Wind stress was calculated using an interactive technique that adjusts the wind speed to a 10-m level and applies a variable drag coefficient depending on the magnitude of the wind speed (Blanton *et al.*, 1989). The hourly wind stress data were smoothed with a low-pass filter prior to analyses at lags of 1, 6, and 24 h. A 3-h filter was used for the 1- and 6-h lagged readings, while a 40-h filter

was used for the 24-h lag, to remove wind fluctuations with periods shorter than a day.

RESULTS

Oceanographic characteristics of Ossabaw Sound

Harmonic analysis of near-bottom currents (Table 2) indicated a large between-channel difference in mean flow. Mean flow was landward in both channels but stronger in the North Channel by a factor of 4. Some of the difference is due to the seaward pressure gradient induced by freshwater discharge in the South Channel.

The tidal currents in the two channels are contrasted by a comparison of the M2, M4 and M6 tidal constituents (Table 2). Most of the energy is contained in the M2, with the South Channel being slightly higher. Phase lag difference indicates that M2 currents in the South Channel lag those in the North Channel by about 23 min. The shallow-water overtide (M4) is more than twice as high in the North Channel. The M4/M2 ratio is higher by a factor of 2 and leads to greater tidal asymmetry in the North Channel.

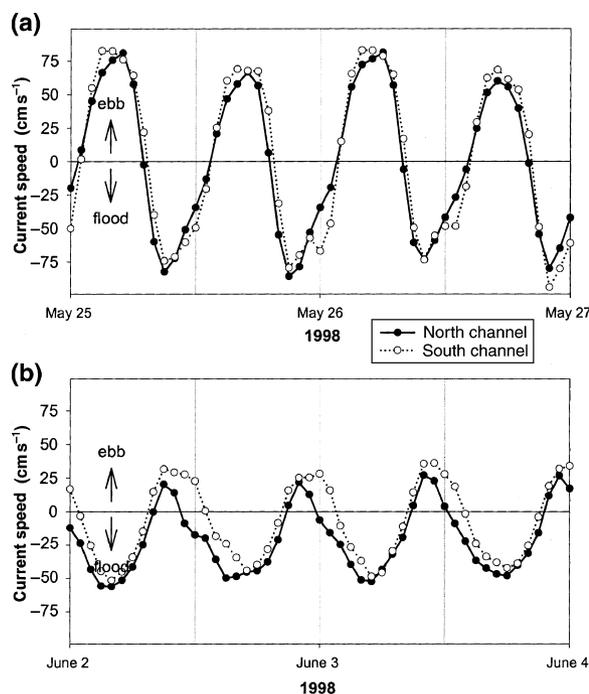
Ebb currents are significantly briefer and floods are significantly longer in the North Channel than in the South during neap tide (Fig. 2). This effect was largest during the neap tide of June 2, 1998. At the time ebb currents in the North Channel switch to flood, currents in the South Channel continue to ebb. This effect is best seen in water-level versus velocity (Fig. 3). During neap tides in the North Channel, the currents change to flood while water level is still falling.

Table 2. North Channel and South Channel tidal velocity constituents for 1998.

Component tide	Freq	North Channel		South Channel	
		amp	pha	amp	pha
Mean	0	-10.15	-	-2.56	-
M2	0.0805	59.73	120	69.44	132
M4	0.1610	8.19	333	4.10	320
M6	0.2415	4.83	237	6.11	247
M4/M2		0.14		0.06	
M6/M2		0.08		0.09	
2M2-M4		267		304	
3M2-M6		122		149	

Record length = 11.825 days; freq, frequency in cycles h^{-1} ; amp, amplitude in cm s^{-1} ; pha, phase in degrees.

Figure 2. Axial tidal currents in the North and South Channels of Ossabaw Sound, GA, during spring (a) and neap (b) lunar phases of the 1998 cruises.



Further comparison between the two channels on June 2, 1998, indicated that salinity ranged more widely along the axis of the South Channel during both high water (8–28 psu) and low water (2–26 psu) than in the North Channel (16–30 psu at high water; 10–26 psu at low water). Temperature ranges were relatively small along the length of both channels, particularly during low slack water (from 26.5°C at the mouth of each channel to maxima of 29 and 29.5°C in the North and South Channels, respectively). On high slack tide, the range in water temperature was slightly greater, with minima of 24 and 25°C at the mouths of the North and South Channels, respectively, and a maximum of 29.5°C at a location 20 km upstream in both channels.

The South Channel, where salinity was consistently lower and more variable among different tidal stages, received freshwater discharge from the Ogeechee River (Fig. 4). The discharge rate varied greatly during 1997 and 1998 (200–30 700 cubic feet per second (cfs)), but it was generally much lower over the winter/spring season prior to plankton sampling in 1997 than it was during the following year. However, differences in the discharge rates during the June plankton sampling collections of those two years were much less extreme (inset of Fig. 4). The abrupt salinity

Figure 3. Axial current velocity plotted against water level in the (a) North Channel and (b) South Channel of Ossabaw Sound, GA on spring and neap tides. Data from moorings H1 and L1 in June 1998. Ebb tides are positive, flood tides are negative.

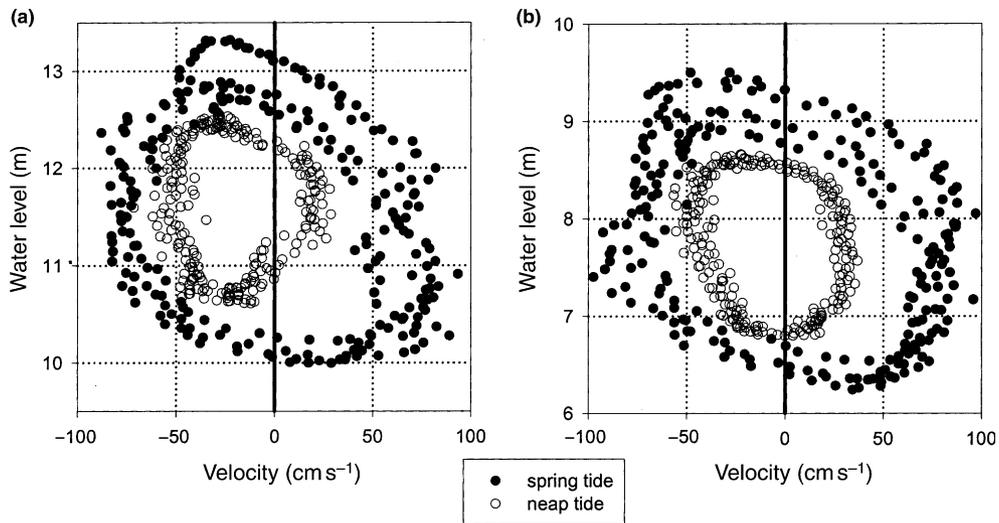
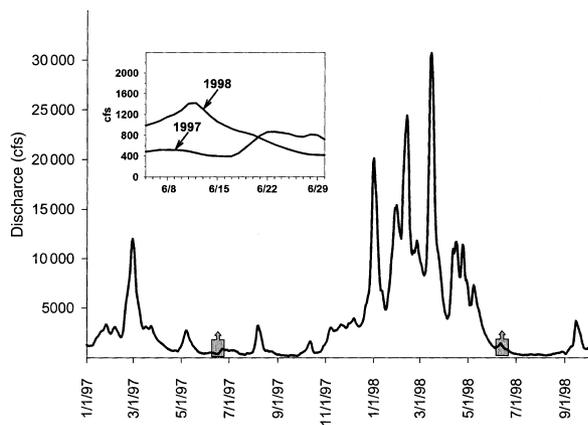


Figure 4. Daily freshwater discharge into Ossabaw Sound during 1997 and 1998. Data within small boxes are expanded in the inset to show flow at the time of post-larval sampling in both years. Streamflow data are from USGS Gauge no. 02202500 in the lower Ogeechee Basin near Eden, GA, approximately 63 km upstream from the study site.



increase of 2–3 psu that was seen in both channels on June 2–3, 1998 (Fig. 5) did not appear to coincide with a corresponding change in the rate of freshwater discharge. Instead, it probably reflects an increase in coastal water salinity.

The axial salinity gradient can be used as a proxy for the strength of the baroclinic pressure gradient. A positive gradient causes a landward force due to the seaward increase in density. We used a simple

one-dimensional equation of salinity continuity to convert the low-high water salinity excursions to salinity gradient (Blanton *et al.*, 2000). The horizontal salinity gradient ($\partial S/\partial x$) was estimated by a simple salt balance equation:

$$\frac{\partial S}{\partial t} + u \frac{\partial S}{\partial x} = 0 \tag{1}$$

where S is the salinity and u is the velocity measured in each channel. The results, averaged for the 50 h centered on the two spring and neap tides covered by the mooring deployment, showed that salinity gradients increased in the South Channel throughout the two spring–neap cycles. The increase is consistent with the observed increase in coastal salinity after June 2 (Fig. 5). Salinity gradients for corresponding time periods were consistently greater in the South Channel compared with those in the North Channel. This is expected for the South Channel, which receives river discharge. After the May 26 spring tide, the difference between the salinity gradients in the two channels almost tripled.

During low discharge (1997), the axial salinity gradient was very small in the South Channel (Table 3) due to the low discharge of the Ogeechee River. The relatively high discharge during 1998 induced a nine times larger gradient in the South Channel. Even the North Channel in 1998 had a gradient nearly four times larger than that observed in the South Channel during 1997.

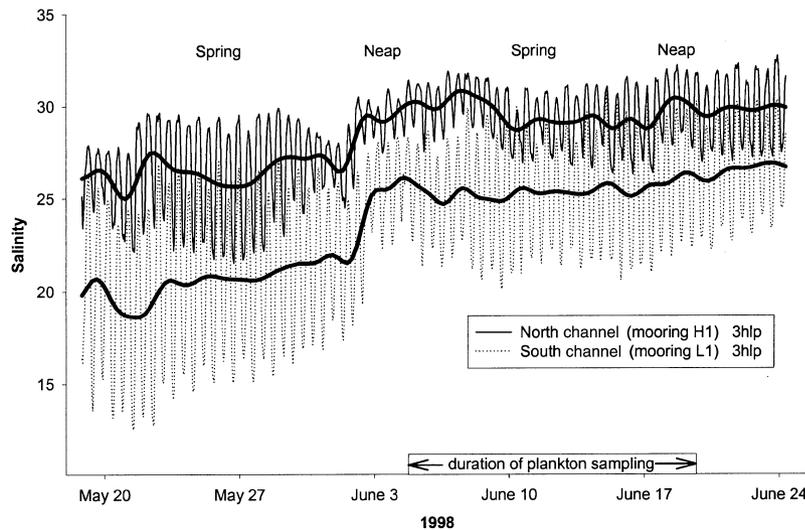


Figure 5. Near-bottom salinity as a function of time in the North and South Channels of Ossabaw Sound, GA. 3-hlp plots show tidal fluctuations in salinity; thick solid lines are 40-hlp data, in which tidal variability has been eliminated.

Table 3. Comparison of mean axial salinity gradient ($\partial S/\partial x$) in North and South Channels calculated from Equation (1).

Experiment	North Channel	South Channel
1997	–	0.10
1998	0.37	0.88

Variation in post-larval density and length

Average densities of post-larvae during 1998 sampling of the South Channel (mean = 299/100 m³) and North Channel (mean = 234/100 m³) were much higher than during the previous year in the South Channel (mean = 13/100 m³) (Table 4). In 1998, densities of post-larvae collected in surface nets on nighttime flooding tides were considerably higher in the South Channel than in the North Channel, from the first sampling night on June 5, 1998 through June 15 (Fig. 6). While post-larvae were abundant in the

Table 4. Comparison of *Litopenaeus setiferus* post-larval densities (no./100 m³) on nighttime flood tides during the three sampling periods.

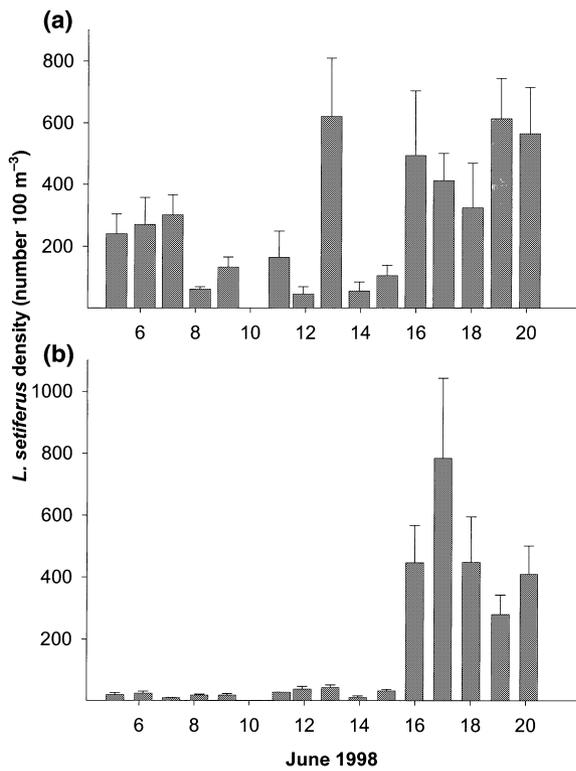
	South Channel 1997	South Channel 1998	North Channel 1998
Mean density (standard error)	12.7 (1.3)	299 (30.6)	234 (39.8)
Minimum–maximum densities	0.4–78.6	6.0–2010	1.9–3430
Number of samples	128	123	114

South Channel during the entire sampling period, they did not reach high abundances in the North Channel until June 16, when comparable densities were noted for both channels.

Post-larvae of *L. setiferus* collected in the South Channel in 1998 were significantly longer than those collected the previous year at the same location (mean = 6.61 versus 5.96 mm; Kruskal–Wallis $\chi^2 = 4200$, $P < 0.001$) (Fig. 7). During 1998, post-larvae collected in the South Channel were also significantly longer than those from the North Channel (mean = 6.61 versus 6.47 mm; Kruskal–Wallis $\chi^2 = 43,349$, $P < 0.001$) (Fig. 7). Although these differences in mean length may be statistically significant, their magnitude is not large (0.6 and 0.15 mm, respectively), and may result from the large number of post-larvae measured. However, comparisons of length-frequency distributions of post-larvae also showed significant differences between the 1997 and 1998 collections in the South Channel (Kolmogorov–Smirnov $Z = 34.6$, $P < 0.001$) and between the two rivers in 1998 (Kolmogorov–Smirnov $Z = 31.1$, $P < 0.001$). In the 1998 samples, the distribution was significantly skewed toward the smaller size classes in the North Channel (Fig. 7).

Temporal changes in post-larval length were observed in both channels (Fig. 8). In 1997, the daily mean length of post-larvae in the South Channel ranged from 5.60 mm (June 21) to 6.35 mm (June 14), with no apparent overall temporal trend (Fig. 8a). The mean length at the beginning of the sampling period was equivalent to that at the end, and a linear regression of length*time was not significant ($r^2 = 0.11$, $P = 0.20$). During 1998, post-larval lengths in

Figure 6. Daily mean density of *Litopenaeus setiferus* post-larvae on nighttime flood tides in the (a) South Channel and (b) North Channel of Ossabaw Sound, GA, during 1998 sampling. Error bars represent 1 standard error.

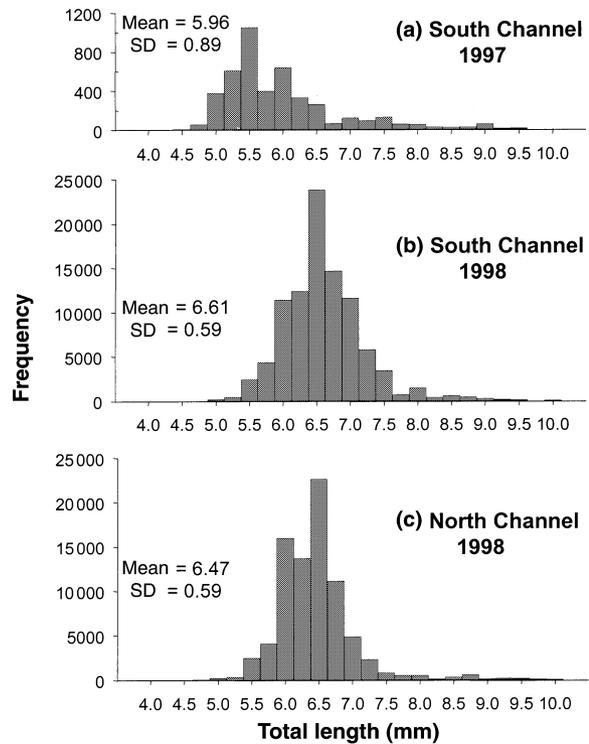


the South Channel were less variable than the previous year, ranging from a minimum of 6.30 mm (June 14) to a peak of 6.79 mm (June 16), with no significant temporal trend ($r^2 < 0.01$, $P = 0.96$). The lengths of post-larvae collected in the North Channel in 1998 varied more widely than those in the South (Fig. 8b). In the North Channel, lengths ranged from 5.46 mm (June 6) to 6.74 mm (June 16), with the peak in length coinciding with the peak in the South Channel. In the North Channel, mean daily post-larval length increased significantly over the 14-day period ($r^2 = 0.46$, $P < 0.001$).

Depth distribution of post-larvae

Hourly plankton tows from the 1998 intensive-phase sampling showed considerable differences in post-larval abundance in surface and bottom waters of the two Ossabaw Sound channels under various combinations of tidal and diel conditions (Fig. 9). Overall, post-larval densities were much higher during neap tides (Fig. 9b,d) than during spring tides (a,c). Peak ingress (i.e. transport on flood tides) occurred in surface

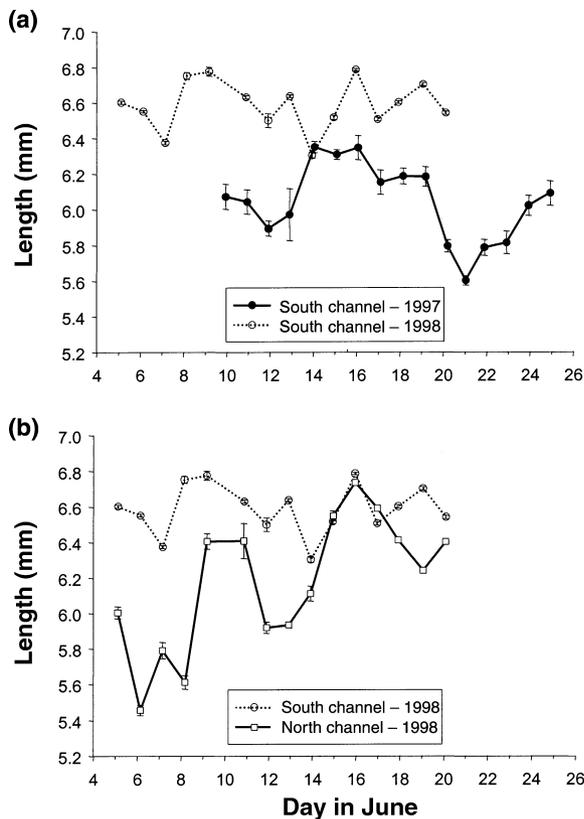
Figure 7. Length-frequencies of *Litopenaeus setiferus* post-larvae collected in 1997 and 1998 in the South and North Channels of Ossabaw Sound, GA.



waters when the tide was flooding during the night (Fig. 9b–d). It should be noted, with regard to these trends, that during the time of sampling, nighttime tidal currents were consistently flooding during the neap tides, but ebbing during the springs.

Data from the 1997 and 1998 intensive-phase cruises were combined in order to statistically evaluate the vertical position of post-larvae relative to diel and tidal periodicity. Both the diel phase and the tidal current phase influenced post-larval position in the water column. During nighttime flood tides, the mean density of *L. setiferus* was an order of magnitude greater at the surface than at the bottom (mean = 284 versus 24/100 m³), but during daylight this comparison was reversed (mean = 4 versus 33/100 m³) (Fig. 10). During the ebbing tide, mean post-larval densities were greater near the bottom (99–199/100 m³) than at the surface (0.1–30/100 m³), regardless of the time of day. A three-way ANOVA (Table 5) on ranked data indicated that depth (surface versus bottom) and diel phase (day versus night) were both significant main effects for post-larval density ($P < 0.001$), although the significant interaction terms depth*diel and depth*tide illustrate the differential influence of light

Figure 8. Daily mean length of *Litopenaeus setiferus* post-larvae collected in 1997 and 1998 in the South and North Channels of Ossabaw Sound, GA.



phase and tidal phase on the depth distribution of *L. setiferus* post-larvae.

Key influences on post-larval density

Step-wise regression analyses were conducted on the data from surface net tows taken on nighttime flooding tides over the neap to spring tidal cycles in 1997 (South Channel) and 1998 (South and North Channels), in order to evaluate which physical factors most influence ingress of post-larval white shrimp. The six predictive variables used in the model were surface temperature, surface salinity, surface chlorophyll *a* concentration, mean tidal currents, cross-shelf and alongshore wind stress (lagged by 6 h).

When the regression model was run on the combined cruises in the Ossabaw Sound system, with the non-significant variables removed, we found that the dependence of post-larval *L. setiferus* density was strongest with the independent variables of surface temperature, surface chlorophyll *a* concentration, mean tidal currents, and alongshore wind stress ($r^2 = 54\%$). All four factors were signi-

ficantly related to log-transformed post-larval density (Table 6).

Water temperature

High densities of white shrimp post-larvae were associated with a critical minimum surface temperature of $\sim 27^\circ\text{C}$ during all three cruises (Fig. 11a). Although temperatures ranged from 23 to 30°C during the study, nearly all ($>96\%$) of the post-larvae were collected at temperatures $\geq 27^\circ\text{C}$. Temperatures were noticeably lower in the North Channel until June 17 when minima were $\geq 27^\circ\text{C}$, coinciding with a peak in post-larval density. In the South Channel, the increase in temperature minima occurred on June 12, followed by an increase in post-larval density (Fig. 11a). Mean density was significantly greater at temperatures $\geq 27^\circ\text{C}$ (mean = $239.4/100\text{ m}^3$) than at lower temperatures (mean = $18.7/100\text{ m}^3$) (*t*-test for unequal variances, d.f. = 322.7, $P < 0.001$). There was also a highly significant ($P < 0.001$) positive correlation between post-larval density and surface water temperature in the combined data from Ossabaw Sound (Fig. 11b).

Predominant nighttime tides

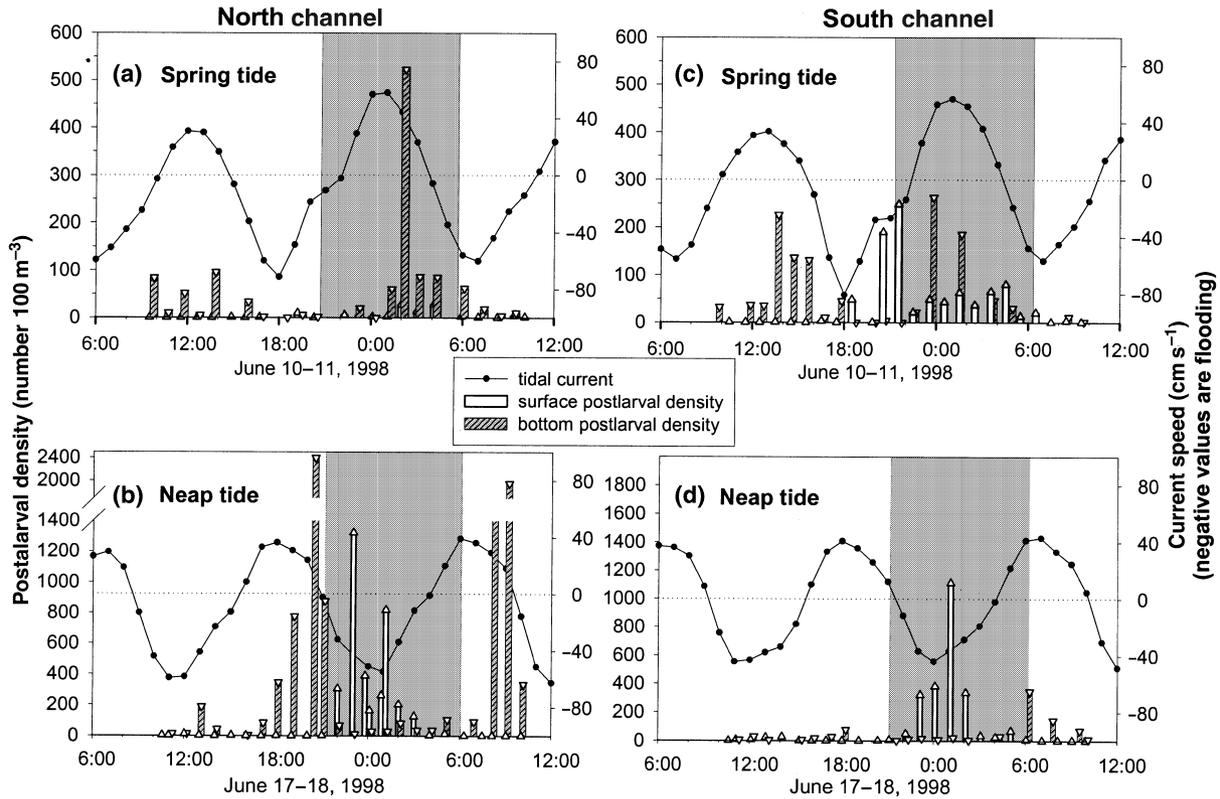
Mean tidal currents, which were defined as the daily average of nighttime hourly current measurements, varied according to lunar period. In general, during new- or full-moon spring tides in June, tidal currents ebb in Georgia estuaries all night long, while on quarter-moon neap tides in June the neap tides flood from sunset to sunrise (Fig. 12). Densities of white shrimp post-larvae were significantly greater when nighttime tides were predominantly flooding (mean = $182.8/100\text{ m}^3$) than when ebb tides were dominant at night (mean = $48.0/100\text{ m}^3$) (*t*-test for unequal variances, d.f. = 474.1, $P < 0.001$).

Wind stress

Water level fluctuations can import large volumes of water through an inlet throat, thus expediting the ingress of larvae. Rising tide is the most obvious example, but wind-induced fluctuations at frequencies lower than tidal play the same role. Cycles in wind stress can either lower or raise sea level in the estuaries (Blanton *et al.*, 1995). These sea level fluctuations due to wind and other subtidal frequency processes are superimposed on the normal rise and fall of the lunar tides, both of which are accompanied by the transport of ocean water into the estuary or export of estuarine water to the ocean.

In our studies, alongshore and cross-shelf wind stress were correlated with larval abundance; however, the systems varied in their response to this factor. During the initial studies conducted in 1994 in the North Edisto Inlet (Wenner *et al.*, 1998), the highest

Figure 9. Comparison of post-larval *Litopenaeus setiferus* densities in surface and bottom plankton tows during spring and neap-tide intensive phase sampling in both channels of Ossabaw Sound, GA in June 1998. The period of darkness (shaded portion of graph) and current velocities are superimposed on the timeline. Flood tides are those with negative values; ebbing tides are positive. Note differences among the graphs in scale of the left vertical axes.



abundances of post-larvae corresponded with downwelling wind stress at lag times of 1, 6 and 24 h. During June 1997, larval abundance in the South Channel was significantly correlated with upwelling wind stress at all three lag times (Table 7). Upwelling-favorable along-shore winds occurred at a time when the axial pressure gradient was extremely small in the South Channel. In the following year (1998), there were no significant associations of wind and post-larvae for the South Channel, but in the North Channel, post-larvae were significantly correlated ($P \leq 0.001$) with onshore wind stress at two of the three lag times. In 1998, the axial pressure gradient was nearly $2\frac{1}{2}$ times greater than present in the North Channel and nine times greater than in the South Channel the previous year. The axial pressure gradient likely overwhelmed any wind-induced import of larvae, rendering any correlation with wind insignificant. Note that the cross-shore stress, when directed onshore, was correlated with high larval abundance in only the North Channel (Table 7), where the axial pressure gradient was smaller than in the South Channel (Table 3).

The wind regime exerted different forcing conditions on the study area during 1997 and 1998 fieldwork (Fig. 13). In 1997, there was an episode of strong downwelling-favorable wind stress with an onshore component in the first part of the period (until June 10). Afterwards, upwelling conditions prevailed. During 1998, on the other hand, upwelling-favorable stress prevailed for the entire period, with three brief exceptions, for the most part with an onshore component. Based on previous model results (Blanton *et al.*, 1999), this suggests that any post-larvae entering the system would have arrived from populations located south of the inlet during the 1998 plankton sampling period. We analyzed the 1998 wind data and sub-surface pressure data in the two channels to identify wind-generated import and export events.

The rotated alongshore wind stress component was compared to water level fluctuations in the North and South Channels of Ossabaw Sound (Fig. 14). For example, beginning on May 22, water level in both channels increased from -0.15 to $+0.15$ m in less than 2 days, signifying an import of offshore water into the

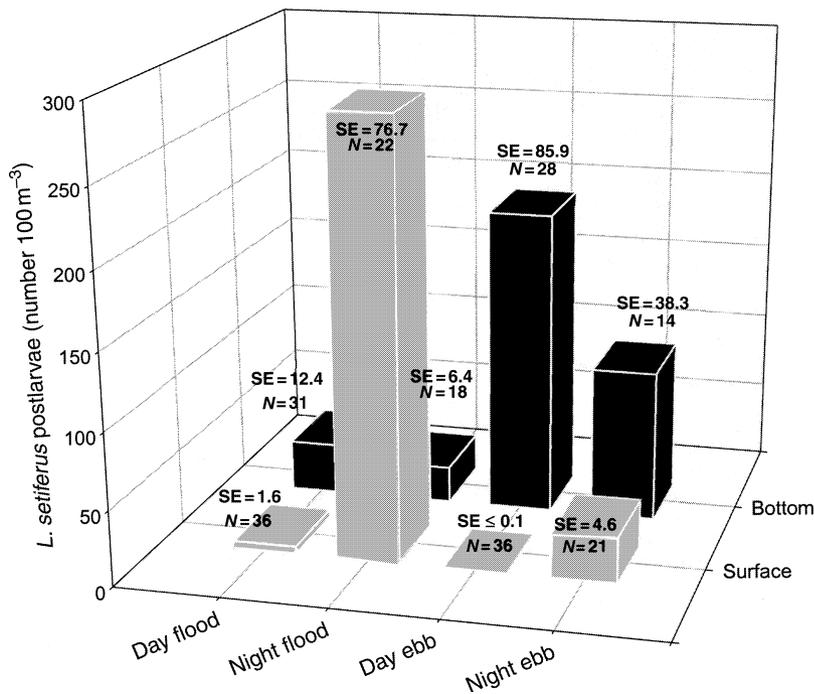


Figure 10. Mean density of *Litopenaeus setiferus* post-larvae collected in the South and North Channels of Ossabaw Sound, GA (combined) during ‘intensive’ sampling in 1997 and 1998. The bar heights represent the means for each combination of depth, day or night, and tidal phase: standard error and number of samples are shown.

Source	Type III sum of squares	d.f.	Mean square	F	Significance
Corrected model	398 203.919	7	56 886.274	35.359	<0.001
Intercept	2 368 823.768	1	2 368 823.768	1472.379	<0.001
Depth	28 166.142	1	28 166.142	17.507	<0.001
Diel	130 249.622	1	130 249.622	80.959	<0.001
Tide	384.242	1	384.242	0.239	0.626
Depth*diel	108 058.339	1	108 058.339	67.165	<0.001
Depth*tide	48 078.518	1	48 078.518	29.884	<0.001
Diel*tide	17.464	1	17.464	0.011	0.917
Depth*diel*tide	309.469	1	309.469	0.192	0.661
Error	318 550.581	198	1 608.841		
Total	2 923 478.000	206			
Corrected total	716 754.500	205			

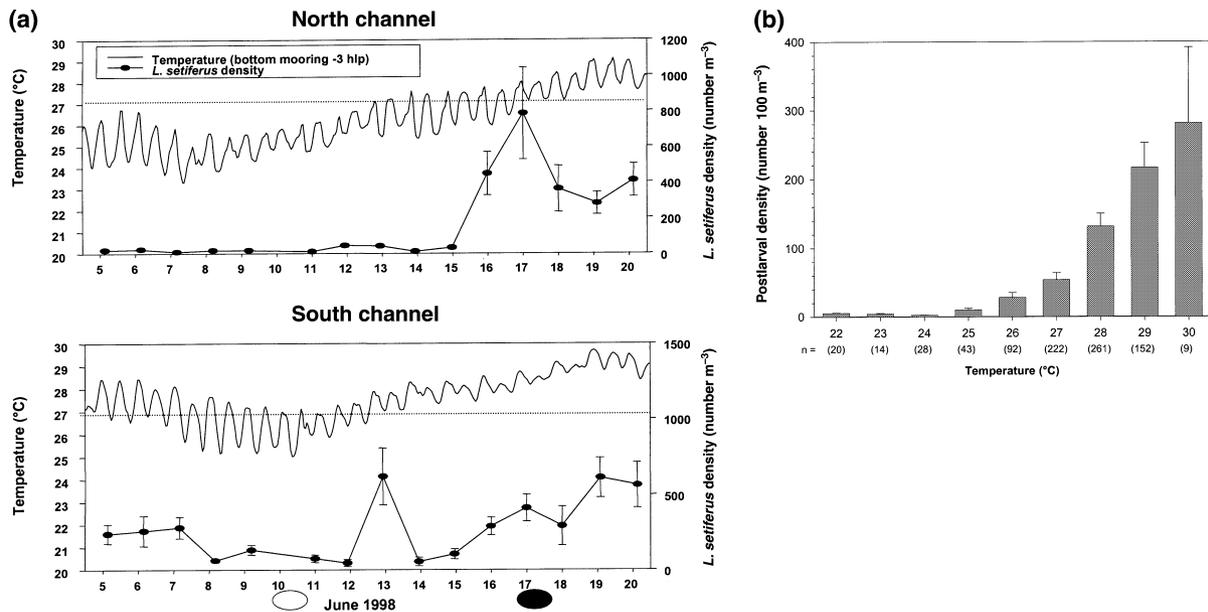
Factors compared are depth (surface, bottom), diel phase (day, night), and tidal phase (flood, ebb).

Table 6. Results of stepwise multiple regression models for the combined cruises in the Ossabaw Sound system.

Model variables	Partial R ²	Cumulative (model) R ²	d.f.	F	P
Surface temperature	0.49	0.49	Regression: 1, residual: 335	325.6	<0.001
Surface temperature, surface Chl <i>a</i>	0.03	0.53	Regression: 2, residual: 334	185.3	<0.001
Surface temperature, surface Chl <i>a</i> , mean tide	0.01	0.54	Regression: 3, residual: 333	129.0	<0.001
Surface temperature, surface Chl <i>a</i> , mean tide, alongshore wind stress (6 h lag)	0.01	0.54	Regression: 4, residual: 332	99.0	<0.001

The physical variables listed were determined to significantly affect log-transformed post-larval abundance, using a forward selection procedure with $P \leq 0.05$ to add and $P \geq 0.10$ to remove.

Figure 11. Mean density of *Litopenaeus setiferus* post-larvae versus surface temperature. (a) Daily mean density compared with bottom water temperatures from CTD casts (3 h low pass filter) during extensive sampling in 1998. Error bars show standard error. (b) Means are based on densities in all tows collected during the 1997 and 1998 cruises in the Ossabaw Sound channels, plotted for each 1°C increment. Standard error bars are shown, and *N* is given in parentheses for each increment.



system. Similar import events occurred on May 29, June 7 and 12, and another prolonged import event began on June 16 and lasted, with only a brief interruption, until June 22. Following the import event of May 22, there was an export of water from Ossabaw Sound to the ocean caused by a fall in water level from +0.15 to -0.10 m, centered on May 26. Similar export events occurred on June 1, 10 and 15.

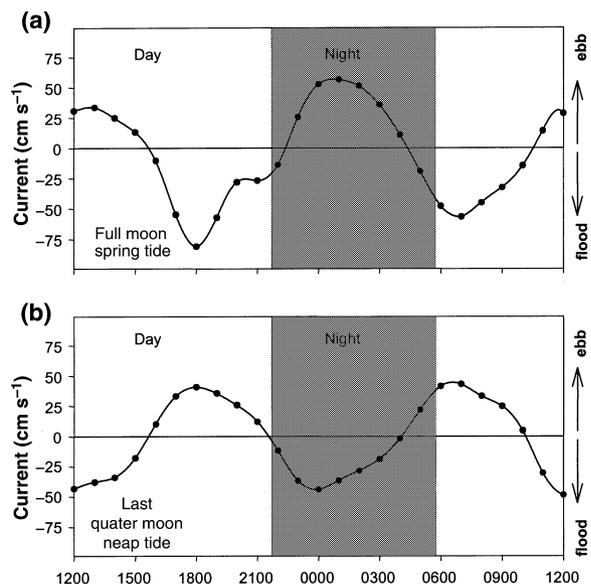
A clear inverse relationship between fluctuations in alongshore wind stress and water depth is illustrated in Fig. 14. For example, the relaxation of the strong northward stress on June 7 caused an increase in mean water level to about +0.15 m. The strong northward stress on June 15 caused water level to decrease to -0.20 m below its mean level. Thus, a northward/southward wind stress fluctuation leads directly to export/import of water through the inlet. However, the association between water import/export and wind is not entirely consistent. For example, when wind was basically northward from May 21 to 26, water level decreased by 0.15 m initially but then rebounded to 0.15 m above its mean, an excursion of about 0.3 m (Fig. 14). These wave-like disturbances undoubtedly play an important role in forcing water into and out of estuaries.

Calculations of spectra and cross-correlated spectra (co-spectra) in cross-shelf and alongshelf wind stress together with water level were made to determine the

time scales of response of wind-driven import and export through Ossabaw Sound (Fig. 15). The along-shelf stress component has a large peak at a period of about 10 days and a smaller peak at 2 days (Fig. 15a). The seabreeze component is barely detectable in this component because the 40-h low-pass filter removes most of the energy at this frequency. The cross-shelf component has a single large peak at 2 days. Thus, from a statistical viewpoint, the predominant wind stress energy consists of a 10-day oscillation in the alongshelf component, probably driven by changing weather systems, superimposed on an onshore-offshore 'wobble' with a period of about 2 days. Note that the spectra for water level only contain peaks at periods of about 10 days (Fig. 15a), coincident with peaks in the alongshore wind stress spectra. There are no peaks in the water level spectra at a 2-day period, indicating that the cross-shelf wind stress has negligible effect on water level at these locations in the two channels.

The cross-spectra (Fig. 15b) indicate that wind-induced import/export events occur primarily at periods greater than 6 days, denoted by coherence squared values above the 90% confidence interval. There is also a suggestion that cross-shelf and alongshelf stress induces fluctuations in water level at the 2-day period (not significant at the 90% confidence level). But, as noted above, the energy of water level fluctuations at the 2-day period is negligible (Fig. 15a).

Figure 12. Schematic representation of the relationship between tidal currents and darkness during (a) spring and (b) neap tides in Georgia estuaries during June (based on current data collected in the South Channel of Ossabaw Sound, June 10–11 and June 17–18, 1998).



Chlorophyll a

The ranges of chlorophyll *a* (Chl *a*) were similar in both channels (>4 to <17 $\mu\text{g L}^{-1}$ in the South Channel; >4 to <19 $\mu\text{g L}^{-1}$ in the North). Tidal influences were apparent in both channels, but more notably in the South Channel. Surface Chl *a* concentrations exhibited significant positive correlations with upwelling favorable winds (Pearson product–moment correlation, 1 h lag, $r = 0.12$; 24 h lag, $r = 0.20$), while near-bottom Chl *a* was significantly related to upwelling (1 h lag, $r = 0.13$; 24 h lag, $r = 0.19$) and offshore favorable winds (24 h lag, $r = 0.12$). Chl *a* was also correlated with current speed for near-bottom and surface samples.

DISCUSSION

Key influences on post-larval density

Three key factors greatly influenced the densities of post-larval white shrimp in time and space within two inlets on the Atlantic coast of the south-eastern US. During the June periods of our study, a sequence of environmental conditions led to the ingress of post-larval white shrimp. Although some combination of the 17 environmental factors measured during our studies must undoubtedly contribute to conditions that stimulate appropriate transport behaviors of post-larval shrimp each spring, we identified only three key predictive factors. Although Chl *a* was significant in multiple regression analyses, maximum Chl *a* concentrations appear to have resulted from tidal or wind-induced resuspension of settled planktonic or epibenthic algal cells (Verity *et al.*, 1998). The wind and tidal resuspension of phytoplankton likely provides enhanced food availability for immigrating organisms, a coincidence that would be beneficial to post-larval shrimp.

The first predictive factor was a critical minimum temperature of coastal waters, after which the lunar tidal stage became a key factor. These conditions, in turn, set the stage for the strong influence of wind stress and its effect on coastal circulation. In response to one or more of these conditions, post-larval densities increased greatly within an inlet. The relative importance and temporal sequence of these influencing factors may change under different conditions. However, the environmental factors and hydrographic conditions that we identified coincided each spring when the post-larvae were offshore in position to be transported into the inlet.

Temperature

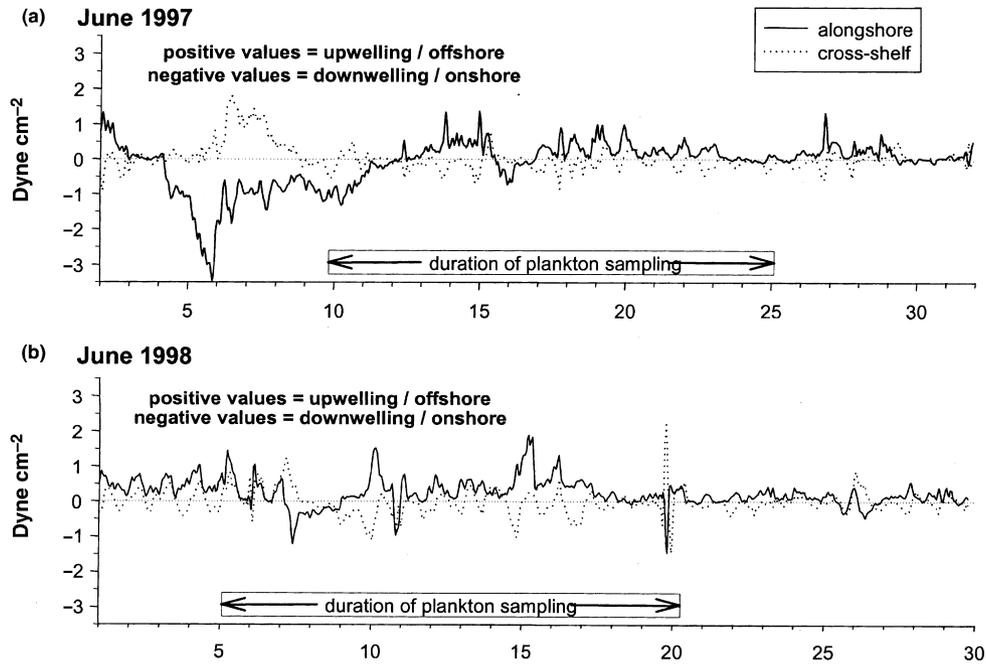
The relationship between water temperature and the ingress of post-larval penaeids has been noted for both brown and white shrimp along the Gulf of Mexico and

Cruise	Cross-shelf wind stress (+ is offshore)			Alongshore wind stress (+ is upwelling)		
	1 h	6 h	24 h	1 h	6 h	24 h
South Channel 1997	ns	ns	-0.189*	0.225*	0.273**	0.400***
South Channel 1998	ns	ns	ns	ns	ns	ns
North Channel 1998	-0.444***	ns	-0.402***	ns	ns	0.241*

Coefficients are shown for wind conditions 1, 6 and 24 h prior to plankton tows during the four different cruises. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

Table 7. Pearson correlation coefficients between wind stress and log-transformed post-larval *Litopenaeus setiferus* density in surface samples collected on nighttime flooding tides.

Figure 13. Alongshore and cross-shelf wind stress (3-hlp filtered) based on wind measurements at Gray's Reef during plankton sampling in the Ossabaw Sound system in 1997 and 1998. This oceanographic buoy is roughly 50 km SSE of Ossabaw Sound, GA.



south-east US coasts. The arrival of brown shrimp in Gulf coast estuaries was found to occur at sustained temperatures $>20^{\circ}\text{C}$ in Louisiana (St. Amant *et al.*, 1963) and between 18 and 22°C in Galveston Bay (Baxter and Renfro, 1966). In an interesting conceptual model, Rogers *et al.* (1993) proposed that temperature and salinity cues from cold front passages enhanced post-larval brown shrimp recruitment to estuaries of the northern Gulf of Mexico. They sug-

gested that cold fronts drove chilled lower salinity water from the shallow estuaries into the coastal zone. Post-larvae that encountered the less saline and colder waters exiting the estuary tended to drop out of the water column and congregate at the mouth of the tidal inlet. After the front passed, post-larvae would move up in the water column in response to onshore movements of warmer more saline waters. This model suggests a complex behavioral response of brown

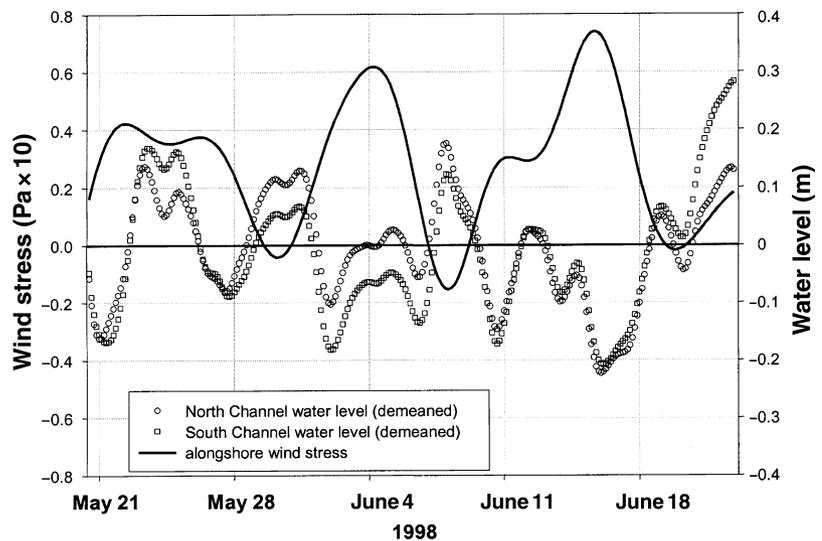
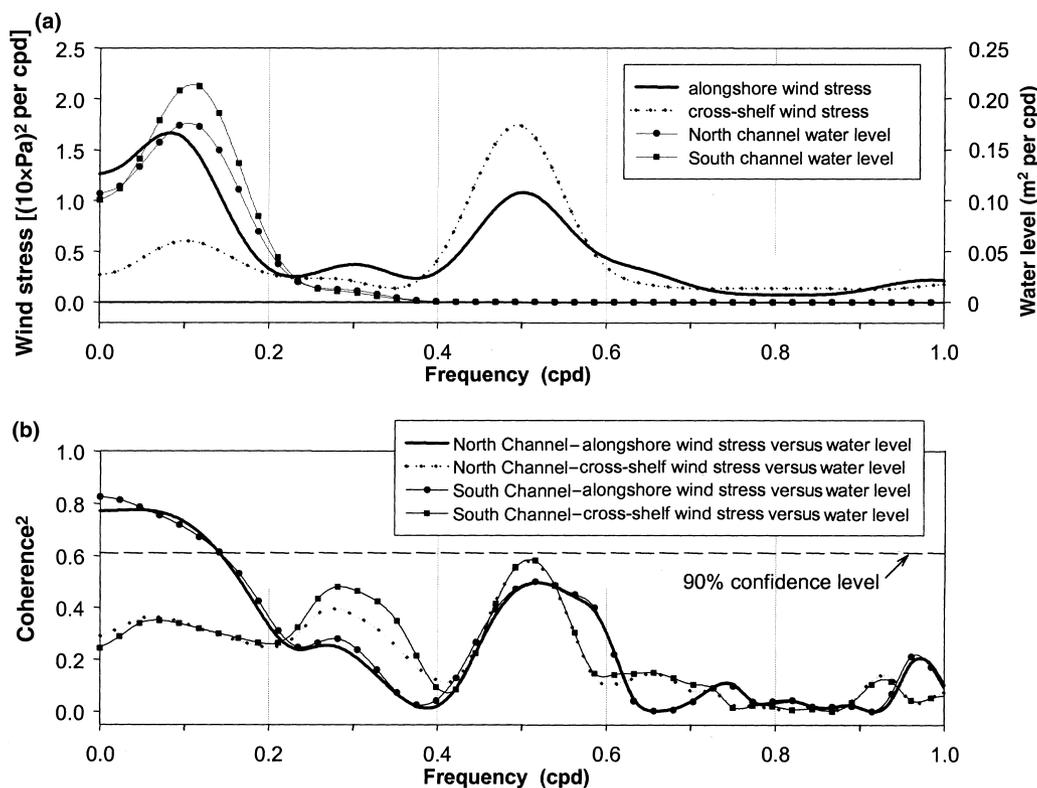


Figure 14. Comparison between fluctuations in alongshore wind stress and demeaned water level in the North and South Channels of Ossabaw Sound, GA during 1998. The coordinate system for wind stress has been rotated -40° , and tidal fluctuations in water level have been removed with a 40-hlp filter.

Figure 15. Cospectra between wind stress and water level in the North and South Channels of Ossabaw Sound, GA during 1998 sampling. The coordinate system for wind stress has been rotated -40° for plots of (a) the power spectra and (b) coherence. Frequency is measured in cycles per day (cpd). Cospectra were calculated by means of a fast Fourier transform of the detrended data in Fig. 14.



shrimp to the cues of temperature and salinity that facilitates movement to the inlet, pooling of larvae, and ingress to the estuary.

Similar interactions of behavior and temperature, in conjunction with wind and tidal currents, appear to aid post-larval transport of white shrimp into estuaries of the south-eastern US. For white shrimp, the increase in bottom water temperature in spring triggers spawning (Muncy, 1984). At an inlet in South Carolina, post-larval ingress occurred only when temperatures exceeded 20°C , with peak ingress from 25 to 30°C (DeLancey *et al.*, 1994). Wenner and Beatty (1993) also noted that peak occurrence of white shrimp in estuarine nursery areas of South Carolina coincided with July temperatures $>26^\circ\text{C}$. Thermally mediated behavior could also contribute to 'pooling' of white shrimp post-larvae on or near the bottom in the immediate near-shore waters until a critical estuarine temperature is reached in the spring. Cool water temperatures have been shown to elicit reduced activity (at 15 – 17°C) and burial into the substrate (at 12 – 16.5°C) by *Farfantepenaeus aztecus*,

and water temperatures at the time of their arrival in Texas bays were similar to those which elicited their emergence from sediments (at 18 – 21.5°C) in the laboratory (Aldrich *et al.*, 1968). Although the same experiments were unable to document similar burrowing behavior in white shrimp, *L. setiferus* did become less active and rested on the bottom at temperatures between 15 and 17°C (Aldrich *et al.*, 1968). The difference in water temperatures at the time when brown and white shrimp post-larvae arrive at coastal inlets suggests that any similar vertical migration behavior may occur at a higher temperature for white shrimp than brown shrimp. Rulifson (1983) showed that juvenile *F. aztecus* leave the water column after a significant cold shock by passively settling to the bottom, although the temperature decreases of ~ 19 – 25°C used for the experiments were much greater than those encountered under natural conditions.

In our previous study of white shrimp ingress into the North Edisto Inlet, most post-larvae were collected during cruises when surface and bottom temperature minima were 27 – 28°C (Wenner *et al.*, 1998). The

uniformity of temperature during each cruise in the North Edisto apparently had little influence on short-term variability of post-larval density. Those results, together with our later collections in the North and South Channels of Ossabaw Sound, provide clear evidence that temperature strongly influences the density of white shrimp in these coastal inlets. The differences in density noted between the South and North Channels in 1998 may be related to the difference in temperature noted between the channels. The higher densities observed in the South Channel occurred throughout the entire sampling period, and they corresponded with higher overall surface temperatures (27°C during high water and 28.5°C during low water). In contrast, surface water in the North Channel was 25°C during high water and 28°C during low water. Our data and that of others (Williams, 1955; Bearden, 1961; Christmas *et al.*, 1966; DeLancey *et al.*, 1994) support the idea that temperature is a key factor that influences post-larval supply to south-eastern estuaries, perhaps by mediating the behavior of post-larvae to stimulate movement off the bottom so that directional motion toward inlets is increased. Once the threshold temperature for a particular species is reached, other key factors, such as those discussed below, may exert considerable further influence on the ingress of post-larvae.

Tidal phase

Several studies have provided evidence that penaeid post-larvae migrate vertically as a means to enhance recruitment to estuaries (Staples and Vance, 1985; Forbes and Benfield, 1986; Dall *et al.*, 1990). Tidally based endogenous rhythms with peaks of movement around flood tide have been found for several species (Copeland and Truitt, 1966; Garcia and Le Reste, 1981; Mair *et al.*, 1982; Forbes and Benfield, 1986). Among penaeid shrimp, Hughes (1972) found that vertical movement of post-larval pink shrimp, *Farfantepenaeus duorarum*, was synchronized with the tides; however, no evidence of a tidally mediated rhythm could be found for *F. aztecus* or *L. setiferus* during static salinity gradient experiments (Keiser and Aldrich, 1976). Other environmental factors have been suggested as cues for post-larval settlement (salinity; Hughes, 1969b) and return to the water column (pressure changes; Forbes and Benfield, 1986). Interactions of temperature and salinity, as well as changes in barometric pressure, have all been suspected of triggering vertical movement of shrimp post-larvae, whose position in the water column strongly affects their onshore transport (Blanton *et al.*, 1995).

Post-larval shrimp may use tidal transport to facilitate movements into the estuary, by moving up in the water column during flood tide and by sinking to near bottom depths on ebb tide, where flow is weakest because of bottom friction, thereby avoiding the stronger ebb currents (Hill, 1991). Post-larvae could also move laterally during ebb to shallow areas where currents are weaker due to friction, thus diminishing their seaward transport. In the semi-diurnal tidal currents of many south-eastern estuaries, vertical movement is sufficient to induce maximum horizontal excursions of a few tens of kilometers (Hill, 1991). The results of our study in the North Edisto River indicated a relationship between white shrimp post-larval density and the tidal component of currents. Rothlisberg *et al.* (1995) proposed that *Melicertus plebejus* (formerly placed in the genus *Penaeus*) responded to tidal pressure by becoming active during a 1–3 h period following the start of flood tide, ceasing activity thereafter, and dropping out of the plankton to bury into the substrate on ebb currents. Rogers *et al.* (1993) hypothesized that if they encountered low salinity water from ebb flows in the nearshore coastal zone, *F. aztecus* post-larvae would move downward in the water column to a point where transport is minimal, or drop onto the substrate itself. Post-larval *F. duorarum* dropped to the substrate when salinity was reduced, presumably to evade displacement by ebb tide (Hughes, 1969b). If rate of change of salinity is a cue for behavior in shrimp, as has been reported for crab megalopae (DeVries *et al.*, 1994), then a clear pattern of vertical distribution supporting tidal stream transport may be particularly difficult to determine in well-mixed estuaries, as opposed to those with significant freshwater inflow.

The amplitudes and phases of the M2, S2 and N2 tidal constituents govern the characteristics of neap and spring tides at any particular site. Such characteristics include the difference between ranges of spring and neap tide, and the 'age' of the tide (i.e. the time lag between the actual occurrence of the spring or neap tide and the occurrence of the specific lunar and solar alignment that causes it). For most locations along the east coast of the US, the co-occurrence of darkness and flood currents in late spring and early summer always occurs near, but not necessarily on, the day of neap tide. This generalization is not universal, however, because no-light conditions are maximized during spring tides at some localities on the opposite side of the Atlantic Ocean.

During neap tide, we observed that the currents in the North Channel changed to flood, while water level was still falling. This effect may be due to selective

withdrawal of subsurface water from the North Channel, a process that becomes more efficient during periods of weak vertical mixing representative of conditions at neap tide (Blanton *et al.*, 2000). As neap tidal currents flood during most of the night, channels that prolong the duration of flood currents by selective withdrawal would presumably retain larvae more efficiently. The strength of withdrawal is proportional to depth, so this process is stronger in the deeper North Channel.

The highest densities of post-larvae observed during our studies occurred in both channels of Ossabaw Sound during the 5-day period centered on the neap tide of June 17, 1998. From June 17 to 19, one of the two semi-diurnal flood tide phases each day occurred entirely during the dark. Thus, during this peak ingress period, the full duration of the flood tide coincided with no-light conditions. As flood tidal currents in Ossabaw Sound are weaker on neap than spring tides, the fact that maximum larval transport into Ossabaw Sound occurred under neap-tide conditions suggests that nighttime behavior outweighs the importance of flood tide current strength as a variable with transport potential. However, as discussed in the next section, there are also subtidal flow conditions that may account for heavy ingress of post-larvae.

Wind component

Although much of the tidal energy available to assist in shoreward movement of post-larvae is periodic, and therefore predictable, the additional transport of oceanic water produced by wind stress is largely stochastic. Theoretical studies (e.g. Klinck *et al.*, 1981) have shown that the Ekman fluxes generated by the alongshore component of wind are responsible for subtidal exchange between ocean and estuary. Examination of data collected by Wenner *et al.* (1998) in the North Edisto Inlet, SC showed that 63% of the variance in post-larval abundance was explained by alongshore wind stress. By contrast, the exchange driven by the cross-shelf component was negligible, with only an additional 6% of the variance attributable to that factor. Large volume exchanges can also occur when continental shelf waves pass through the system and cause an influx and efflux of water into estuaries by means of water level excursions (Schwing *et al.*, 1988). Thus, a downwelling favorable wind or a remotely forced shelf wave that induces a subtidal increase in inflow should increase the potential for larval ingress.

A comparison of the 1998 post-larval ingress data (Fig. 6) with conditions favorable for landward subtidal transport (Fig. 14) supports this hypothesis. After June 12, water temperature in the North Channel

reached the threshold level of 27°C that was observed in the South Channel since the beginning of the study. During the following neap-tide conditions (June 17–19), maximum post-larval densities occurred in both channels (Fig. 6). This peak coincided with the time that water level in the system *increased* by more than 0.2 m (Fig. 14), thereby inducing an additional influx of water that would reinforce the flood current over that time period. Contrast this neap tide with the preceding one, when water level in the system *decreased* by almost 0.3 m, representing a relatively large subtidal current out of the system that would counteract the flood current. Such a large subtidal efflux through the estuarine entrance would presumably inhibit the efficiency by which post-larvae might be entrained in the flood tidal flow.

We would expect that the direction of subtidal currents (into or out of the system) becomes a significant factor when water influx coincides with the time of favorable temperature conditions and nighttime flood tides. However, we were unable to demonstrate this from our study. The normal ingress period for white shrimp lasts for 4–6 weeks. As weather systems strong enough to induce large subtidal exchanges occur, on average, once every 4–7 days (Blanton *et al.*, 1989), we would expect about 5 or 6 cycles of exchange during a normal ingress season. This makes it difficult to predict, with any confidence, how many of those cycles of subtidal influx will coincide with conditions of nighttime flood tides and favorable temperatures during a given ingress season. For our study, which sampled post-larvae for 2-week intervals in two different years, there was only one such coincidence.

Being able to forecast stock abundance based on environmental conditions associated with the post-larval recruitment period would be helpful in stock assessments. The ability to predict larval shrimp responses to changes in the environment is one of the first steps toward understanding how factors encountered during early life-history stages may influence annual differences in shrimp abundance within their distributional range. In addition, identification of critical requirements for post-larval stages may assist resource managers in protecting estuarine and coastal habitats from anthropogenic influences during critical larval ingress periods. Information on the complex interactions between diverse biological and abiotic processes are essential to the conservation of estuarine habitats and species health in the face of expanding human populations along the coasts. Understanding the dynamics, interactions and coupling between cyclic and stochastic oceanographic processes and the behavior and population biology of white shrimp post-

larvae may be helpful in future models of estuarine ingress by penaeid shrimp to other systems within the region. Obviously, further research needs to be done in order to determine how the processes critical to short-term recruitment dynamics relate to long-term trends in the population.

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