Key Factors Influencing Transport of White Shrimp Postlarvae in Southeastern U.S. Estuaries

Final Report

to
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prepared by

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INTRODUCTION

The most valuable fishery in the southeastern United States is directed at the penaeid shrimp resource. In South Carolina and Georgia, two species are targeted, the white (_Litopenaeus_ _setiferus_) and brown (_Farfantepenaeus_ _aztecus_) shrimps, with white shrimp dominating catches. Coastal oceanographic and meteorological processes greatly influence early life history stages of 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; and Rothlisberg *et al*., 1995). There is evidence that the magnitude of the postlarval stocks is related to subsequent adult harvests (Delancy *et al*., 1994). A recent study developed a model to predict white shrimp harvests, based on environmental parameters and indices of abundance (Belcher and Fortuna, in prep.). As might be expected with a short-lived species like the white shrimp, spawning stock, relative abundance, and resulting recruitment are the most important factors used to define the adult stock size and expected harvest. The fact that the index of abundance first becomes important to the model in May suggests that the prediction of stock size is primarily dependent on the spawning stock size, and secondarily on the ensuing larval recruitment. Thus, successful recruitment of planktonic larvae appears to be a critical determinant of adult shrimp stock size, yet our ability to understand and predict their interannual and spatial variations is limited. The interaction between the behavior of postlarval white shrimp and the hydrographic processes that transport them to their estuarine nursery grounds produces complex temporal patterns of ingress and 3-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 postlarvae is a complex issue in which more than one mechanism may be involved, simultaneously or in series. Suggested mechanisms have involved selective tidal transport cued by synchronized salinity changes (Hughes, 1969 a,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 to facilitate transport (Rogers *et al*., 1993). The interaction of diel vertical migration with tidal and 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, it is necessary to have a pool of larvae available in a withdrawal 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 component that enhances the cross-shelf transport of coastal water (Blanton, 1996). The movement of surface water offshore is indicated by shallow low-density lenses with a cross-shelf scale width of about 20 km, a result that has been verified in previous numerical simulations (Blanton *et al*., 1989). This mechanism appears to be responsible for removing large quantities of coastal water seaward.

Based on our previous research, tidal circulation in the vicinity of an idealized tidal inlet was modeled using a 3-D 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 across 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 (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. This study pointed out that the source location of larvae depended more on the wind acting on the scale of inlet separation than on a larger scale such as the width of the continental shelf.

Shoreward currents capable of advecting larvae into the vicinity of inlets occur in both upwelling and downwelling conditions. However, only near-bottom shoreward currents are present during upwelling. Thus, whether or not larvae are carried shoreward in either upwelling or downwelling depends critically on the vertical migratory behavior of the organism (Blanton *et al*., 1995; Wenner *et al*., 1998). Recent results from our work on penaeid shrimp transport in the North Edisto River of South Carolina verified the importance of vertical positioning in the water column of white shrimp postlarvae. Downwelling winds having an onshore stress component were associated with the largest ingress of white shrimp (Wenner *et al*., 1998). White shrimp postlarvae, in order to derive maximum benefit from the downwelling regime, would have to spend most of their time near the surface in order 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 alongshore equatorward component.

Vertical migration of blue crab larvae has been documented as a means to enhance transport from offshore into an estuarine nursery (Epifanio, 1988). It has been hypothesized that weakly swimming larvae move upstream via tidally-timed vertical migration. A number of field and laboratory studies have addressed the concept that penaeid shrimp undergo diel vertical migration (Renfro and Brusher, 1982; Mathews *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 postlarvae of *P. merguiensis* 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).

Our North Edisto study showed that, in addition to wind-driven transport, density of white shrimp postlarvae changes with tidal stage (Wenner *et al*., 1998). This suggests that postlarvae may be using tidal transport to facilitate movements into the estuary. The present study addresses the importance of similar transport mechanisms through channels with different salinity and tidal current regimes. Specifically, we examine and compare conditions under which white shrimp postlarvae 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 postlarvae during ingress; to describe the hydrographic conditions and the distributions of zooplankton and phytoplankton (chlorophyll *a*) that existed during ingress of white shrimp postlarvae; and to identify the combination of mechanisms that contributed to postlarval transport.

DESCRIPTION OF THE STUDY AREAS

This report provides information obtained from sampling over a five-year period in the North Edisto River, SC (1994) and the Ossabaw Sound, GA estuarine systems (1997-1998) (Figure 1). The results regarding postlarval white shrimp ingress into the Ossabaw Sound system will be compared with previous results obtained from the North Edisto Inlet.

The North Edisto River forms a short deep estuary with ~28 km^2 of open water surrounded by *Spartina*-dominated salt marsh. The estuary is connected to the ocean through a narrow (1 km), deep (22 m) inlet throat (Figure 1). It has a fairly simple bathymetry with a tidal prism of approximately 0.9×10^8 m^3, based on estimates of total lagoon and open water areas given by Nummedal *et al*. (1977). Little freshwater runoff enters the estuary (Mathews and Shealy, 1978), and strong semi-diurnal tidal currents through the inlet throat of 130 cm s^{-1} (flood) and 150 cm s^{-1} (ebb) maintain vertically homogenous water throughout the tidal cycle (Blanton *et al*., 1994). The mean tidal range in the North Edisto estuary is approximately 1.7 m. Compared to Ossabaw Sound, the North Edisto system receives an insignificant amount of freshwater discharge (Wenner *et al*., 1998).

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 (Figure 1). A mean annual freshwater discharge of about 70 m^3 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 toward the ocean. At its mouth, the South Channel has a depth of 7-8 m at low water and a width of about 1.5 km. 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 2.7×10^8 m^3 (Table 1). As confirmed by our study, tidal currents typically range from ~50 cm sec^{-1} to 75 cm sec^{-1} (Dörjes and Howard, 1975). Ebb currents are usually stronger than flood in both channels of Ossabaw Sound. However, we will show later that near-bottom flood currents in the North Channel can be stronger and last longer during neap tide.

Table 1. Comparison of morphological parameters for North Edisto and Ossabaw Sound (based on Nummedal *et al*., 1977 and Oertel and Dunstan, 1981}. The tidal prism for the North Edisto is for mean tide level, while values shown for Ossabaw Sound are for spring and neap tide, respectively.

	maximum throat depth (m)	total lagoon area (10^6 m^2)	open water area (10^6 m^2)	ratio of open water to total	tidal prism (10^6 m^3)
North Edisto	22	132	28	0.21	90
Ossabaw Sound	10	274	72	0.26	442/167

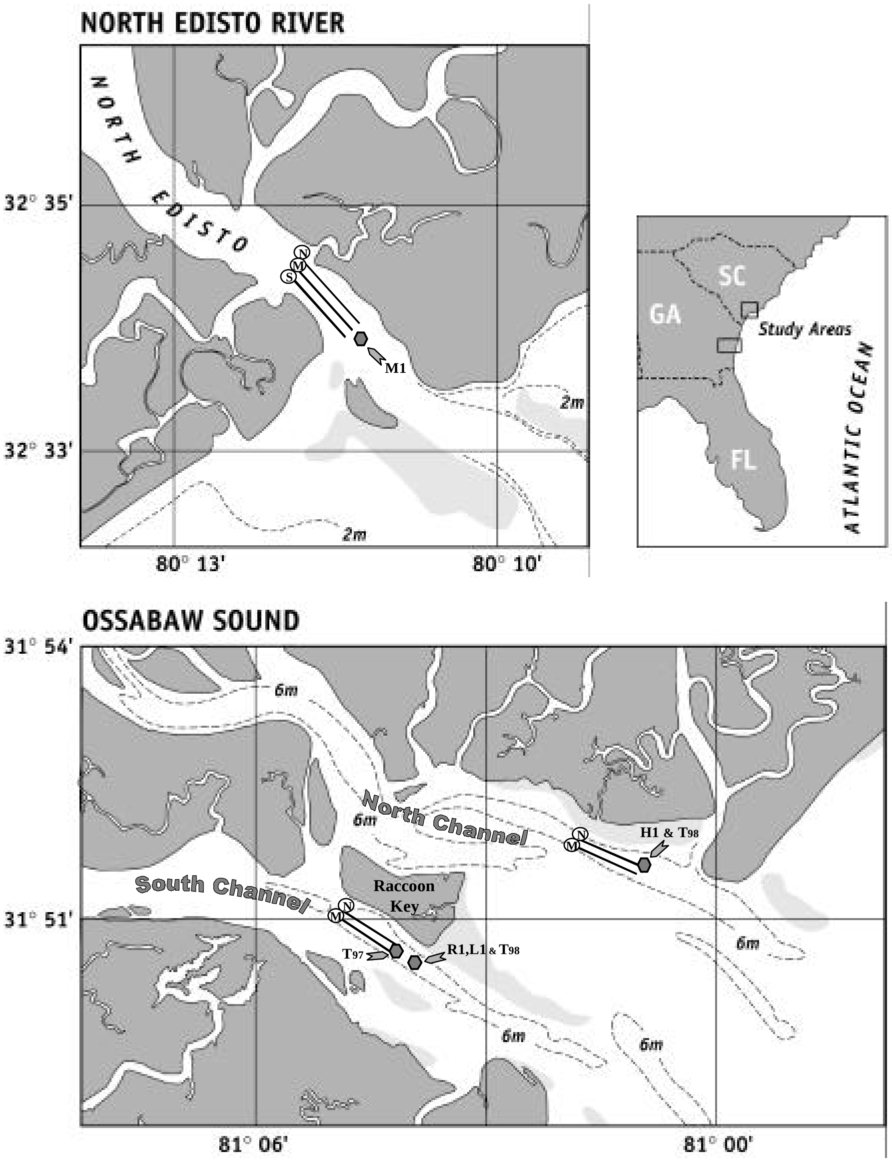


Figure 1. Map of the sampling locations in the North Edisto River (SC) and Ossabaw Sound (GA). Symbols show the specific locations of plankton, hydrographic and acoustic data collection; an explanation of station designations and details of data collected at each station are given in Table 2.

METHODS

Table 2. Site and station designations for biological, acoustic, and hydrographic sampling efforts in the North Edisto, SC and Ossabaw Sound, GA estuaries, along with the dates and locations of data collection. (codes for instrument deployments: B = bottom, MW = midwater, S = surface; v = current velocity, p = subsurface pressure, t = water temperature, c = conductivity)

sampling description	***dates***	***station designation***	***location***
1994 North Edisto River			
plankton sampling	June 15-30	N	32°34.27'N 80°11.63'W
	June 15-30	M	32°34.20'N 80°11.67'W
	June 15-30	S	32°34.14'N 80°11.70'W
hydrographic mooring [B: p,t,c]	June 7-July 5	M1	32°33.84'N 80°10.92'W
wind measurements	June 1-July 20	FBIS1	32°40.80'N 79°53.40'W
1997 Ossabaw Sound - South Channel			
plankton sampling	June 9-25	N	31°50.98'N 81°04.57'W
	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
TAPS acoustics	June 2-July 1	T_{97}	31°50.71'N 81°04.18'W
wind measurements	June 1-July 6	NDBC-41008	31°24.13'N 80°52.23'W
1998 Ossabaw Sound - South Channel			
plankton sampling	June 5-20	N	31°51.00'N 81°04.62'W
	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
TAPS acoustics	May20,22,25,28	T_{98}	31°50.53'N 81°04.02'W
wind measurements	May 1-June 29	NDBC-41008	31°24.13'N 80°52.23'W
1998 Ossabaw Sound - North Channel			
plankton sampling	June 5-20	N	31°51.82'N 81°01.35'W
	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
TAPS acoustics	May19,22,25,28	T_{98}	31°51.65'N 81°00.99'W
wind measurements	May 1-June 29	NDBC-41008	31°24.13'N 80°52.23'W

Postlarval Sampling

Postlarval ingress, as used here, describes the movement of shrimp postlarvae from the coastal ocean into the estuary. In the case of the Ossabaw Sound study, the sampling scheme was divided into *extensive* and *intensive* phases. In the extensive phase, we determined the temporal pattern of density of white shrimp postlarvae by collecting a series of nighttime surface plankton tows taken over several 14-day periods. In addition to this nightly ingress sampling, intensive periods of around-the-clock sampling were conducted in the Ossabaw Sound system. Surface and near-bottom tows were collected to examine the effects of diel and tidal periodicity on postlarval ingress, and to determine the importance of vertical migration to ingress. Sampling occurred in June each year, to coincide as closely as possible with peak ingress of postlarval white shrimp (*Litopenaeus setiferus*). The cruises were each ~14 days in duration, in order to sample over a full cycle of neap/spring tides (Table 2).

Extensive Sampling – Postlarval Ingress

Surface plankton tows were collected over several 14-d periods, during which consecutive 5-min tows were made against the flooding current in the inlet channels. Tows were made 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 by 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.

During the 1994 North Edisto cruise, plankton tows were made at three stations evenly spaced across the inlet throat (N, M, and S), approximately 2 km upriver from the mouth (Table 2, Figure 1). Since no significant differences in postlarval abundance were seen among the three station locations (Wenner *et al*., 1998), they were pooled in subsequent analyses. In Ossabaw Sound, 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 (Figure 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 (Figure 1).

Intensive Sampling – Diel, Tidal, and Vertical Patterns of Distribution

During the course of the 14-d extensive sampling periods, additional intensive periods of around-the-clock surface and near-bottom plankton tows were made in Ossabaw Sound in 1997 and 1998. 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.

Sampling Gear

During the North Edisto cruise, surface collections were made by a 0.505 mm mesh conical nitex net attached to a 0.6 m diameter bongo frame in which a General Oceanics Model

2010 flowmeter (with a standard speed rotor) was mounted. The net was towed against the tidal current (upcurrent), and the vessel speed was adjusted to maintain the top of the net opening as near to the surface as possible. During subsequent cruises in Georgia, a rectangular neuston frame (1 m wide, 0.5 m high), equipped with an identical 0.505 mm mesh plankton net and flowmeter, 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.

Postlarvae were also collected near the bottom of the water column during the intensive sampling phases at the Ossabaw Sound stations, 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 sec) 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 input into software 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 downcurrent.

Sample Processing

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 postlarvae were sorted from the samples using Bogorov trays under 60x magnification. For bottom samples that contained substantial volumes of sandy sediments, Ludox medium was used to separate plankton from the sand. Postlarvae 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 postlarvae were split and subsampled prior to estimating the total number. After the shrimp postlarvae 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 m^3. For samples collected in 1997 and 1998, the total length (tip of rostrum to tip of telson) of up to 30 postlarvae were measured from each sample, using an ocular micrometer in a dissecting microscope.

Oceanographic and Meteorological Data Aquisition

Moored Instruments

Oceanographic conditions were monitored and recorded every six minutes using instrument arrays deployed on moored stations (Table 2). The stations were located slightly seaward of the path of the net tows that sampled for the postlarvae. The moorings were deployed 1-2 weeks prior to plankton sampling by the R/V *Bluefin*, a 22 m research vessel operated by

Skidaway Institute of Oceanography. Moorings were removed at the conclusion of plankton sampling.

Moorings were deployed for 37 days in both the North and South Channels (Figure 1 and Table 2). L1 was located in 8.5 m of water in the South Channel. Temperature and conductivity were recorded at three depths by SEACATs (SeaBird Electronics, Inc.). 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.) was attached to the mooring 1.0 m above the bottom. The instrument array at station H1 was deployed in 12.3 m of water in the North Channel and was similar to that in the South Channel, except that it lacked the floating SEACAT instrument.

For the North Edisto study, mooring M1 was deployed for 28 days in 14 m of water in the main channel of the inlet throat (Figure 1, Table 2). SEACATs and S-4s were also used in this experiment. No current meters were deployed in the inlet throat. Instead, a pair of current meters was deployed along the foot of the ebb tide delta for one tidal cycle. Tidal currents for periods other than these were approximated using NOAA current predictions for Deveaux Bank (~ 2 km from the M1 mooring), after making minor adjustments based upon a comparison of current measured at M1 during previous cruises with the coincidental NOAA predictions (NOAA, 1993).

CTD Casts

During the extensive phases of plankton sampling, each vessel was equipped with a Model 25 Sealogger® CTD instrument (Sea-Bird Electronics, Inc.), which was used prior to the start of each plankton tow to obtain a vertical profile of conductivity, temperature, fluorescence and depth. Locations of the tow stations are shown in Figure 1 and Table 2. Salinity and density were computed from the conductivity, depth and temperature readings, using standard algorithms. The fluorometers, which measure chlorophyll *a* fluorescence, were calibrated against phytoplankton cultures prior to the cruises, which 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 lab with a Turner Designs fluorometer. These data were used to derive calibration curves to convert *in situ* fluorescence from CTD vertical profiles into chl *a* readings (in $\mu g\ l^{-1}$).

Immediately prior to the start of each plankton tow, the CTD unit was lowered through the water column and real-time data were displayed (at 1 Hz) on a personal computer, giving us the ability to immediately ascertain the vertical structure of the water column. Vertical structure was also sampled at a rate of 4Hz and stored as a binary data file on the computer. Following the cruise, downcast data were averaged by depth into 1.0 m bins, allowing hundreds of data points to be summarized into relatively few values, while maintaining sufficient vertical resolution.

During the intensive phases (24-hr sampling), hourly CTD casts were taken from the R/V *Bluefin* while it was anchored downstream of station M, where plankton tows were being conducted. The R/V *Bluefin* anchored 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 was made in lieu of those otherwise taken from the vessel that towed the plankton nets, immediately prior to each tow.

Low Tide / High Tide CTD Transects

Three days prior to plankton sampling in Ossabaw Sound, a series of CTD profiles was taken at mid-channel stations in the South Channel (1997,1998) and the North Channel (1998). These data were used to define estuarine salinity and temperature structure. By using two vessels, coverage in the North and South Channels was simultaneous. Surveys were conducted at low water and again during the following high water, during the neap tides associated with the first-quarter moon. This defined the salinity distribution when flood currents at night had the maximum duration. Each survey commenced at a station near the ocean, and subsequent vertical profiles were made at 2-km intervals along the axis of each channel, usually up to 20 km upstream. Profiles were timed to coincide with local low water at each station, with a resultant elapsed time of roughly 2.5 hr for surveys in the South Channel and 2.3 hr in the North Channel. Following completion of the low tide survey, the sampling vessel returned to the mouth of the river and commenced the subsequent high water survey at the time of the next high tide. The equipment and methods used to obtain the profiles are the same as described above.

Wind Measurements

Hourly readings of wind speed and direction were obtained from the National Oceanic and Atmospheric Administration’s C-MAN (Coastal-Marine Automated Network) station FBIS1 at Folly Beach, about 30 km east-northeast of the North Edisto Inlet. Meteorological data from this station are representative of local coastal wind conditions during the North Edisto cruise (Blanton *et al*., 1995; Wenner *et al*., 1998) and are well correlated with temporal patterns in plankton distribution (Verity *et al*., 1998). Comparable wind data for the Ossabaw cruises was obtained from NOAA’s National Data Buoy Center, Station 41008 at Gray’s Reef. This buoy is located approximately 50 km south-southeast of Ossabaw Sound.

Acoustical Sampling

During June 1997, the Tracor Acoustical Profiling System (TAPS) (Holliday and Pieper, 1995) was deployed to describe temporal distributions of the plankton community in the South Channel of Ossabaw Sound. The TAPS unit was mounted on a bottom frame in an up-looking mode and placed at station T_{97} near the mouth of the inlet (Table 2; Figure 1), in approximately 7 m depth. A power and transmission wire connected the TAPS to a battery system and laptop computer on Raccoon Key. Data were recorded in 0.125 m depth bins for six frequencies (265, 420, 700, 1100, 1850, & 3000 kHz) at 1-min. intervals. Because of the large amount of data recorded (969 columns for each minute), files were closed and saved each hour. The TAPS unit was deployed for 31 days beginning on 2 June, prior to plankton net sampling, to obtain a continuous temporal recording during sample collection. Equipment failure from 20-22 June resulted in the loss of data for 43 hours before the system was restored.

Contour plots of backscattering strength (dB) for all six frequencies in the entire data set were compiled sequentially to observe temporal patterns. Calculations of the inverse function to compute biovolume estimates were performed using all six frequencies for selected data sets to compare with results from plankton net sampling. MATLAB software programs were used for calculations of acoustic backscatter and inverse functions (Holliday, 1977; Greenlaw, 1979; Holliday *et al*., 1989; Pieper *et al*., 1990). Contour plots, with a standardized color scale (-80 to -20 for backscatter; 0-10 for log of biovolume mm^3 m^{-3}) allowed visual comparison of results between channels and years, and also with results from the North Edisto River (Barans *et al*., 1997).

In May, 1998, ten days prior to the initiation of plankton net sampling in both the North and South Channels of Ossabaw Sound, temporal and spatial data on plankton distributions were obtained with a 4-frequency (265, 420, 700 and 1100 kHz) TAPS in a downward-looking mode. Acoustic backscatter was measured along transects across both channels near T_{98} (Table 2, Figure 1) from 1 m below the transducer (just below the surface) down to a maximum depth of 20 m. Data was collected through the water column in 0.125-m bins at 1-min intervals, during both day and night, primarily during flooding tides between 18-28 May 1998. The TAPS unit, which was attached to the side of the boat, was moved perpendicular to the axis of the river. Repetitive transects of acoustic measurement stations were made alternately across each of the two rivers, during the flood tide on spring and neap tides. Temporary range lights set up on the shorelines facilitated relocation along the same transect lines during day and night sampling. A total of 34 transects were made across the North (8 day; 9 night) and South (10 day; 7 night) Channels. Data sets were stored in batch files of 1-hr duration on a portable computer and returned to the lab for processing. Biovolume was determined for specific large scatterer sizes (0.79 and 1.99) in mm of Equivocal Spherical Radius (ESR). Since the highest frequency (1100 kHz) was valid only in depth ranges <7 m, inverse calculations were based only on the three lower frequencies (265, 420, and 700 kHz), which are adequate for calculations of particle sizes >0.5 mm ESR. A typified bottom profile mask was used for each river to assist visual interpretations, although minor variations in track lines (and resulting depth profile) did occur. Tidal velocity during each TAPS recording was determined from S4 current meters on the nearby hydrographic moorings. Plots were viewed for patterns in plankton distributions under different tidal, diel, lunar, depth, and spatial 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 (Table 2) 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 was computed from the first form by applying a low-passed digital Lanczoz filter with a 40-hr cutoff. This form of the data 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 clockwise from north, to align it with the coastline (50º for the North Edisto study site, 40º for the Ossabaw system). In the case of the Ossabaw system, this aligns the cross-shelf component to within 5 degrees of the orientation of the North and South Channels (Figure 1). Wind stress was calculated using an interative 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 the low-pass filter described above prior to analyses at lags of 1, 6, and 24 hr. A 3-hr filter was used for the 1- and 6-hr lagged readings, while a 40-hr filter was used for the 24-hr lag, to remove wind fluctuations with periods shorter than a day. Stress units are in 10*Pa (= dynes*cm^{-2}).

RESULTS

Oceanographic Characteristics of Ossabaw Sound

Harmonic analysis of near-bottom currents (Table 3) indicated a large between-channel difference in the 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.

Oceanic tides generate higher-frequency overtides as they propagate into shallow water of shelves and estuaries. Non-linear terms associated with friction and preserving the continuity of flow are responsible for the production of the quatradiurnal (M4) and sextadiurnal (M6) lunar tides, as well as several others (Friedrichs and Aubrey, 1988; Parker, 1991). Overtide generation is important in environments where the ratio of tidal amplitude to water depth becomes significant, as it does in the North and South Channels. Overtides with strengths of 10% or higher relative to M2 (the principal lunar semidiurnal constituent) lead to tidal currents with a high degree of distortion compared to the normal sinusoid characteristic of a current with only the M2 constituent (eg. Blanton *et al*., 2001).

The tidal currents in the two channels are contrasted by a comparison of the M2, M4 and M6 tidal constituents (Table 3). 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 minutes. 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 two and leads to greater tidal asymmetry in the North Channel and indicates a higher transfer of M2 tidal energy to M4 (Friedrichs and Aubrey, 1988; Parker, 1991). Nevertheless, the distortion is not high when compared to that observed in the surrounding tidal creeks (Blanton *et al.*, 2001).

Table 3. North Channel and South Channel tidal velocity constituents for 1998. Record length = 11.825 days. freq = frequency in cycles per hour; amp = amplitude in cm s^{-1}; pha = phase in degrees.

component tide	freq	North Channel amp	 pha	South Channel 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

	North Channel	South Channel
M4/M2	0.14	0.06
M6/M2	0.08	0.09
2M2-M4	267	304
3M2-M6	122	149

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

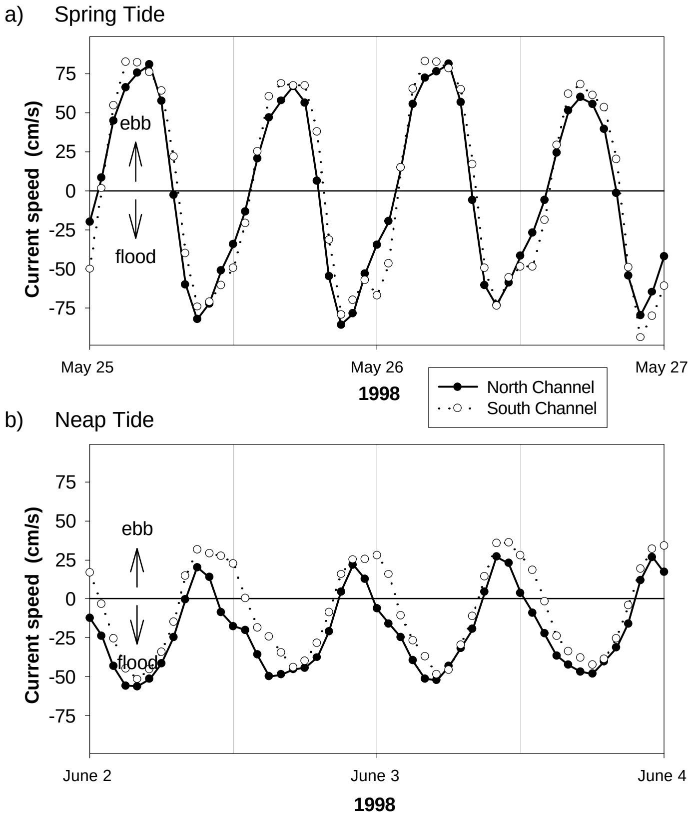


Figure 2. Axial tidal currents in the North and South Channels during spring (a) and neap (b) lunar phases of the 1998 cruises.

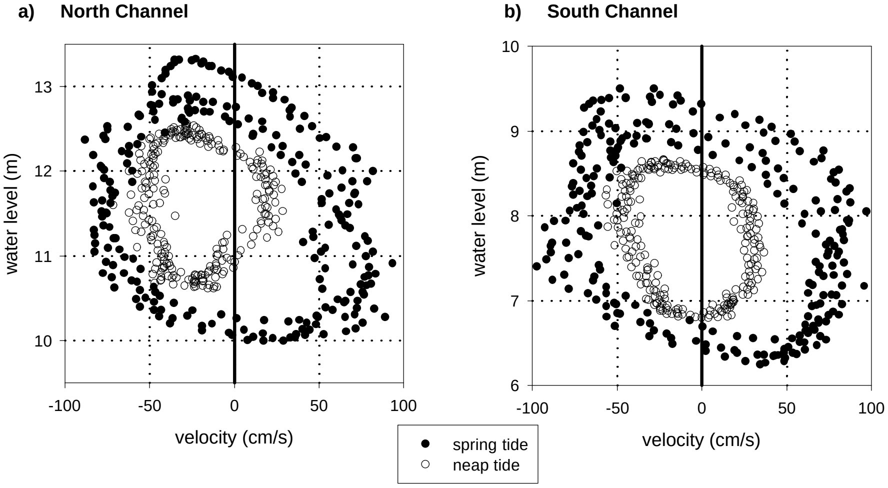


Figure 3. Axial current velocity plotted against water level in a) the North Channel and b) the South Channel on spring and neap tides. Data from moorings H1 and L1 in June 1998. Ebb tides are positive, flood tides negative.

Comparisons of temperature and salinity distributions between the two adjacent estuarine systems at the time of maximum and minimum oceanic intrusion (i.e. high and low slack water) illustrate the range of conditions potentially encountered by shrimp postlarvae during their transport. On June 2, 1998, water temperature at the entrance to the South Channel was slightly higher than in the adjacent North Channel, while salinity was lower (Figures 4 and 5). During these slack water CTD transects, the highest temperature (29.5°C) and lowest salinity (<2 psu) occurred 22 km upriver in the South Channel during slack low water, while the coolest temperature (23.5°C) and highest salinity (>30 psu) occurred at the mouth of the North Channel at slack high water. At the larval sampling station in the South Channel, surface water temperature was 29 °C at high slack tide and 28.5°C during low slack. At the North Channel larval sampling station, surface water was 28.5°C during high water and 28°C

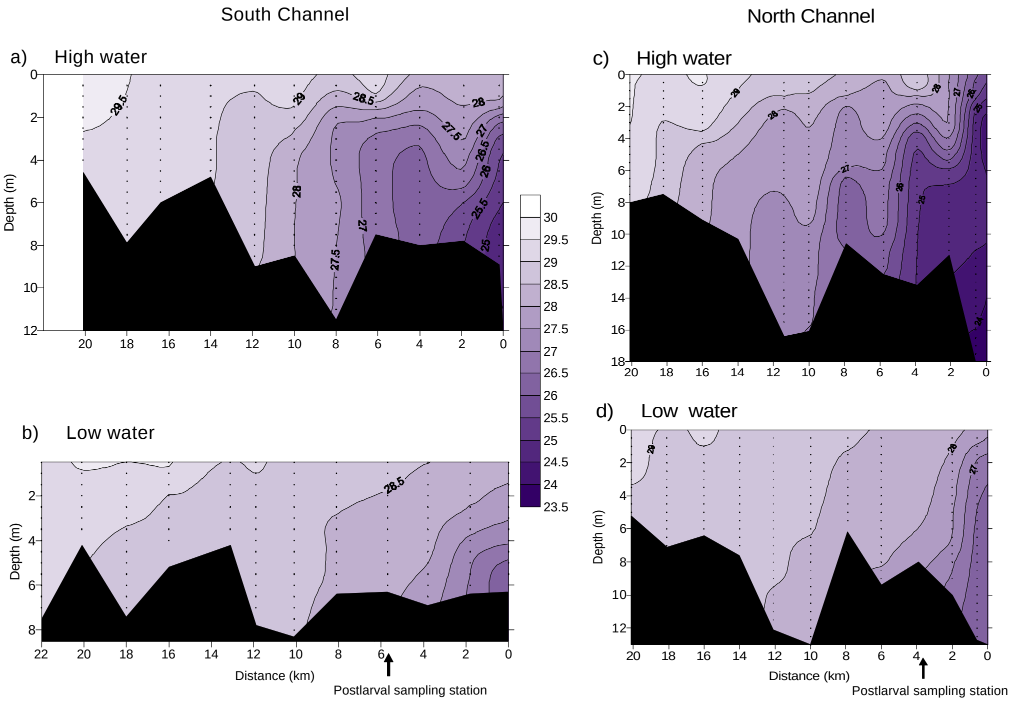


Figure 4. Vertical and horizontal distribution of water temperature in the South and North Channels of Ossabaw Sound at high and low slack water on June 2, 1998. The location of postlarval sampling in each river is indicated by the arrows. The unit of temperature is degrees Celsius.

during low water. Note that bottom temperature during high slack water was about 1-2°C lower in the entrance to the North Channel.

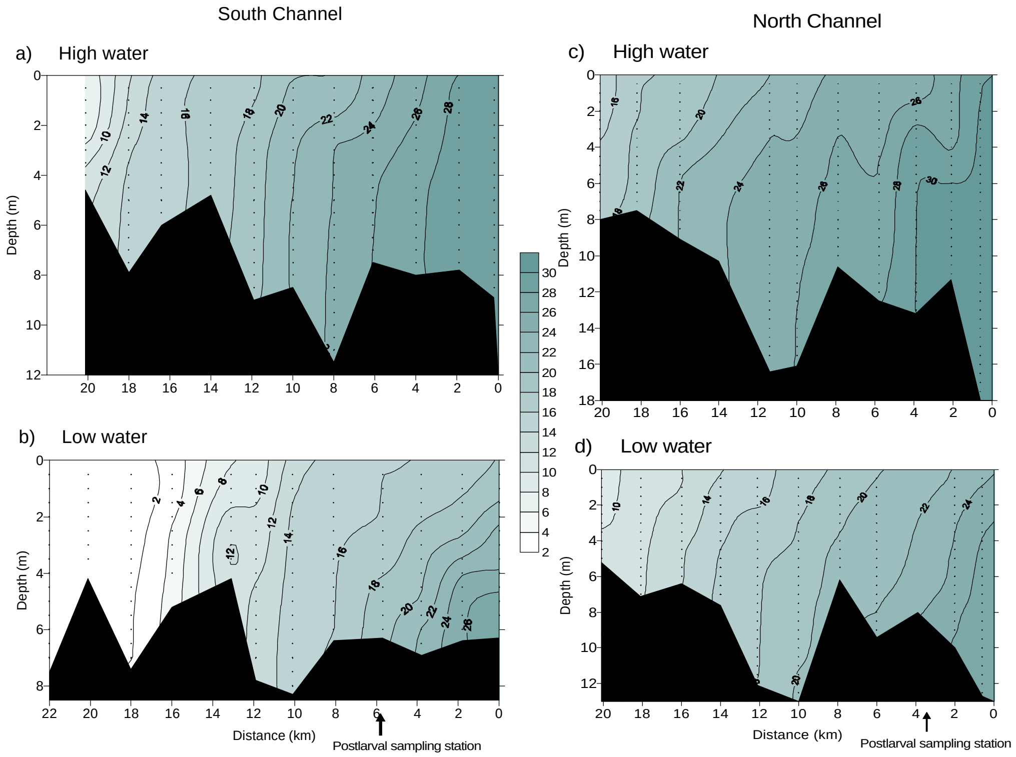


Figure 5. Vertical and horizontal distribution of salinity in the South and North Channels of Ossabaw Sound at high and low slack water on June 2, 1998. The location of postlarval sampling in each river is indicated by the arrows. The unit of salinity is psu.

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 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 (Figure 6). The discharge rate varied greatly during 1997 and 1998 (200 - 30,700 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 Figure 6). The abrupt salinity increase of 2-3 psu that was seen in both channels on June 2-3, 1998 (Figure 7) 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.

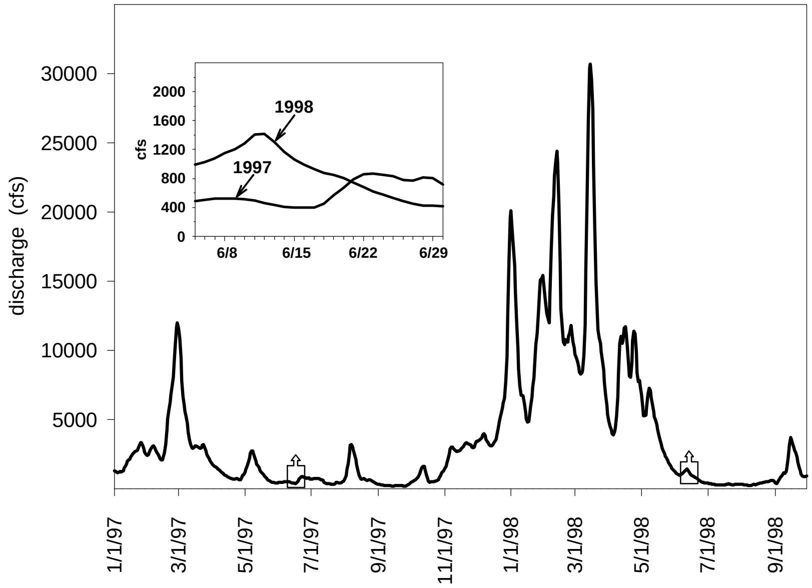


Figure 6. Daily freshwater discharge into Ossabaw Sound during 1997 and 1998. Data within small boxes are expanded in the inset to show flow at the time of postlarval sampling in both years. Streamflow data are from USGS Gauge #02202500 in the lower Ogeechee Basin near Eden, GA, approximately 65 km upstream from the study site.

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 ($\frac{\partial S}{\partial x}$) was estimated by a simple salt balance equation:

$$\frac{\partial S}{\partial t} + u\frac{\partial S}{\partial x} = 0 \qquad \text{[Equation 1]}$$

where S is the salinity and u is the velocity measured in each channel respectively. The results are presented in Table 4, averaged for the 50 hours centered on the two spring and neap tides covered by the mooring deployment.

Table 4. Comparison of axial salinity gradients ($\frac{\partial S}{\partial x}$) in North and South Channels calculated from Equation 1. Gradient is in units of psu km^{-1}. The mid-date for the fortnightly tide is listed in the time column. The ($\frac{\partial S}{\partial x}$) difference is South minus North.

time	North Channel	South Channel	tide	$\frac{\partial S}{\partial x}$ difference
May 26, 1998	0.53	0.76	Spring	0.23
June 3, 1998	0.11	0.81	Neap	0.70
June 11, 1998	0.27	0.88	Spring	0.61
June 18, 1998	0.41	1.01	Neap	0.60

Salinity gradients increased in the South Channel throughout the two spring-neap cycles. This is contrary to expectations, since river discharge in this channel steadily decreased as salinity increased. However, coastal salinity also increased after June 2 (Figure 7). Salinity gradients for corresponding time periods were consistently greater in the South Channel compared to 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 (Table 4).

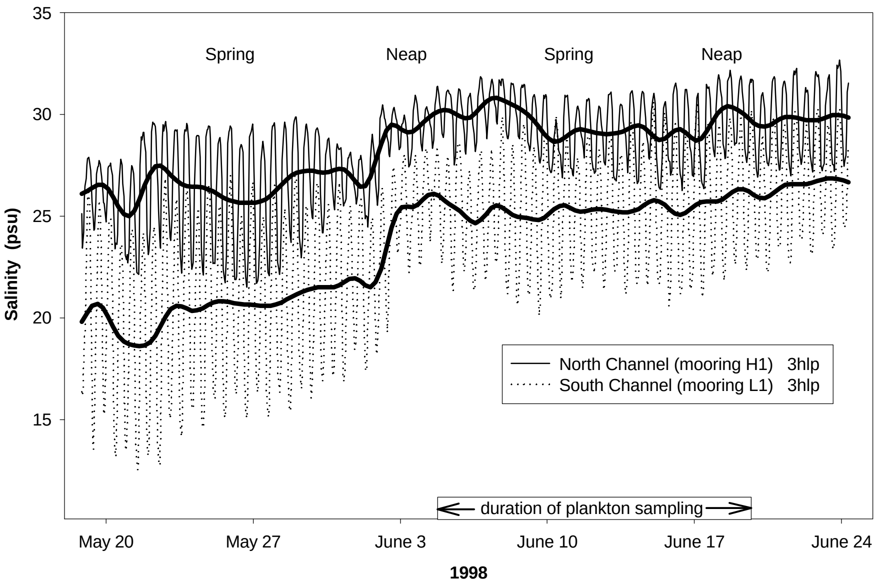


Figure 7. Near-bottom salinity as a function of time in the North and South Channels. 3 hlp plots show tidal fluctuations in salinity; thick solid lines are 40 hlp data, in which tidal variability has been eliminated.

Chlorophyll *a* Concentrations

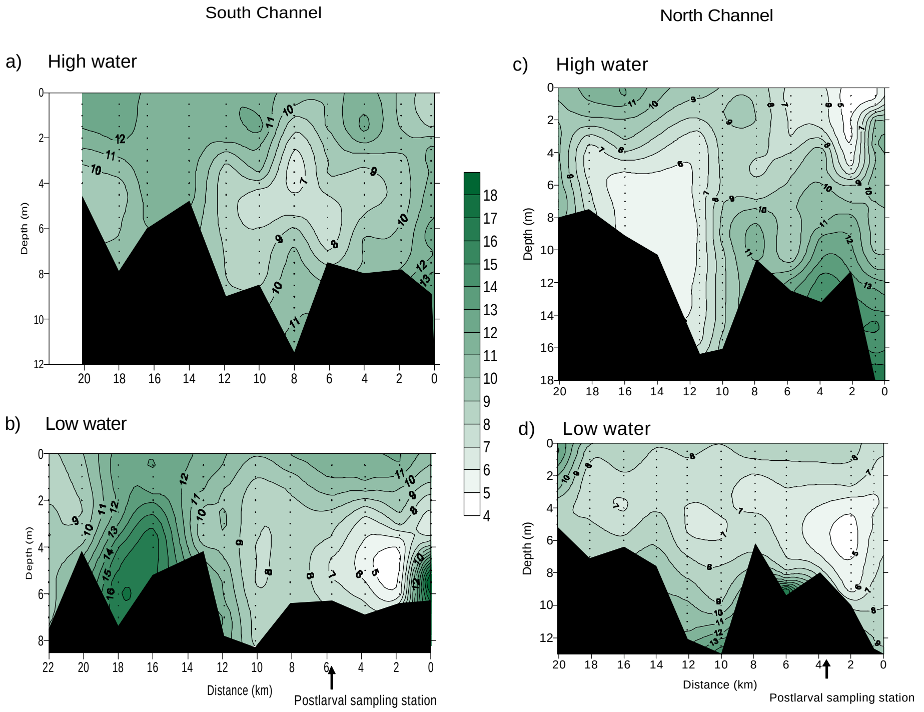


Figure 8. Vertical and horizontal distribution of chlorophyll a concentration in the South and North Channels of Ossabaw Sound at high and low slack water on June 2, 1998. The location of postlarval sampling in each river is indicated by the arrows. The unit of chl a concentration is micrograms per liter.

Chlorophyll *a* (chl *a*) varied considerably along the two channels during the high and low water surveys (Figure 8). The ranges in chl *a* concentration were similar in both channels (>4 to <17 ìg l^{-1} in the South Channel; >4 to <19 ìg l^{-1} in the North). Tidal influences were apparent in both channels, but more notably in the South Channel, where the range of concentrations was narrower at high slack water (>6 to <14 ìg l^{-1}). Maximum chl *a* concentrations have previously been shown to result from tidal and/or wind-induced resuspension of settled planktonic or epibenthic algal cells (Verity *et al.*, 1998). However, since our river CTD surveys were conducted on slack water, tidal effects were likely to have been minimal, compared to times of maximum current velocity. During high slack water, "patches" of water with relatively low chlorophyll *a* levels (5-7 μg l^{-1}) were found some distance upriver from the inlet mouth at mid-water or near bottom depths (Figure 8). In the North Channel, even lower concentrations occurred in surface waters near the mouth of the inlet. Peak chlorophyll *a* values (12-18 μg l^{-1}) were generally found at the bottom directly in the inlet mouth; the one exception was the low slack run in the North Channel, where the maximum occurred 10 km upriver at the bottom.

The time-series plot of daily mean surface and bottom chl *a* concentrations during June 1998 plankton sampling exhibited considerable variability over that 2-week period (Figure 9). Among repeated measurements made on each particular sampling day, chl *a* concentrations were higher and more variable at the bottom than in surface waters (see error bars, Figure 9). Similar temporal patterns were noted between the two channels, for both surface and bottom values. Differences between surface and bottom concentrations were greater in the North Channel than in the South during the first half of the survey period, but they were smaller during the second half. Mean bottom/surface differences were greater during the 1998 cruises in Ossabaw Sound (4.7 and 5.8 μg l^{-1} greater at the bottom in the South and North Channels, respectively) than in 1994 North Edisto and 1997 South Channel samples (~2.5 μg l^{-1}).

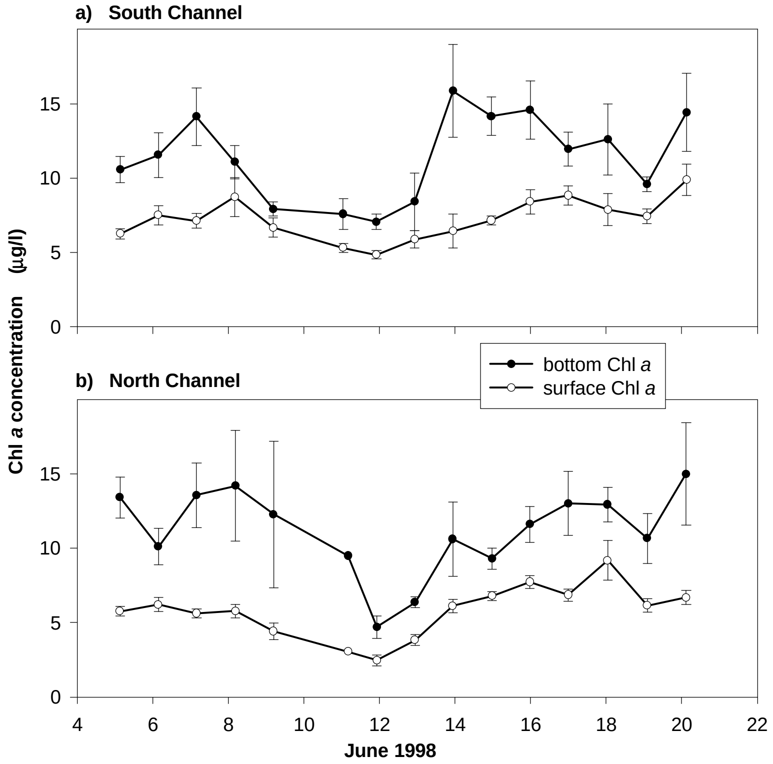


Figure 9. Mean daily chlorophyll *a* concentrations at the surface and bottom of the North a) and South b) Channels during nighttime flooding tides. Error bars represent the standard error of the mean.

Surface chl *a* concentrations exhibited significant positive correlations with upwelling favorable winds, while near-bottom chl *a* was significantly related to upwelling and offshore favorable winds (Table 5). Similar correlations were also observed in the North Edisto estuary and coastal waters (Verity *et al.*, 1998).

Table 5. Pearson correlation coefficients between chlorophyll *a* concentrations at the time of plankton collection and wind conditions 1, 6, and 24 hr earlier. Comparisons are made separately for surface and bottom waters, and are based on nighttime flood tide samples from all four sampling cruises combined. (Significance levels indicated by * = p 0.05; ** = p 0.01; *** = p 0.001; ns = not significant).

	alongshore wind stress (upwelling is positive)			cross-shelf wind stress (offshore is positive)		
	1 hr	6 hr	24 hr	1 hr	6 hr	24 hr
Surface water chlorophyll *a* concentration	0.118*	ns	0.200***	ns	ns	ns
bottom water chlorophyll *a* concentration	0.128**	ns	0.191***	ns	ns	0.118*

In both surface and near-bottom waters, chlorophyll *a* concentrations were significantly correlated with water temperature (positively) and salinity (negatively), when the four cruises were considered together (Table 6). Chl *a* was also correlated with current speed for near-bottom samples. For surface samples, however, correlations were only significant when each of the four cruises was considered individually, but not when the correlation was done on all samples combined. This is most likely due to the fact that the North Edisto River had relatively high currents but low chl *a*, while the opposite was true in the Ossabaw Sound system.

Table 6. Pearson correlation coefficients between chlorophyll *a* concentrations and water temperature, salinity and current velocity. Comparisons are made separately for surface and bottom waters, and are based on nighttime flood tide samples from all four sampling cruises combined. (Significance levels indicated by * = p 0.05; ** = p 0.01; *** = p 0.001; ns = not significant).

	surface temperature	surface salinity	current velocity
surface water chlorophyll *a* concentration	0.207 ***	-0.203 ***	ns
	bottom temperature	bottom salinity	current velocity
bottom water chlorophyll *a* concentration	0.134 **	-0.169 ***	0.171 ***

Plankton Distribution – the Acoustic Data

Several patterns were easily discernable in the backscattering record on all frequencies during June, 1997 in the South Channel. Typically, the high frequency (1.10, 1.85, and 3.00 MHz) scatterers had greatest densities along the bottom and rose proportionally higher into the water column with increasing current velocity. Maximum currents were inferred to be temporally situated between the times of high and low water, which are indicated by the sine curve of water height above the TAPS unit in the backscatter and biovolume plots (Figure 10; on the y-axis). The three higher frequencies indicated more highly concentrated scatterers during ebb than during flood currents, especially noticeable at the 3.00 MHz frequency. The cyclic vertical pattern was also influenced by the spring-neap cycle, with more dense scatterers covering more of the water column during high velocity spring tides of June 23 (Figure 10), when currents were much stronger than during June 13 neap tides (Figure 11). Night patterns tended to include stronger and more widely distributed low frequency scatterers throughout the water column than were seen during the day (Figure 10; example of one 24-hr period). During daylight, low frequency scatterers (265, 420, and 700 KHz) occurred in well-defined layers in mid-water and along the bottom. These layers were nearer the surface during maximum current and lower in the water column during slack water periods, often just above the higher frequency scatterers.

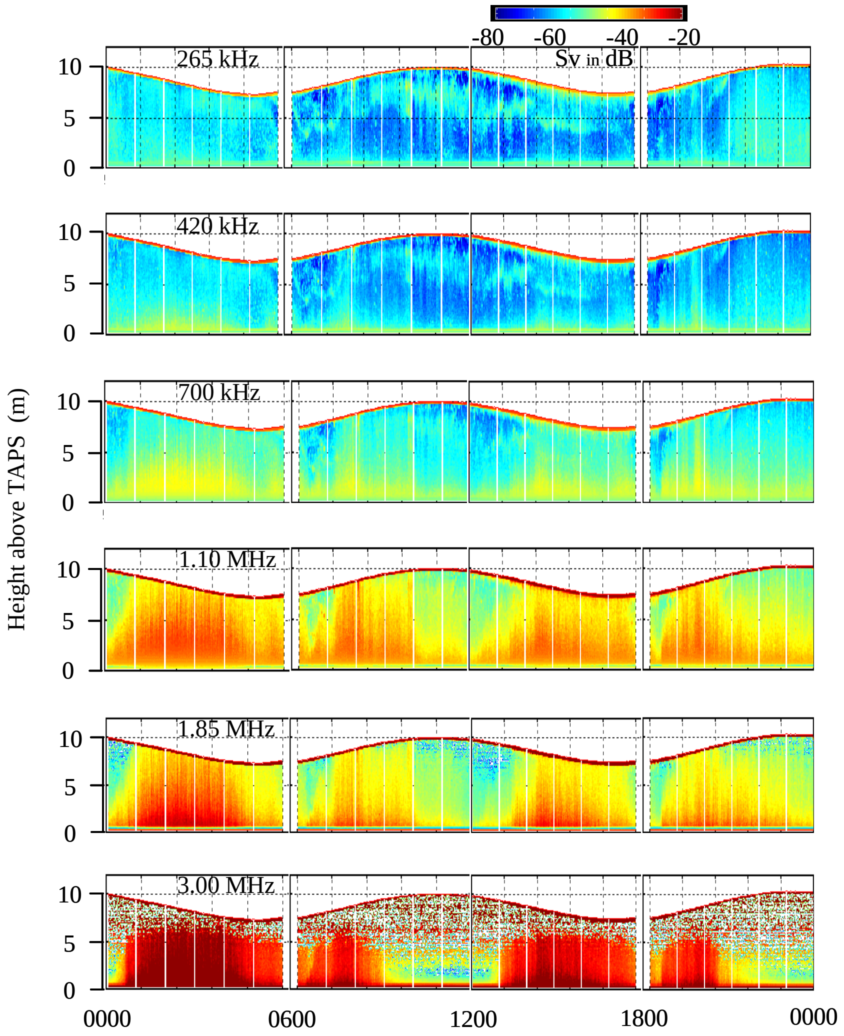


Figure 10. Acoustic backscatter intensity for six frequencies on spring tides of June 23, 1997 at station T97 in the South Channel. Color key is volume backscatter strength (dB) from low (dark blue) to high (bright red).

Patterns in the distribution of plankton, as estimated from biovolume calculations, concurred with patterns in backscatter and indicated that small plankton or particles (< 0.32 mm ESR) occurred higher in the water and in greater densities during maximum currents than during minimal currents or slack water (Figure 12; example of one 24-hr period). During spring tide conditions, the density of small plankton/particles was noticeably greater on flood than on ebb currents. The 0.79-mm ESR plankton was found in two distinct bands, one along the bottom that, to a lesser extent, reflected the pattern of the small sizes (< 0.32 mm ESR). The second band of particles was higher in the water column and above, but typically not within, the aggregations of small particles. During the spring tide, the band of 0.79-mm ESR plankton high in the water column was of greater density and nearer the surface than during the neap tide, especially during flood tides. Typically, the large (1.99-5.0 mm ESR) plankton was more widely distributed throughout the water column and in lower densities than the 0.79 mm plankton, especially during the day. Overall, most particles in the South Channel were small (< 0.32 mm ESR), with lower densities of the 0.79 and 1.99 mm ESR plankton.

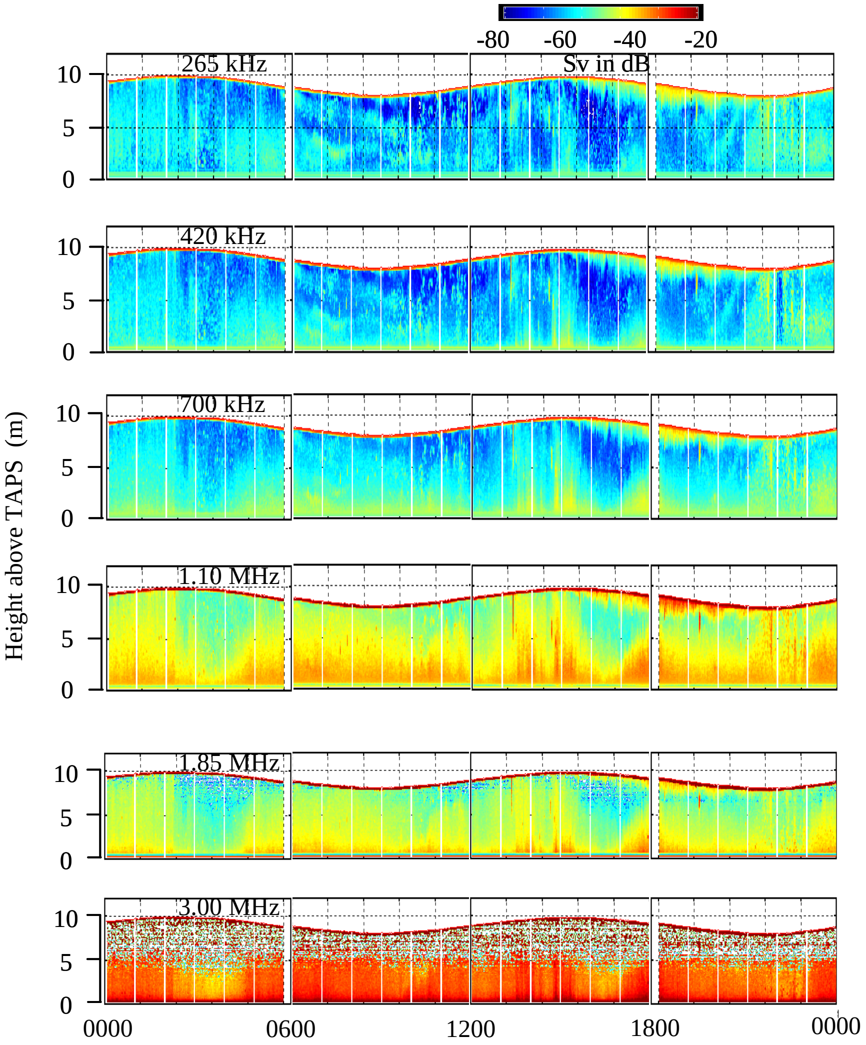


Figure 11. Acoustic backscatter intensity for six frequencies on neap tides of June 13, 1997 at station T_{97} in the South Channel. Color key is volume backscatter strength (dB) from low (dark blue) to high (bright red).

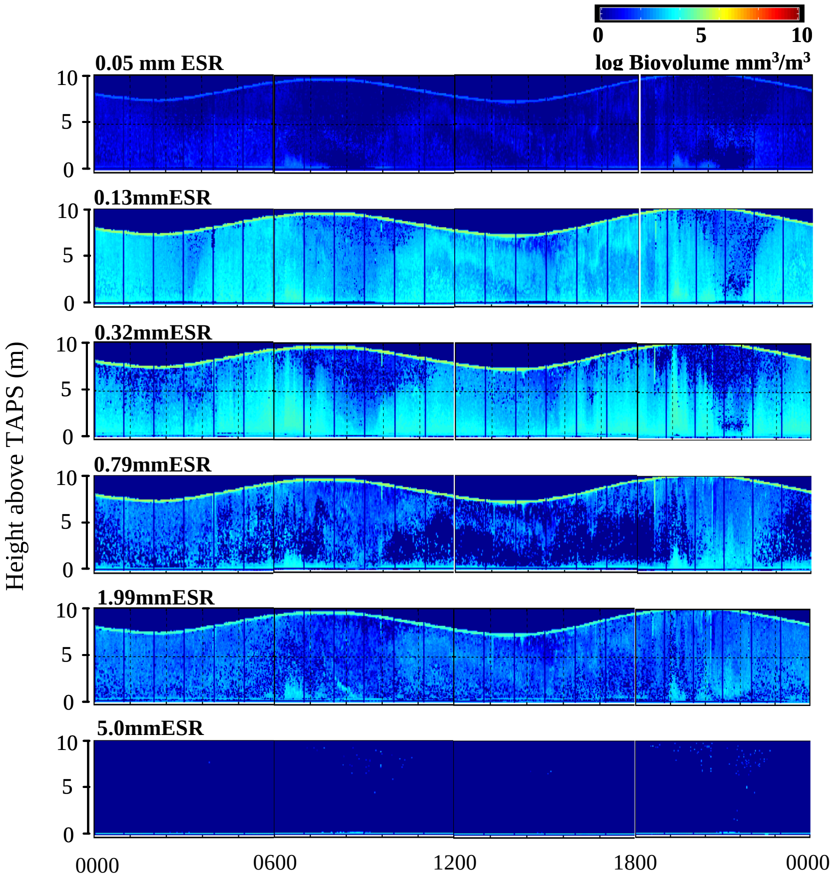
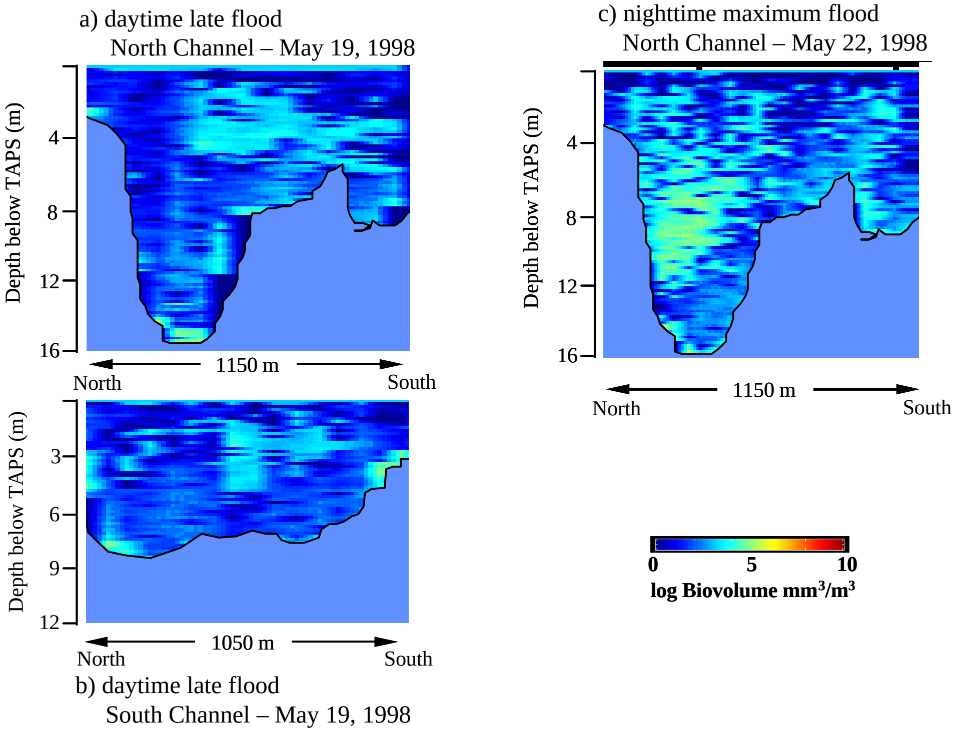


Figure 12. Biovolume estimates for six particle size classes (Equivalent Spherical Radius) on June 19, 1997 at station T97 in the South Channel. Color key is in a logarithmic scale of density.

The vertical distributions of 0.79-mm ESR plankton (closest to postlarval shrimp size) across each channel in May 1998 exhibited several patterns. In the day, scatterers were typically clumped in discrete layers within the water column, aggregated neither near the surface nor the bottom (Figure 13 a&b). During the nights, both channels generally had more scatterers that were more widely distributed throughout the water column (vertically and horizontally) than during daylight hours. The 0.79-mm ESR scatterers appeared more frequently and in higher concentrations in deeper waters of both channels early in the flood tidal cycle and higher in the water column late in the flood tidal cycle. The nighttime transects on 22 May, especially mid- to late tides, had higher densities of scatterers and larger patches of 0.79-mm ESR scatterers (Figure 13 c) than during similar tidal conditions on other nights (not shown). The one exception was a



a) daytime late flood North Channel – May 19, 1998

b) daytime late flood South Channel – May 19, 1998

c) nighttime maximum flood North Channel – May 22, 1998

Figure 13. Biovolume estimates for the 0.79 mm ESR size class across the North Channel (a & c) and South Channel (b) under different tidal and diel conditions. Color key is in a logarithmic scale of density.

very large patch of plankton near slack water following a daytime flood tide in the North Channel on 28 May. In the North Channel, densities of the 0.79-mm ESR scatterers were greater in the deep part of the channel on early flood tides than in shallow near-shore waters. Later in the flood tide, the densest patches occurred higher in the water column and toward the shoal on the southern margin of the channel (not shown). The horizontal shift in distribution over the tidal progression was much less distinct in the South Channel, but the general pattern in depth distribution, from deep to shallow locations later in the flood phase, appeared to be similar (not shown). Although descriptions of temporal and spatial patterns from multi-frequency acoustic data were inferred to be closely related to water velocities associated with tidal currents, inconsistencies in the patterns suggest that the plankton distributions also respond to other factors. Also, large patches of 0.79 mm ESR plankton form during each tidal cycle in mid-water, well away from both the surface and the bottom.

Comparison of Postlarval Lengths

Postlarvae of *L. setiferus* collected in the South Channel in 1998 were significantly longer than those collected the previous year at the same location ($\bar{c}$ = 6.61 vs. 5.96 mm; Kruskal-Wallis χ^2=4200, p<0.001) (Figure 14a&b). During 1998, postlarvae collected in the South Channel were also significantly longer than those from the North Channel ($\bar{c}$ = 6.61 vs. 6.47 mm; Kruskal-

Wallis χ^2=43,349, p<0.001) (Figure 14b&c). Although these differences in mean length may be statistically significant, their magnitude is not large (0.6 and 0.15 mm, respectively), and that significance may result from the large number of postlarvae measured. However, comparisons of length-frequency distributions of postlarvae 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 (Figure 14b&c).

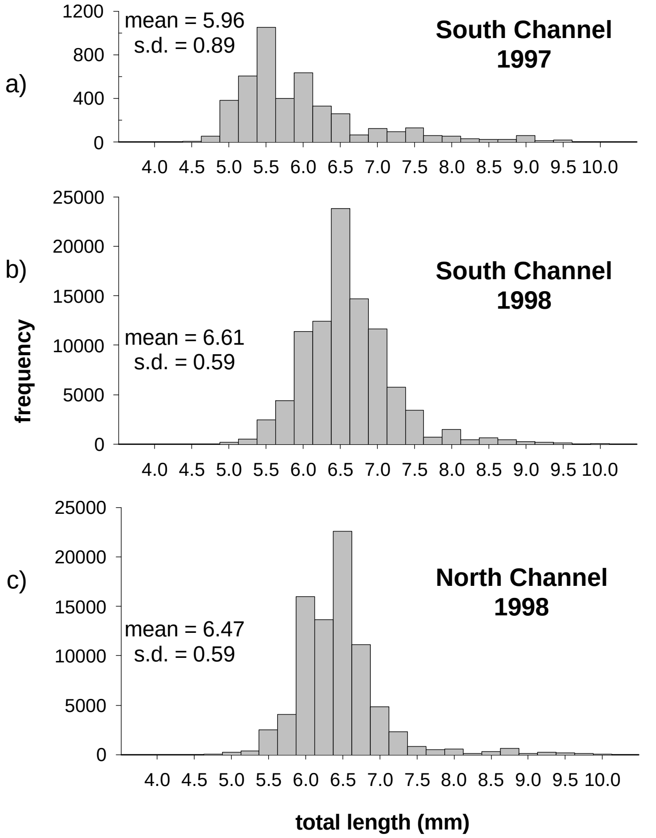


Figure 14. Length-frequencies of *L. setiferus* postlarvae collected in 1997 and 1998 in the South and North Channels of Ossabaw Sound.

Temporal changes in postlarval length were observed in both rivers (Figure 15). In 1997, the daily mean length of postlarvae in the South Channel ranged from 5.60 mm (June 21) to 6.35 (June 14), with no apparent overall temporal trend (Figure 15a). 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 non-significant (r^2=0.11, p=0.20). During 1998, postlarval lengths in the South Channel were less variable than the previous year, ranging from a minimum of 6.30 (June 14) to a peak of 6.79 (June 16), with no significant temporal trend observed (r^2<0.01, p=0.96). The lengths of postlarvae collected in the North Channel in 1998 varied more widely than those in the South (Figure 15b). 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 postlarval length increased significantly over the 14-d period (r^2=0.46, p<0.001).

Temporal Variation in Postlarval Density

Average densities of postlarvae during the 1998 sampling cruise in the South Channel ($\bar{c}$ = 299/100 m^3) and North Channel ($\bar{c}$ = 234/100 m^3) were much higher than previous studies during June 1997 in the South Channel ($\bar{c}$ = 13/100 m^3) or during June 1994 in the North Edisto River ($\bar{c}$ = 24/100 m^3) (Table 7). Densities of postlarvae collected in surface nets on nighttime flooding tides were considerably higher in the South Channel than in the North from the first sampling night on June 5, 1998 through June 15 (Figure 16). While postlarvae were abundant in the 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.

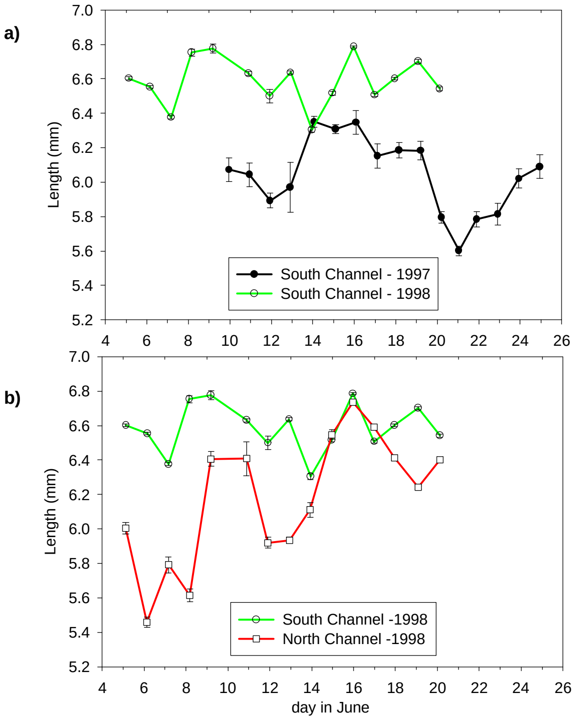


Figure 15. Daily mean length of *L. setiferus* postlarvae collected in 1997 and 1998 in the South and North Channels of Ossabaw Sound.

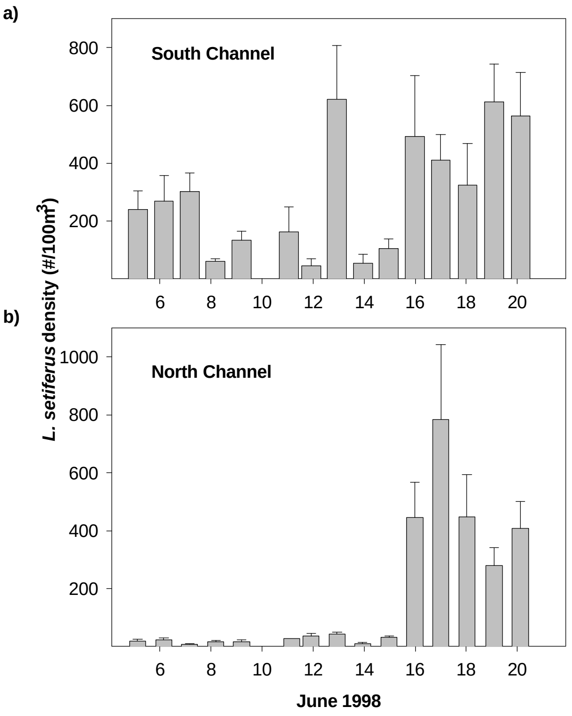


Figure 16. Daily mean density of *L. setiferus* postlarvae on nighttime flood tides in the South Channel (a) and North Channel (b) during 1998 sampling. Error bars represent the standard error.

Table 7. Comparison of *Litopenaeus setiferus* postlarval densities on nightime flood tides during the four sampling periods.

	North Edisto River 1994	South Channel 1997	South Channel 1998	North Channel 1998
Litopenaeus setiferus density (no./100 m^3)				
mean density (standard error)	24.1 (2.6)	12.7 (1.3)	299 (30.6)	234 (39.8)
minimum - maximum densities	0 – 156	0.4 – 78.6	6.0 – 2010	1.9 – 3430
number of samples	141	128	123	114

Depth Distribution of Postlarvae

Hourly plankton tows from 1998 intensive-phase sampling showed considerable differences in postlarval abundance in surface and bottom waters of the two Ossabaw Sound channels under various combinations of tidal, diel, and lunar conditions (Figure 17). Overall, postlarval densities were much higher during neap tides (Figure 17b&d) than during spring tides (a&c). Peak ingress (i.e. transport on flood tides) occurred in surface waters when the tide was flooding during the night (Figure 17b,c,&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.

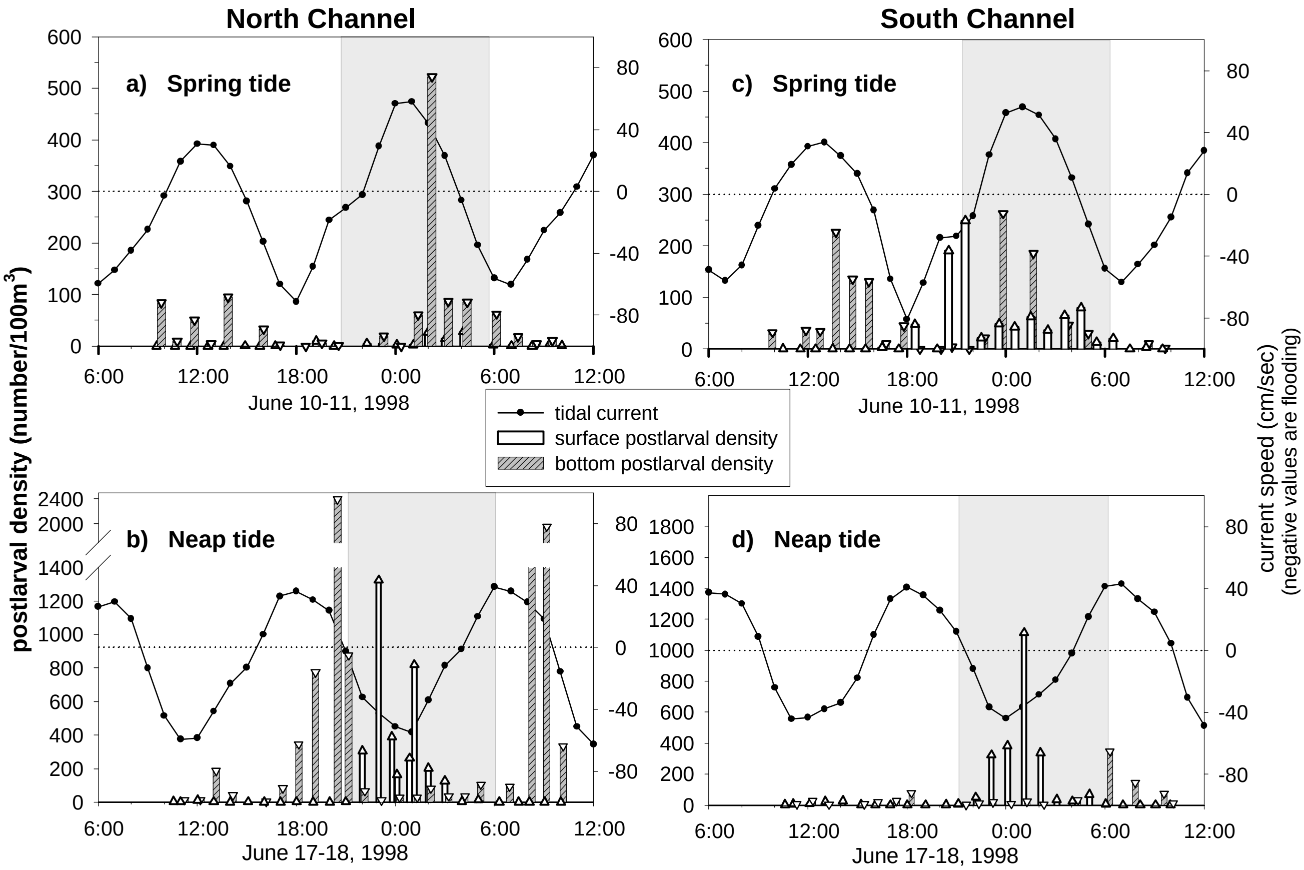


Figure 17. Comparison of postlarval *L. setiferus* densities in surface and bottom plankton tows during spring and neap tide intensive phase sampling in both channels of Ossabaw Sound in June 1998. The period of darkness (shaded portion of graph) and current velocities are superimposed on the timeline. Flood tides are those with negative values; ebbing tides are positive. Note differences among the graphs in scale of the left vertical axes.

Data from the 1997 and 1998 intensive-phase cruises were combined in order to statistically evaluate the vertical position of postlarvae relative to diel and tidal periodicity. Both the light phase and the tidal current phase influenced postlarval 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 ($\bar{c}$ = 284 versus 24/100 m^3), but during daylight this comparison was reversed ($\bar{c}$ = 4 versus 33/100 m^3) (Figure 18). During the ebbing tide, mean postlarval densities were greater near the bottom (99-199/100 m^3) than at the surface (0.1-30/100 m^3), regardless of the time of day. A three-way ANOVA (Table 8) on ranked data indicated that depth (surface/bottom) and diel phase (day/night) were both significant main effects for postlarval density ($p<0.001$), although the significant interaction terms depth*diel and depth*tide illustrate the differential influence of light phase and tidal phase on the depth distribution of *L. setiferus* postlarvae.

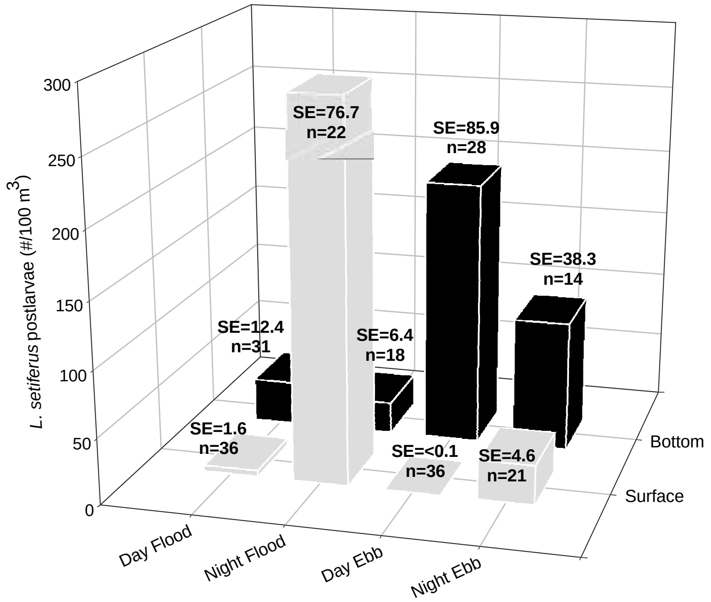


Figure 18. Mean density of *L. setiferus* postlarvae collected in the South and North Channels (combined) during "intensive" sampling in 1997 and 1998. The bar heights represents the means for each combination of depth, light phase, and tidal phase; standard error and number of samples are shown.

Table 8. Three-way analysis of variance on ranked values of *L. setiferus* postlarval density in samples collected during intensive phase sampling in the South Channel and North Channel in 1997 and 1998 (n=206). Factors compared are depth (surface, bottom), diel phase (day, night), and tidal phase (flood, ebb).

source	type III sum of squares	df	mean square	F	sig.
corrected model	398,203.919	7	56,886.274	35.359	<0.001
intercept	2,368,823.768	1	2,368823.768	1,472.379	<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			

Key Influences on Postlarval Density

Step-wise regression analyses were conducted on data from surface net tows on nighttime flooding tides over the neap to spring tidal cycles in June 1994 (North Edisto River), June 1997 (South Channel) and June 1998 (South and North Channels) in order to evaluate physical factors that may influence ingress of postlarval white shrimp. The six predictive variables that were used in the model were surface temperature, surface salinity, surface chlorophyll *a* concentration, mean tidal currents, cross-shelf and alongshore wind stress (6-hr lag).

After removal of non-significant variables, alongshore wind stress, surface temperature, and cross-shelf wind stress explained 77% of the variance in the North Edisto model, and these variables were significantly related to log-transformed postlarval density (Table 9). When the model was run on the combined cruises in the Ossabaw Sound system, the predictors of surface temperature, surface chlorophyll *a* concentration, mean tidal currents, and alongshore wind stress explained 54 % of the variance in the regression model, and all four were significantly related to log-transformed postlarval density.

Table 9. Results of stepwise multiple regression models for the North Edisto cruise and for the combined cruises in the Ossabaw Sound system. The physical variables listed were determined to significantly affect log-transformed postlarval abundance, using a forward selection procedure with p 0.05 to add and p 0.10 to remove.

model variables	**partial R^2**	**cumulative (model) R^2**	**df**	**F**	***p***
North Edisto River					
alongshore wind stress $_{\text{(6hr lag)}}$	0.627	0.627	regression: 1 residual: 110	185.24	<0.001
alongshore wind stress $_{\text{(6hr lag)}}$, surface temperature	0.085	0.712	regression: 2 residual: 109	135.01	<0.001
alongshore wind stress $_{\text{(6hr lag)}}$, surface temperature, cross-shelf wind stress $_{\text{(6hr lag)}}$	0.059	0.771	regression: 3 residual: 108	121.44	<0.001
Ossabaw Sound system (1997 and 1998)					
surface temperature	0.493	0.493	regression: 1 residual: 335	325.56	<0.001
surface temperature, surface Chl *a*	0.033	0.526	regression: 2 residual: 334	185.27	<0.001
surface temperature, surface Chl *a*, mean tide	0.012	0.538	regression: 3 residual: 333	129.02	<0.001
surface temperature, surface Chl *a*, mean tide, alongshore wind stress $_{\text{(6hr lag)}}$	0.006	0.544	regression: 4 residual: 332	99.04	<0.001

Water Temperature

High densities of white shrimp postlarvae were associated with a critical minimum surface temperature of ~27°C during all four cruises (Figure 19). Although temperatures ranged from 22-30°C during the study, nearly all (>96.2%) of the postlarvae were collected at temperatures ≥ 27°C. Mean density was significantly greater at temperatures ≥27°C ($\bar{c} = 146.7/100\ \text{m}^3$) than at lower temperatures ($\bar{c} = 18.4/100\ \text{m}^3$) (t-test for unequal variances, df=574.3, p <0.0001). There was also a highly significant (p<0.001) positive correlation between postlarval density and surface water temperature in the combined data from Ossabaw Sound and the North Edisto River (Figure 20).

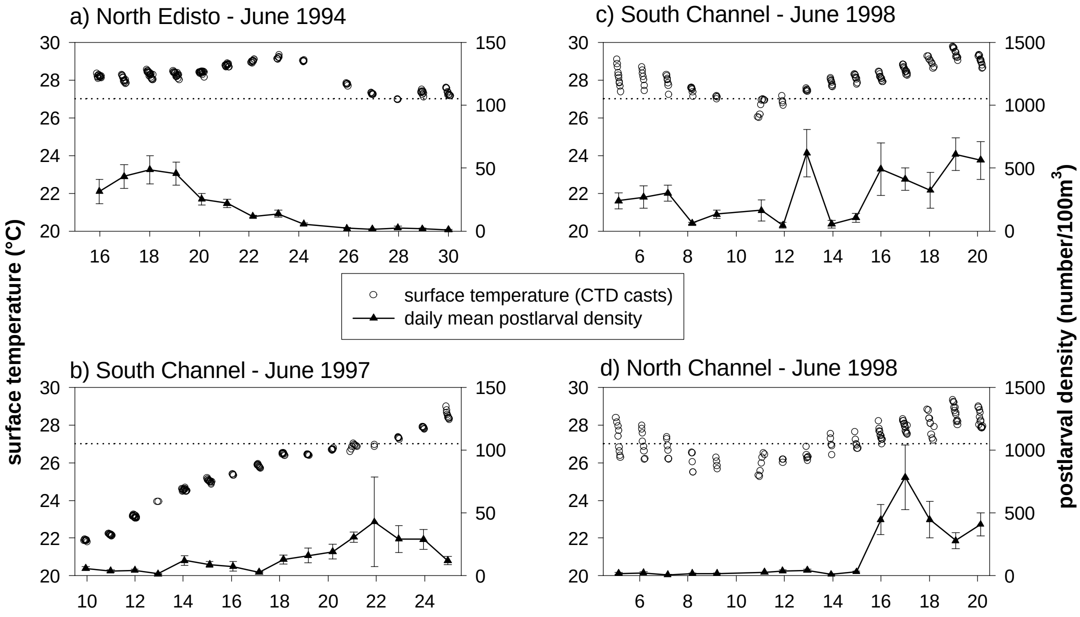


Figure 19. Daily mean *L. setiferus* postlarval densities compared with surface water temperatures during each of the four extensive-phase plankton cruises. Error bars show standard error; note the difference in scale of the right vertical axes of a & b versus c & d.

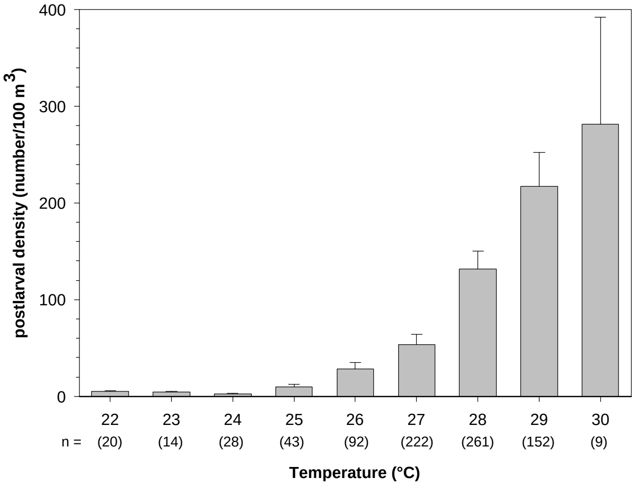


Figure 20. Mean density of *L. setiferus* postlarvae versus surface temperature. Means are based on densities in all tows collected during the 1994, 1997 and 1998 cruises, plotted for each 1°C increment. Standard error bars are shown, and n is given in parentheses for each increment.

Predominant Nighttime Tides

Mean tidal currents, which were defined as the daily average of nightime hourly current measurements, varied according to lunar period. In general, during new- or full-moon spring tides in June, tidal currents ebb in South Carolina and Georgia estuaries all night long, while on quarter-moon neap tides in June the neap tides flood from sunset to sunrise (Figure 21). Densities of white shrimp postlarvae were significantly greater when nighttime tides were predominantly flooding ($\bar{c}$ = 182.8/100 m^3) than when ebb tides were dominant at night ($\bar{c}$ = 48.0/100 m^3) (t-test for unequal variances, df=474.1, p<0.001).

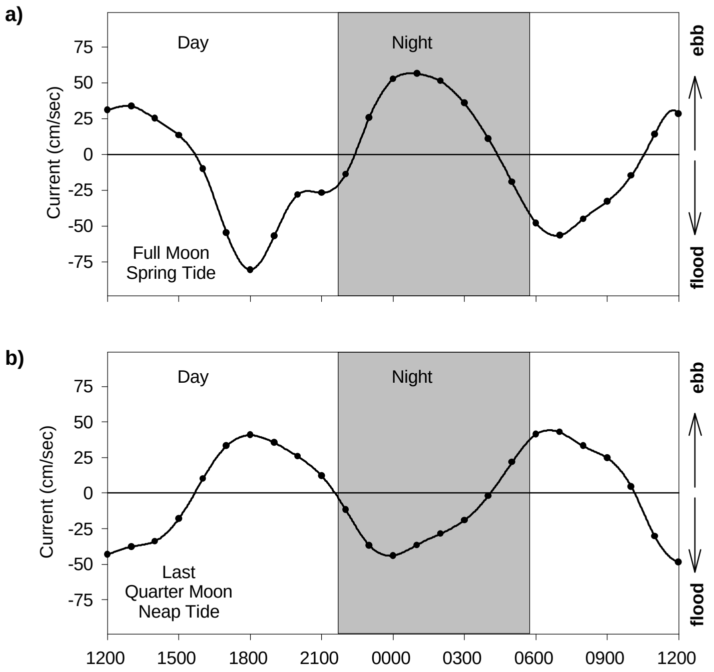


Figure 21. Schematic representation of the relationship between tidal currents and darkness during a) spring and b) neap tides in South Carolina and Georgia estuaries during June (based on current data collected in the South Channel of Ossabaw Sound, June 10-11 and June 17-18, 1998).

Windstress

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 (sub-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 through the inlet to the estuary. The flux strength is related to the cross-sectional area of the inlet throat and the tidal prism through the equation of continuity:

$$uA_z = A_{xy}\frac{\partial h}{\partial t} \qquad \text{[Equation 2]}$$

where u is channel velocity, A_z is the cross-sectional area through the inlet, A_{xy} is the horizontal surface area of the estuary's water surface, and $\frac{\partial h}{\partial t}$ is the rate of change of water level. Thus, the flux through the inlet is proportional to the ratio of the mean horizontal water surface area of the estuary to the mean cross-sectional area of the inlet. Both A_z and A_{xy} are functions of time, and the latter can vary greatly during a tidal cycle when water level typically changes by 2-3 m in Georgia and South Carolina estuaries. However, subtidal fluctuations are typically 0.2-0.3 m (an order of magnitude less).

In our studies, alongshore and cross-shelf windstress were correlated with larval abundance; however, the systems varied in their response to this factor. During the initial studies conducted in North Edisto Inlet (1994), the highest abundances of postlarvae corresponded with downwelling windstress at lag times of 1, 6 and 24 h (Table 10). During June 1997, larval abundance in the South Channel was significantly correlated with upwelling windstress at all three lag times. In the following year (1998), there were no significant associations of wind and postlarvae for the South Channel, but in the North Channel, postlarvae were significantly correlated (*p* 0.001) with onshore windstress at two of the three lag times.

Table 10. Pearson correlation coefficients between wind stress and log-transformed postlarval *L. setiferus* density in surface samples collected on nighttime flooding tides. Coefficients are shown for wind conditions 1, 6 and 24 h prior to plankton tows during the four different cruises. (Significance levels indicated by * = *p* 0.05; ** = *p* 0.01; *** = *p* 0.001; ns = not significant).

	cross-shelf wind stress (+ is offshore)			**alongshore wind stress** (+ is upwelling)		
Cruise	1 h	6 h	24 h	1 h	6 h	24 h
North Edisto River 1994	ns	-0.323 ***	-0.336 ***	-0.776 ***	-0.792 ***	-0.782 ***
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 *

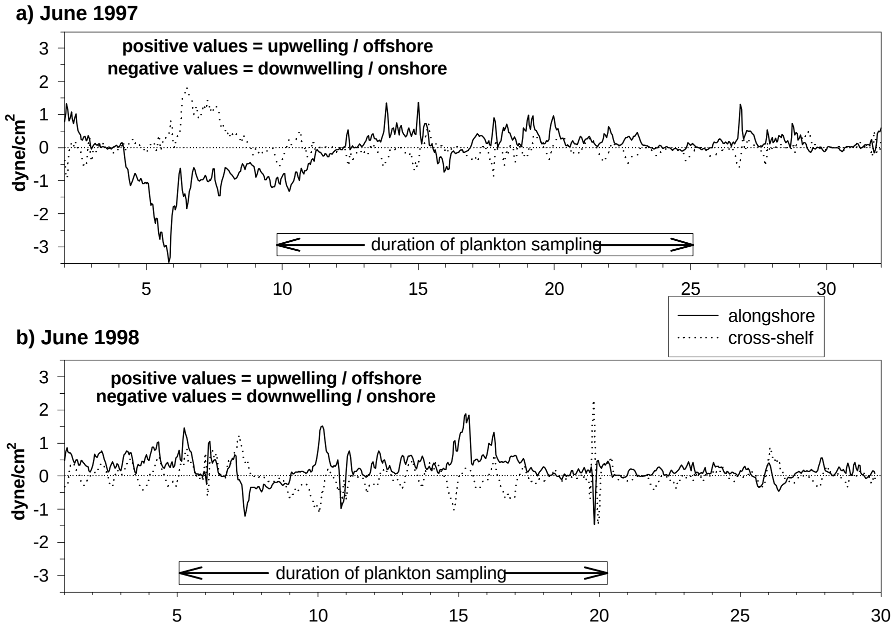


Figure 22. Alongshore and cross-shelf wind stress (3 hlp filtered) based on wind measurements at Gray's Reef during plankton sampling in the Ossabaw Sound system in 1997 and 1998.

The wind regime exerted different forcing conditions on the study area during 1997 and 1998 fieldwork (Figure 22). In 1997, there was an episode of strong downwelling-favorable wind stress with an onshore component in the first part of the period (until 10

June). 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 postlarvae 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.

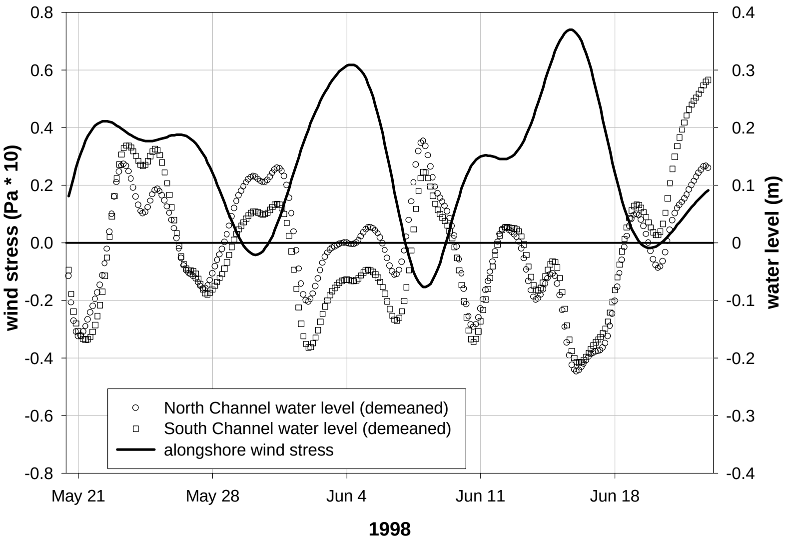


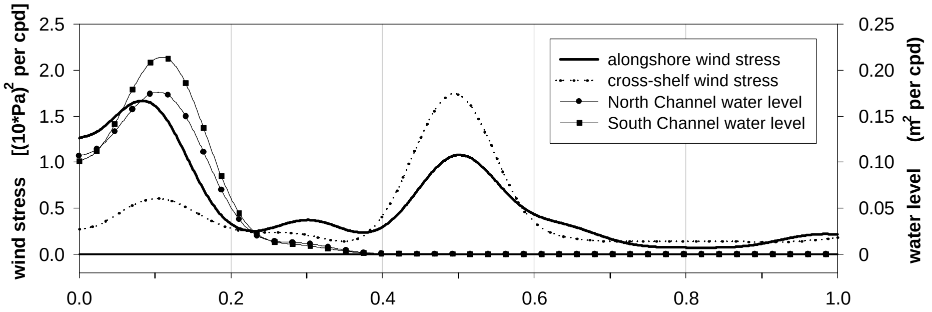
Figure 23. Comparison between fluctuations in alongshore wind stress and demeaned water level in the North and South Channels during 1998. The coordinate system for wind stress has been rotated -40 degrees, and tidal fluctuations in water level have been removed with a 40-hlp filter.

The rotated alongshore wind-stress component was compared to water level fluctuations in the North and South Channels of Ossabaw Sound (Figure 23). Fluctuations in water level are directly related to $\frac{\partial h}{\partial t}$ in Equation 2. For example, beginning on 22 May, water level in both channels increased from -0.15 m to +0.15 m in less than two days, signifying an import of offshore water into the system. Similar import events occurred on 29 May, 7 June and 12 June, and another prolonged import event began on 16 June and lasted, with only a brief interruption, until 22 June. Following the import event of 22 May, there was an export of water from Ossabaw Sound to the ocean caused by a fall in water level from +0.15 m to -0.10 m, centered on 26 May. Similar export events occurred on 1 June, 10 June and 15 June.

A clear inverse relationship between fluctuations in alongshore wind stress and water depth is illustrated in Figure 23. For example, the relaxation of the strong northward stress on 7 June caused an increase in mean water level to about +0.15 m. The strong northward stress on 15 June 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 through Equation 2. However, the association between water import/export and wind is not entirely consistent. For example, when wind was basically northward from 21-26 May, 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 (Figure 23). 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 (Figure 24).

a) power spectra



b) coherence

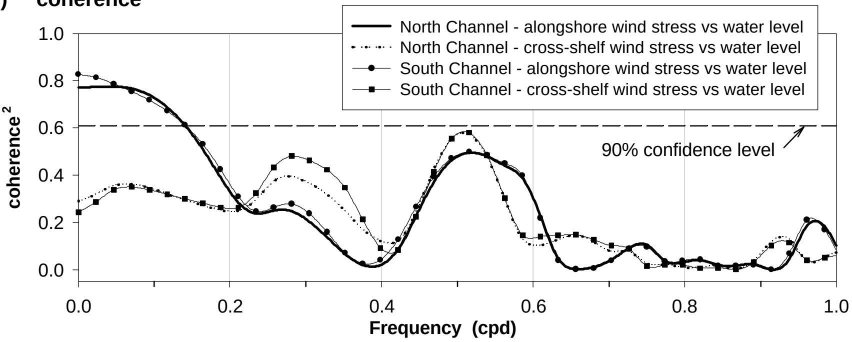


Figure 24. Cospectra between wind stress and water level in the North and South Channels during 1998 sampling. The coordinate system for wind stress has been rotated -40 degrees for plots of (a) the power spectra and (b) coherence. Frequency is measured in cycles per day (cpd). Cospectra were calculated by means of a fast fourier transform of the detrended data in Figure 23.

The alongshelf stress component has a large peak at a period of about 10 days and a smaller peak at 2 days (Figure 24a). The seabreeze component barely shows up in this component because the 40-hlp 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 (Figure 24a), 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 (Figure 24b) 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 (Figure 24a).

DISCUSSION

Plankton Acoustics

Postlarval white shrimp that entered the South Channel during June 1997 became some small or large part of the plankton assemblage, which had distinct and predictable distributions. Postlarvae near the bottom during daylight or ebb currents would have been exposed to extremely dense concentrations of resuspended fine materials or phytoplankton (<0.40 mm ESR) during the high currents of either flood or ebb tides. Fine materials were always most dense nearest the bottom and became more dense in concentration at levels higher in the water column with increased water velocity. The cyclic patterns in vertical distributions in the South Channel were similar to those found in the North Edisto Inlet (Barans *et al*., 1997), but reflected the lower water velocities in the South Channel. Palmer and Gust (1985) found tidal currents of ~0.6 m/s resuspended benthic meiofauna (nematodes, copepods, foraminiferans, bivalves, etc.), with more being resuspended during spring than neap tides. Currents in the South Channel exceeded this velocity and could easily cause resuspension of fine materials.

During the daytime, there were two distribution patterns of the 0.79 mm ESR size class (postlarval shrimp and other similar sized taxa), one along the bottom mixed with and one above the small 0.32 mm ESR particles, which probably represent several different taxa. Postlarvae probably feed on several species included within these smaller particles and may be distributed in the water column just above the greatest concentrations of the small plankton. These closely related spatial distributions were noted in the North Edisto Inlet (Stender *et al*., 2000). Postlarvae that rise off the bottom during nighttime would be within a water column full of similar sized plankton (0.79 mm ESR) for the duration of darkness. Many planktonic organisms are more widely distributed in the water column at night than during the day for varying reasons, including predator avoidance (Lampert, 1993). The wide distribution of 0.79-mm ESR size class throughout the water column at night and the dense fluctuating layers of plankton during the daytime were similar to patterns described for the North Edisto Inlet (Barans *et al*., 1997).

If many of the postlarval shrimp do not fully settle to the bottom during daytime or nighttime flood tides, they may become part of dense patches of plankton in mid-water that appear to follow distinct patterns. Our acoustic findings in both channels during 1998 indicated that many 0.79-mm ESR plankton change from light concentrations near bottom to mid-water or near surface patchy concentrations as the tide stage progresses from early to late flood. This pattern of sequential increases in height off the bottom may be consistent with selective tidal transport reported for white shrimp postlarvae (Wenner *et al*., 1998) and other plankton species. Near bottom positions of plankton early in the flood tide could represent some residual of near bottom positions during the recently ended ebb tide cycle. Also, the increase in height of dense plankton patches off the bottom across both inlets was somewhat consistent with the relationship between vertical height and water velocity that was observed in the stationary temporal data set of 1997. The exception was that large plankton patches remained high in the water column during decreasing current velocities of late tides in the across channel data sets. A more comprehensive temporal and spatial data set focused on a single channel will be necessary to determine any relationship between patch height and position across the inlet with cyclic factors.

The complex vertical and horizontal distributions of postlarval sized plankton (0.79 mm ESR) suggest that the behavior of inlet plankton, probably many species acting as a group, form dense patches with temporal patterns, which were not always consistent over the brief time period of our study. Very often large patches of plankton formed in the estuarine mid-water column, which would not have been sampled with either the surface or the bottom collection nets. These patches may or may not have contained significant densities of postlarval white shrimp moving between their believed surface and bottom positions. This preliminary acoustical research indicates that distributional patterns of plankton can be complex, and that further research is necessary to elucidate the distributional patterns of individual taxa within the ingressing assemblages.

Key Influences on Postlarval Density

Three key factors greatly influenced the densities of postlarval white shrimp in time and space within two inlets on the Atlantic coast of the southeastern US. During the June periods of our study, a sequence of environmental conditions led to the ingress of postlarval white shrimp. Although some combination of numerous environmental factors must undoubtedly contribute to conditions that stimulate the appropriate transport behaviors of postlarval shrimp each spring, we identified only three key factors during this study. The first 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, postlarval 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 have identified, more or less, coincided each spring when the postlarvae were offshore in position to be transported into the inlet. The relationship between postlarval densities and each of the three key factors is discussed below.

Temperature

The relationship between water temperature and the ingress of postlarval penaeids has been noted for both brown and white shrimp along the Gulf and southeast coasts. The arrival of brown shrimp in Gulf coast estuaries was found to occur at sustained temperatures > 20°C in Louisiana (St. Amant *et al*., 1963) and between 18-22°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 postlarval brown shrimp recruitment to estuaries of the northern Gulf of Mexico. They suggested that cold fronts drove chilled lower salinity water from the shallow estuaries into the coastal zone. Postlarvae 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, postlarvae would move up in the water column in response to onshore movement of warmer more saline waters. This model suggests a complex behavioral response of brown 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 postlarval transport of white shrimp into estuaries of the southeastern US. For white shrimp, the increase in bottom water temperature in spring triggers spawning (Muncy, 1984). At an inlet in South Carolina, postlarval ingress occurred only when temperatures exceeded 20°C, with peak ingress from 25-30°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°C. Thermally mediated behavior could also contribute to “pooling” of white shrimp postlarvae 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 *F. 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 behavior in white shrimp, *L. setifierus* did become less active and rested on the bottom (Aldrich *et al*., 1968). The difference in water temperatures at the time when brown and white shrimp postlarvae 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 19.3-24.7°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 postlarvae 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 postlarval 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 postlarval supply to southeastern estuaries, perhaps by mediating the behavior of postlarvae 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 it's postlarvae.

Tidal Phase

Several studies have provided evidence that penaeid postlarvae 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 LeReste, 1981; Mair *et al*., 1982; Forbes and Benfield, 1986). Among penaeid shrimp, Hughes (1972) found that vertical movement of postlarval pink shrimp, *F. 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 postlarval 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 postlarvae, whose position in the water column strongly affects their onshore transport (Blanton *et al*., 1995).

Postlarval 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). Postlarvae could also move laterally during ebb to shallow areas where currents are weaker, thus diminishing their seaward transport. In the semi-diurnal tidal currents of many southeastern 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 postlarval density and the tidal component of currents. Rothlisberg *et al*. (1995) proposed that *P. plebejus* 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* postlarvae would move downward in the water column to a point where transport is minimal, or drop onto the substrate itself. Postlarval *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 with flood conditions are maximized during spring tides at some localities on the opposite side of the Atlantic Ocean.

The highest densities of postlarve observed during our studies occurred in both channels of Ossabaw Sound during the 5-day period centered on the neap tide of 17 June 1998. From 17-19 June, 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. Since 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 postlarvae.

Wind component

Although much of the tidal energy available to assist in shoreward movement of postlarvae is periodic, and therefore predictable, the additional transport of oceanic water produced by wind stress is largely stochastic. Theoretical studies (eg. 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. By contrast, the exchange driven by the cross-shelf component is negligible. 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 postlarval ingress data (Figure 16) with conditions favorable for landward subtidal transport (Figure 23) supports this hypothesis. After 12 June, 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 (17-19 June), maximum postlarval densities occurred in both channels (Figure 16). This peak coincided with the time that water level in the system *increased* by more than 0.2 m (Figure 23), 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 postlarvae might be entrained in the flood tidal flow.

Our data are consistent with the hypothesis that the direction of subtidal currents (into or out of the system) becomes a significant factor when influx coincides with the time of favorable temperature conditions and nighttime flood tides. The normal ingress period for white shrimp lasts for 4-6 weeks. Since 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 postlarvae for 2-week intervals in three different years, there was only one such coincidence.

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