SPATIAL AND TEMPORAL DISTRIBUTION OF DECAPOD LARVAE IN THE SATILLA RIVER ESTUARY, GA

by

JENNIE ELIZABETH SEAY

(Under the Direction of Merryl Alber)

ABSTRACT

The distributions of larvae of two decapod crustaceans were studied during a two-year, multi-seasonal investigation of the Satilla River estuary. The physical parameters of the estuary were investigated and related to the biological aspects of the larvae to determine the distribution and transport of planktonic larvae within the system. Measured parameters included vertical profiles of salinity, temperature, and density taken with a Conductivity-Temperature-Depth recorder, depth-averaged velocities using an Acoustic Doppler Current Profiler, assessments of the flow field with Global Positioning System tracked drifters, and collections of plankton from within the estuary. Larval densities of *Uca* spp. varied based on season, tide, and depth and the developmental stages of larvae were vertically stratified within the water column to facilitate their expulsion from or reinvasion to the estuary. *Petrolisthes armatus* larval densities varied based on year, season, and location and were located within the water column to aid in their retention.

INDEX WORDS: Satilla River, Larval distribution, *Uca* spp., *Petrolisthes armatus*

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DEDICATION

I would like to dedicate this thesis to all those who have helped me achieve so much over the years. To those who have inspired me to fulfill my dreams, to those who have encouraged me to keep going, and to those who have comforted me along the way, I dedicate this work to you. I would especially like to say thank you to my friends and family who have always shown me such wonderful love and support.

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CHAPTER 1

INTRODUCTION

This study investigated the distribution and transport of two species of decapod crab larvae within the Satilla River estuarine system to better understand their life cycles and their relationship to the physical conditions of the estuary. The study focused on the larval distribution of the brachyuran crab, *Uca* spp., and the recently invasive anomuran crab, *Petrolisthes armatus* (Gibbes, 1855). In both cases, the physics of the flow field and the life cycle of the crab were used to explain the observed larval distribution and abundance patterns.

Crabs play a significant role in the ecology of the estuarine systems in which they live. They range in size from small pea crabs, *Pinnotheres ostreum* (Say, 1817), whose females measure 8-12 mm and live inside oyster shells to free-swimming blue crabs, *Callinectes sapidus* (Rathbun, 1896) measuring 130-140 mm (Van Den Avyle, 1984). Crabs are found in every habitat throughout the estuary and beyond; in marsh grasses, on hard substrates, in muddy flats, in the open water at the mouth of the estuary and on the continental shelf. Crabs are active at many different trophic levels, acting as prey, predators, and scavengers (Van Den Avyle, 1984, Scharf & Schlicht, 2000). *Uca* spp. are known to affect sediment biogeochemistry and nutrient regeneration by aiding in the bioturbation of the marsh and estuarine sediments (Grimes et al., 1989; Kostka et al., 2002, Gribsholt et al., 2003; McCraith et al., 2003).

This study investigated the similarities and differences in the life cycles and larval movements of decapod larvae and examined the physical mechanisms that affect their distribution in the estuaries of Georgia. Due to the economic importance of *Callinectes*

sapidus as a commercial fishery in Georgia, as well as the vast amount of previous *C. sapidus* research, this study also recorded any observations of blue crab larvae found within the Satilla River estuary. *C. sapidus* larvae are released by the females directly into the coastal ocean during an ebbing tide, resulting in larval development in the coastal ocean and reinvasion of the estuary as megalopae (Van Den Avyle, 1984). Consequently, few larvae were found in the Satilla River and its tributaries (Provenzano, 1983; Garvine et al., 1997; Epifanio & Garvine, 2001; Epifanio, 2003; Forward et al., 2003; Tilburg et al., 2005).

Fiddler Crabs

Crabs of the genus *Uca*, commonly known as fiddler crabs, live in the muddy and sandy banks marsh creeks, rivers and estuaries along the east coast of the United States from Maine to Florida (Grimes et al., 1989). Three *Uca* species are included in this study, *Uca minax* (LeConte, 1855), *Uca pugnax* (Smith, 1870) and *Uca pugilator* (Bosc, 1802), all of which inhabit Georgia's coast and spawn at the same time of year. Since detailed dissection and examination of morphological characteristics is required for identification of the larvae of the three *Uca* speciesbeyond the level of genus (Sandifer, 1975), they are collectively referred to as *Uca* spp. in this study. Although *Uca* are not commercially significant, they play a major role in the ecology of the estuarine environment. They influence the nutrient and energy flows through the environment by creating a network of burrows, feeding on the fine particles in the mud, and producing fecal pellets (Grimes et al., 1989; Kostka et al., 2002). In addition, *Uca* spp. are usually the most abundant larvae found in planktonic samples from inside the estuary and on the continental shelf, making them a useful indicator of typical crab larval dispersal and transport (Dittel & Epifanio,

1982; Queiroga & Blanton, 2005). Due to their abundance, research on *Uca* has been extensive along the east coast of the United States. However, few studies have been conducted in Georgia and most (e.g., Teal, 1958, Wolf et al., 1975) have focused on adult populations.

Porcelain Crab

Another crab that is now present along the coast of Georgia is the anomuran crab, *Petrolisthes armatus*, commonly known as the green porcelain crab. *P. armatus* is a non-indigenous species that first appeared in Georgia's coastal waters in 1994 and South Carolina's coastal waters in 1995 (Knott et al., 1999; Coen & McAlister, 2001). Since these initial sightings, it has established successful breeding populations in all of Georgia's major estuarine systems and is often the dominant crab, numbering thousands per square meter, on oyster reefs and hard substrates in shallow subtidal and intertidal waters along the coasts of both states (Knott et al., 1999; Hollebone, 2006). It is unclear what environmental conditions and transport mechanisms allowed the introduction and rapid establishment of the green porcelain crab in Georgia and South Carolina and the long-term effects of this new species on the marsh ecosystem are unknown. Examination of the distribution and transport of its larvae may provide insight into its life cycle and ultimately how it has been able to quickly become a dominant species in the southeast coastal region.

Life cycles of Decapod Crustaceans

Most decapod crustaceans are motile organisms that live on or close to the substrate. After mating, egg development occurs on the abdomen of the female crab. Once the eggs reach maturity they are released into the water and become part of the

plankton. There are typically two different larval types found in decapod crabs, the zoea and the megalopae. The zoea larvae grow by molting and undergo different stages until they reach the megalopal stage, which settles onto the substrate. These megalopae then molt again into juvenile crabs, which continue to grow by molting until they reach sexual maturity. The amount of time spent in the plankton by each larval stage varies between species and as a result of environmental conditions. Since the survival of planktonic larval stages helps to determine future population numbers, growth dynamics of juveniles, distribution ranges and demographics (Pechenik, 1999), it is important to examine the larval stages to gain a more in-depth understanding of the biology of these crabs.

The presence of planktonic larval stages in estuarine crabs has many advantages, as well as some disadvantages. Mass dispersal of newly-hatched planktonic larvae allows for the distribution of the species and the colonization of new habitats, and decreases predation threats and the probability of interbreeding leading to genetic problems within the species (Pechenik, 1999). The dispersal of offspring also decreases potential competition with the adult population and between the developing juveniles (Pechenik, 1999). Disadvantages of planktonic larval stages include the loss of many offspring, unfavorable advection to areas where they are unable to survive or from which they are unable to re-enter the estuary (Pechenik, 1999). Most planktonic larvae do not survive. In one of the most well studied crabs, the blue crab, surviving larvae average one in every million (Van Den Avyle, 1984).

Life cycle of *Uca* spp.

There are 15 species of fiddler crabs along the North American east coast; however *Uca pugnax*, *Uca pugilator* and *Uca minax* are the most abundant species in the southeast (Grimes et al., 1989). Post-settlement, the adult habitat of each species is largely determined by the composition and dampness of the substrate and the salinity of the water reaching that substrate (Teal, 1958; Capaldo, 1993). *U. minax* prefers muddy substrate and brackish water, while *U. pugnax* prefers a muddy substrate covered with vegetation, and *U. pugilator* lives in sandier substrate in the higher marsh and creek banks (Teal, 1958).

Male and female fiddler crabs differ slightly in size, averaging 23 and 18 mm wide, respectively. The males are distinct due to the enlarged cheliped, the front claw used to attract the females for mating (Grimes et al., 1989). Mating takes place inside the male's burrow, while the exoskeleton of the female fiddler is in a hardened state. Gravid females have been seen as early as April in the southern part of the range and in July through August in the more northern part of the east coast range (Grimes et al., 1989). Female fiddler crabs carry an egg mass (sponge) on their abdomen containing the fertilized eggs, which can number from 1,500 to 23,700 (Grimes et al., 1989). Studies of fiddler crabs in Delaware Bay have shown that the females show periodicity in larval release. Spawning usually occurs on a semilunar cycle at the new and full moons in conjunction with the high slack tide, allowing the newly hatched larvae to move out of the estuary on the fast currents of the ebbing spring tide (Wheeler, 1978; Christy, 1982; Salmon et al., 1986; Forward, 1987). The zoea of *Uca* spp. are able to vertically migrate within the water column in order to facilitate their export from the estuary (O'Connor &

Epifanio, 1985; Capaldo, 1993; Garrison, 1999). Larval development of *Uca* consists of five zoeal stages, each lasting from 7 to 31 days, and one megalopal stage, lasting 4 to 31 days, total larval development ranging from 32 to 180 days (Van Den Avyle, 1984). Studies in Chesapeake Bay and Delaware Bay (Lambert & Epifanio, 1982; O'Connor & Epifanio, 1985) have shown that fiddler crab larvae are exported from the estuary onto the continental shelf where they develop and then return to the estuary as megalopae. Differences in vertical distribution of stages of *Uca* zoea have been observed with earlier stage larvae at the surface and later stage larvae at depth in order to facilitate movement out of and into the estuary, respectively (Van Den Avyle, 1984). Laboratory tests have shown that salinity may govern the ability of the larvae to molt (O'Connor & Epifanio, 1985). Thus, development can only occur when larvae are in the ideal salinity conditions such as those in the coastal ocean. By developing in the coastal ocean, the larvae are able to avoid predation by juvenile fish inhabiting the estuary and prevent exposure to the extreme temperature and salinity changes that occur within the tidally influenced estuarine system (Christy, 1982).

Lifecycle of *Petrolisthes armatus*

Petrolisthes armatus is a small crab measuring 12 to 14 mm wide (Coen & Heck, 1983). Its small size allows it to hide easily in the crevices of an oyster reef and it is assumed to filter feed using its third maxillipeds (Coen & Heck, 1983; Coen & McAlister, 2001). Densities of *P. armatus* on substrates in Georgia and South Carolina have been measured as high as 20,000 individuals per square meter (Coen & McAlister, 2001; Hollebone, 2006). The rapid establishment of dense populations of *P. armatus* in southeastern United States estuaries may be partially due to an abbreviated larval phase

in its lifecycle. *P. armatus* has only two zoeal stages and one megalopal stage during its larval development (Gore, 1969). It has been hypothesized that its zoeal stages may not be transported out of the estuary at all, thus increasing the number of larvae available to settle in the adult habitat and making the establishment of dense populations more likely (Bishop, personal communication).

No published research has been completed on the mating practices of *P. armatus* or the number of eggs produced per female. Larvae reared in the laboratory reached the juvenile crab stage in 17 to 49 days, with faster maturation of larvae when temperatures were higher (Gore, 1969).

Physical Processes Affecting Larval Transport

As larvae are released by female crabs into the water column, the physical processes within the estuary and the coastal ocean act to transport them to different areas. Although larvae are able to swim short distances using their maxillipeds, their swimming speeds (3 – 12 mm/s) are typically much less than the horizontal velocities within an estuary or coastal ocean (~.5 m/s) (Capaldo, 1993). *Uca* spp. and *P. armatus* larvae are under the control of the tides, winds, and buoyancy driven flow, all of which result in currents that transport them throughout their environment (Epifanio & Garvine, 2001). Vertical velocities within the water column are typically an order of magnitude less than horizontal velocities (Dyer, 1997), allowing larvae to overcome the vertical flow within the estuary and modify their horizontal position by taking advantage of vertical shear in the water column. While larvae are able to swim and can alter their vertical position in the water column, the physical forces present in the estuary largely control their transport of the larvae. The currents present within the estuary as well as in the coastal ocean are

caused by various environmental factors and ultimately lead to the movement of larvae around as well as out of and back into the estuary.

Tides, caused by the gravitational forces of the sun and the moon, are responsible for the largest velocities in the estuarine environment. Tides result in horizontal currents that move water into or out of the estuary, resulting in a raising or lowering of the water (Dyer 1997). The type of tide an area receives is due to its latitudinal position, coastal geometry, and bottom topography. Although residual water movement due to the tides is typically negligible, the estuaries in Georgia are predominantly ebb-dominated with larger velocities during ebb tide than during flood tide. The presence of extensive marshes results in significant oceanward transport of surface-dwelling passive particles originating from the marsh surface during ebb tide (Dame et al., 2000; Zheng et al., 2003). This means that the timing of larval release during the ebb tide can result in larvae that exit the estuary quickly with an outgoing flow, while timing of larval release during the flood tide can result in retention of larvae within the estuary and transport upstream (Queiroga & Blanton, 2005).

Although currents are caused by the tides, they also result from gravitational circulation created by freshwater inputs from rivers and shear created by the wind along the surface (Queiroga & Blanton, 2005). Gravitational circulation occurs in estuaries due to the slope of the surface water and differences in the densities of the relatively freshwater originating upstream of the estuary and the more saline water originating in the coastal ocean. Gravitational circulation results in a residual seaward flow of the surface water, a residual upstream flow of the water near the bottom, and an area of no net motion at mid-depth (Dyer, 1997).

Surface wind stress can affect transport within the estuary both locally and remotely. Winds oriented along the longitudinal axis of the estuary result in surface velocities that can transport surface-dwelling larvae into or out of the estuary. Upwelling and downwelling due to large-scale wind forcing parallel to the coastline can result in an increase or decrease in sea level at the mouth of the estuary, causing transport into or out of the estuary on subtidal scales (Queiroga & Blanton, 2005).

The United States east coast is a passive geological margin and the continental shelf can extend for over 200 km offshore. Onshore transport occurs in the coastal ocean, specifically in the surf zone along the coast, due to incoming waves causing net transfer onto the shore of particles within that zone. There is also a net longshore movement of water within the surf zone due to the slight angle at which the waves hit and then leave the beach (Queiroga & Blanton, 2005). Onshore transport may prevent larvae entrained in the water from exiting the estuary, whereas longshore transport will move the larvae down the coastline once they reach the coastal ocean.

Physical Processes in the Satilla River Estuary

The Satilla River, in coastal Georgia, drains a watershed of 9140 km^2 and contains 3.79×10^5 km^3 of water during mid-tide. Freshwater makes up approximately 50% of the total volume of the river (Alber & Sheldon, 1999; Blanton et al., 2003). Some previous work has been done regarding the physical processes in the Satilla River estuary. Alber and Sheldon (1999) examined the flushing times, the average amount of time fresh water spends in an estuary, of various Georgia estuaries. They determined that the flushing time for the Satilla River estuary ranges from a few days in February to almost a hundred days in January and that flushing times are related to the amount of discharge of fresh water

being added to the system. Flushing of the estuary aids in the movement of larvae out of the estuary so faster flushing times would result in faster transport of larvae out to the coastal ocean. Zheng et al. (2003) used a numerical model to examine the near-surface tidal currents and investigate the flooding-drying process in the intertidal zone of the Satilla River estuary. Blanton et al. (2003) investigated the physics of the river to examine the transport and flux of salt and suspended sediments through a curve in the Satilla estuary. They found faster flow during spring tides than during neap tides and faster flow during ebb tide than flood tide. The physical mechanisms in the Satilla River were used to explain how suspended particles are transported. Net sediment transport of sediments appeared to be upriver due to resuspension of sediment at the beginning of the flood tide (Blanton et al., 2003).

Previous Research on Larval Distribution and Transport

The theories surrounding the dispersal and transport of decapod larvae have evolved over many years of research. The explanation for recruitment of offspring to adult habitats has grown from one of simple retention to a complex process involving tides, buoyancy driven currents, and wind driven forces. The *Uca* larvae are possibly able to alter their horizontal position by changing their vertical position in the dynamic environment (DeCoursey, 1976; Garrison, 1999). *C. sapidus* are expected to remain at the surface throughout the duration of their development and travel out to the continental shelf and return to the estuary due to wind-driven transport. Computer models have helped predict the paths taken by the larvae and the numbers of larvae returning to the estuary (Tilburg et al., 2005).

A timeline of research in larval development and transport is important to show how the theories for larval distribution and recruitment have changed and evolved and how the study of decapod larvae has progressed. Numerous studies have examined decapod larval transport along the east coast of the United States, although very little has been done in Georgia. The majority of this research has concentrated on the Chesapeake Bay and the Delaware Bay, with some studies focusing on the coasts of the Carolinas and the Gulf Coast.

Sandifer (1975) first examined the importance of planktonic larval stages in the recruitment of adults to their habitat. He examined a variety of caridean shrimp and estuarine crabs, including *C. sapidus* and *Uca* in the York River estuary. He concluded that only two methods of recruitment could exist; either the larvae are retained near the adult habitat or the animals move into the habitat from other areas as juveniles or adults. Two later studies, DeCoursey's (1976) and Provenzano's (1983) did not support Sandifer's (1975) conclusion that larvae are retained in the estuary allowing recruitment to adult habitats. DeCoursey's (1976) examined the vertical migration behavior of *Uca* larvae in North Inlet, SC and found a tidally rhythmic vertical movement that suggested larvae are able to determine their vertical distribution in the water column and therefore their horizontal position and transport out of the estuary. Provenzano's (1983) study found that the amount of *C. sapidus* larvae in the surface waters was greatest during a nighttime high slack tide, allowing the blue crab larvae to move out of the estuary on the subsequent ebb tide for development in the coastal ocean.

Dittel and Epifanio (1982) examined the seasonal abundance and vertical distribution of both *C. sapidus* and *Uca* in the Delaware Bay, finding that the abundance

of *Uca* reached its maximum in July while the abundance of *C. sapidus* was highest in August. They also found only zoea stage I (ZI) of *C. sapidus* within the estuary, which was predominantly in the surface waters, while all stages of *Uca* were found at all depths and were much more prevalent. These conclusions also did not support the two methods for recruitment set forth by Sandifer (1975) because only ZI *C. sapidus* were found within the estuary demonstrating that larval development does not occur within the parent estuary, but out in the continental ocean. Dittel and Epifanio (1982) postulated that *C. sapidus* leave the estuary in the ebbing surface waters during ZI of larval development and return to the estuary as post-larvae using on-shore drift of deeper waters.

Brookins and Epifanio (1985) examined the abundance of *C. sapidus* and *Uca* larvae over consecutive tidal cycles in Delaware Bay. They found that both crabs spawn their larvae at high slack water, allowing the larvae to be exported from the estuary on the ebb tide. *Uca* zoea were the most abundant larvae collected during the study period and were most numerous at the surface during ebb tide. *C. sapidus* zoea were collected at very low numbers during this study period. No pattern of stratification regarding depth was seen during ebb or flood tide for the zoeal stages of either species; however, megalopae of both *C. sapidus* and *Uca* were collected at depth. Williams (1971) and Mense and Wenner (1989) conducted studies in North and South Carolina concerning the annual occurrences of blue crab larvae and their distribution. They concluded that *C. sapidus* zoea were never seen within the estuaries and that reinvading megalopal densities were based on salinities.

More recent studies have supported the theory that megalopae do not move to deep water, but reenter the estuary using surface water. Studies in Delaware Bay showed

that settlement into adult habitats of both *C. sapidus* and *Uca* is accomplished by megalopae occupying the surface water (Little & Epifanio, 1991; Jones & Epifanio, 1995). *Uca* larvae were examined in Delaware Bay to determine the possibility of vertical migration as a method of facilitating horizontal transport. It was determined that higher densities of *Uca* larvae were present near the bottom during flooding tides than during ebbing tides, possibly deterring transport back into the estuary (Garrison, 1999). Roman and Boicourt (1999) have shown that larvae can move out and re-enter the same estuary after development in the coastal ocean. Crab larval densities of various species were studied in the Chesapeake River plume. The seasonal physical changes of the plume were examined to determine the methods used by larvae, which are transported out to the shelf during developing stages and then re-enter the estuary to replenish adult populations. Wind events, which cause periods of downwelling and upwelling along the shore resulting in transport of surface water toward or away from the coast, were recognized as the forces that move larvae off-shore and down-shelf and then back on-shore and up-shelf, returning them to the parent estuary (Roman & Boicourt, 1999). A study in the Gulf of Mexico also showed that wind stresses may be related to return and settlement of *C. sapidus* megalopae into the parent estuaries (Perry et al., 2003).

Studies along the Georgia coast

It is important to examine crab larval distribution in Georgia due to the differences between coastal Georgia and the areas where the majority of previous studies have taken place. Coastal Georgia greatly differs from Chesapeake Bay and Delaware Bay in its geography. Whereas the bays have large riverine inputs into one large bay covering a vast area, coastal Georgia has various separated points of riverine input

creating a variety of smaller estuaries. Georgia's coast is bordered with barrier islands and small estuaries and differs from North Carolina's coast which has bar built islands and Delaware Bay and Chesapeake Bay which are both drowned river systems. The coast of Georgia has a wider continental shelf, resulting in larger tides along Georgia's coast.

The distribution of adult fiddler crabs has been analyzed in the Georgia salt marshes (Teal, 1958). The settlement patterns of the megalopal stage of brachyuran crabs have been investigated near Sapelo Island in Georgia (Wrona et al., 1995), but no work has been published on the distribution and transport of the zoeal stages of either brachyuran or anomuran crabs along Georgia's coast.

Objectives

The major objective of this study was to investigate and describe the dispersal and transport of the larvae of *Uca* spp. and *Petrolisthes armatus* in the Satilla River estuarine system, focusing on the physics of the flow field and the behavior of the larvae that govern transport.

Uca larvae must reach the higher salinity of the coastal ocean in order to develop and reach post-larval maturity (O'Connor & Epifanio, 1985; Capaldo, 1993; Forward et al., 1994). As a result of its lifecycle, consisting of release within the estuary, development in the coastal ocean, and settlement back within the estuary, *Uca* larvae are dependent on the physical flow field for transportation to the coastal ocean and back to the estuary once they have reached post-larval development by molting. Since fiddler crabs are essential to the marsh ecosystem and serve many important roles in the natural food web, a better understanding of their life cycles and those forces that transport them is vital. *P. armatus'* rapid invasion and establishment along Georgia's coast necessitates

an investigation into its lifecycle and processes which govern the dispersion of this species. Knowledge of the physics affecting the Satilla River estuary and the way in which the crab larvae are transported will result in a greater understanding of the lifecycles of these crabs as well as the important roles the physics of the estuary play their dispersal, transportation, and ultimate success.

Questions

Specific questions of this study included: 1) Where are the majority of the crab larvae both temporally and spatially within the estuary? 2) What are the primary physical processes that affect the location and transport of the crab larvae? 3) Do *Uca* and *P. armatus* zoea larvae vertically migrate and if so how does this affect their dispersal and transport?

Predictions

This paper aims to answer the previously stated questions and makes the following predictions: 1) *Uca* larvae move out of the estuary for development, 2) *Uca* larvae will be stratified vertically within the water column with the earlier stage larvae closer to the surface and the later stage larvae below the surface, 3) *P. armatus* larvae are not vertically stratified within the tidal creeks, and 4) *P. armatus* larvae are more common when salinities are higher.

Materials and Methods

Study Area

The Satilla River estuary is located in the middle of coastal Georgia. This area was chosen for this study because it represents a typical Georgia estuary exhibiting an input of freshwater combined with a semidiurnal tidal cycle. Some research has also been

performed on the physics of this system, providing a general knowledge of the physical mechanisms within the estuary.

The Satilla River drains a watershed of 9140 km^2 and has a 1 to 1.5 meter semi-diurnal tidal amplitude. The volume of the estuary is 379,000 km^3 and the freshwater volume is 194,000 km^3. Average depth of the estuary is 4 meters, but may reach 10 meters at the deepest. The effects of the tidal influx extend 50 km inland and the lower 25 km of the estuary is 1 km wide. The average freshwater inflow is 70 m^3/s, but changes seasonally (Blanton et al., 2003). Vertical stratification is weak, varying from a salinity gradient of less than 0.1 PSU/m to 0.8 PSU/m, making the estuary partially mixed whose vertical stratification depends on the location, tide, and freshwater input

The Little Satilla River and Jointer Creek are adjacent tributaries of the Satilla River. Both tributaries are located to the north of the Satilla River and close to where it meets with the coastal ocean. While some freshwater enters the tributaries from mixing with the Satilla River, the Little Satilla River receives small amounts of freshwater inflow from upstream and Jointer Creek has no upstream fresh water source.

Sampling in the Little Satilla and Jointer Creek tributaries took place during two day periods in April, June, July, August, and September of 2005 and a one day period in August 2006. Sampling in the Satilla River took place during two days in March and August of 2006 (Table 1.1). During each sampling period except June and July of 2005, samples were collected during a full tidal cycle on each day at various stations. Sampling in June and July 2005 involved deploying drifters and collecting physical data whereas sampling during all other dates involved plankton tows and physical data collection from a 27-foot boat, the R/V WaterDawg, at each designated station (Fig. 1.1).

Collections in 2005 were conducted in the surface waters in the Little Satilla River and Jointer Creek at stations A, B, and C (Fig. 1.1). In March of 2006, two transects were made of the Satilla River (Fig. 1.1) and in August 2006 surface and deep waters were sampled in the Little Satilla River and Jointer Creek at stations A, B, C and D, as well as along the two transects of the Satilla River.

Table 1.1: Table showing months of data collection in Jointer Creek and the Little Satilla River (X) and the Satilla River (O) during 2005 and 2006.

Data collected	**2005**												**2006**											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
CTD				**X**				**X**	**X**						**O**					**XO**				
FSI CT				**X**				**X**	**X**						**O**					**XO**				
ADCP				**X**				**X**	**X**						**O**					**XO**				
Drifter						**X**	**X**																	
Plankton tow (surface)				**X**				**X**	**X**						**O**					**XO**				
Plankton tow (depth)																				**XO**				

Sampling in the Little Satilla River and Jointer Creek was conducted to include the flood and ebb tide at each station. The Satilla River was sampled to include both sides of an island lying in the center of the river to observe the differences in flow on either side. Each station was sampled after both the ebb and flood tide.

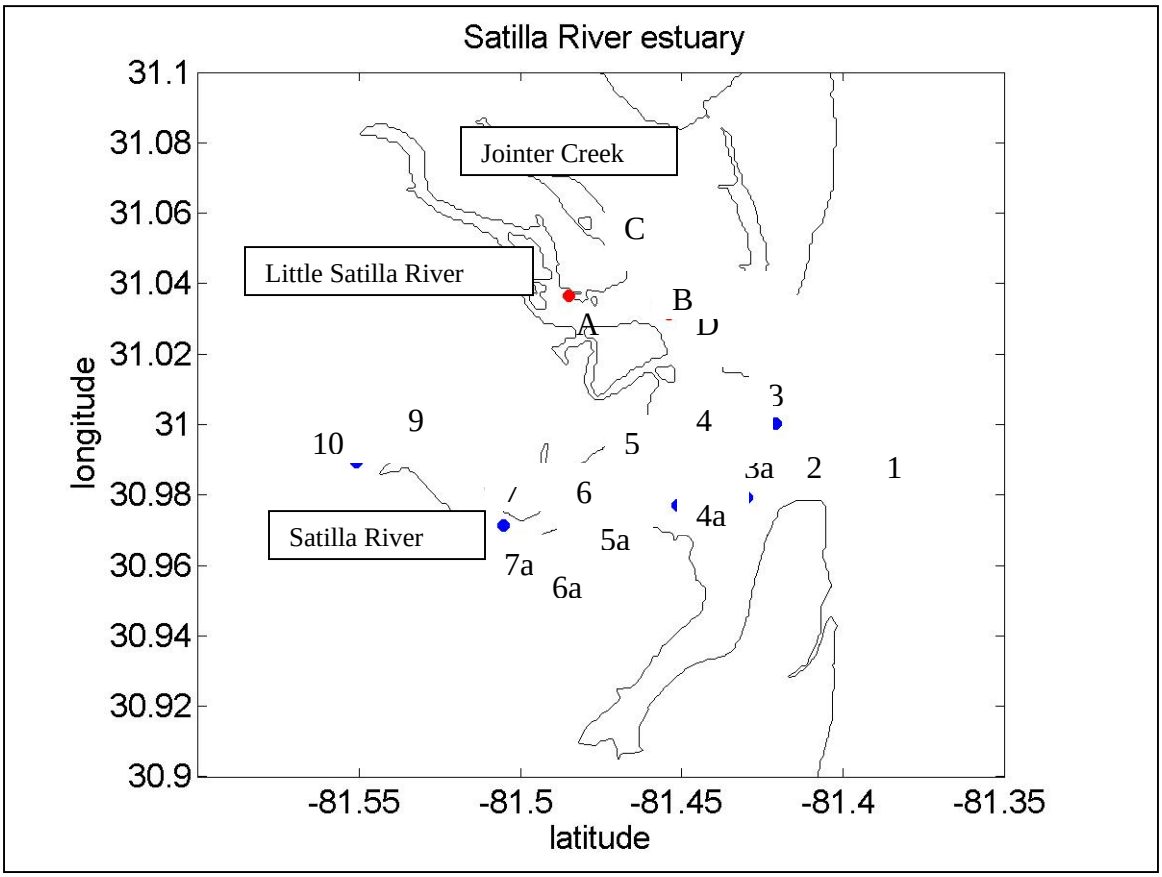

Figure 1.1: Map of Satilla River estuary showing the location of the 4 sampling stations in the Little Satilla River and Jointer Creek (red) and transect of Satilla River (blue).

Physical Data Collection and Analysis

Salinity, temperature, and depth were observed at each station using an SBE-25 CTD (Conductivity, Temperature, and Depth recorder). Continual temperature and salinity readings were made using a continuously deployed FSI CT (Conductivity and Temperature recorder) at 0.5 meters depth and the current velocities at various depths were taken using an ADCP (Acoustic Doppler Current Profiler) for the duration of each cruise.

The measurements of salinity and temperature changes with depth were used to create horizontal and vertical profiles of the study area that illustrate the stratification

seen in the Satilla River estuary. The surface salinity and temperature data collected using the FSI CT's were plotted on a map to show the variations in surface temperature and salinity seen throughout the sample area during the different times of the study. The ADCP was used to determine the depth-averaged velocities of the water at the time each biological sample was taken. When the ADCP was non-functional, the measured tidal heights at St. Simon's Lighthouse were used to generate a prediction of the depth-average velocities.

Drifters equipped with GPS (Global Positioning System) trackers were also deployed in the Little Satilla River and Jointer Creek during June and July of 2005. The drifters, positioned in the surface waters, were allowed to flow with the current for a tidal cycle. The GPS trackers recorded the paths taken by each drifter. The resulting routes were plotted on a map of the study area to show the general flow of water over one tidal cycle in the section of the estuary being studied.

Biological Data Collection and Analysis

Plankton samples were taken at each station using plankton nets with a mesh size of 240 μm equipped with flowmeters to measure the volume of water being sampled. The nets were used to make five or ten minute plankton tows from the 27-foot R/V WaterDawg at each previously determined station (Fig. 1.1). The samples taken in 2005 and March of 2006 were of the surface only. In August 2006 samples were taken using a simultaneous surface net and a net attached to a sled for sampling at a depth near the bottom. As each sample was collected, it was washed using a 180 μm-mesh sieve. The plankton sample was then placed in a container and treated with 500 ml of ethyl alcohol in 2005 and 500 ml of formalin in 2006 for preservation.

The samples were split using a Folsom splitter following the guidelines of Griffiths et al. (1984). Each sample was split 4 or 6 times resulting in 2^4=16 or 2^6=64 sub-samples and two sub-samples from each sample were counted. If the difference between the sub-samples was greater than 25%, then a third sub-sample was counted. The samples were counted using a dissecting microscope and the *Uca*, *C. sapidus*, and *P. armatus* larvae were separated from the sample and divided into their respective larval stages. The mean values of total larvae of each genus were divided by the volume of water sampled to obtain a density of crab larvae at each station. The larval density at each stage of larval development was also determined using the same method.

Average larval densities were calculated and compared for various spatial and temporal conditions. The variance of the whole population estimate was determined (Equation 1.1) and standard error (SE) (Equation 1.2) was calculated from the variance. T-tests were performed on different mean values to determine the level of significant difference between samples from different locations and during different times.

$$VARIANCE(N) = 2\text{^}T * (2\text{^}T - n)(X / n) \qquad \textbf{Equation 1.1}$$

$$SE = \sqrt{VARIANCE(N)} \qquad \textbf{Equation 1.2}$$

Where N is the whole population estimate,

T equals the number of splits made,

n equals the number of sub-samples counted, and

X equals the mean of the counted sub-samples.

Comparisons were made between the larval densities collected during the different years and seasons of sampling as well as during the different tidal regimes and

at different locations within the estuary to determine the spatial and temporal distributions.

The results of this study are presented in separate chapters focusing on the physical parameters measured in the Satilla River estuary, the results and discussion for *Uca* spp., and the results and discussion for *P. armatus*. The two species are compared in the conclusion.

CHAPTER 2

PHYSICS

Results

The physical data collected during this study includes temperature, salinity, the depth-averaged velocity, and the surface flow patterns present in the Satilla River estuarine system. The results of the physical data are grouped by location (Little Satilla River and Jointer Creek tributaries and the Satilla River) and by date.

Data from monitoring stations (filled blue and green circles in Fig. 2.1) managed by the US Geological Survey (USGS) were used to examine the stream flow (Figs. 2.2) and precipitation (Figs. 2.3) in the Satilla River and the Little Satilla River over the period of this study. Data from the National Oceanic and Atmospheric Association (NOAA) monitoring site at Gray's Reef (filled red circle in Fig. 2.1) was used to determine the prevailing winds in the area during the sampling periods. Spatial scales of atmospheric systems in this region are typically greater than 200 km, so the use of observed winds at Gray's Reef (which is approximately 60 km NE from the Satilla River) as a measure of the prevailing wind conditions provides an acceptable estimate of wind conditions in the Satilla River estuary.

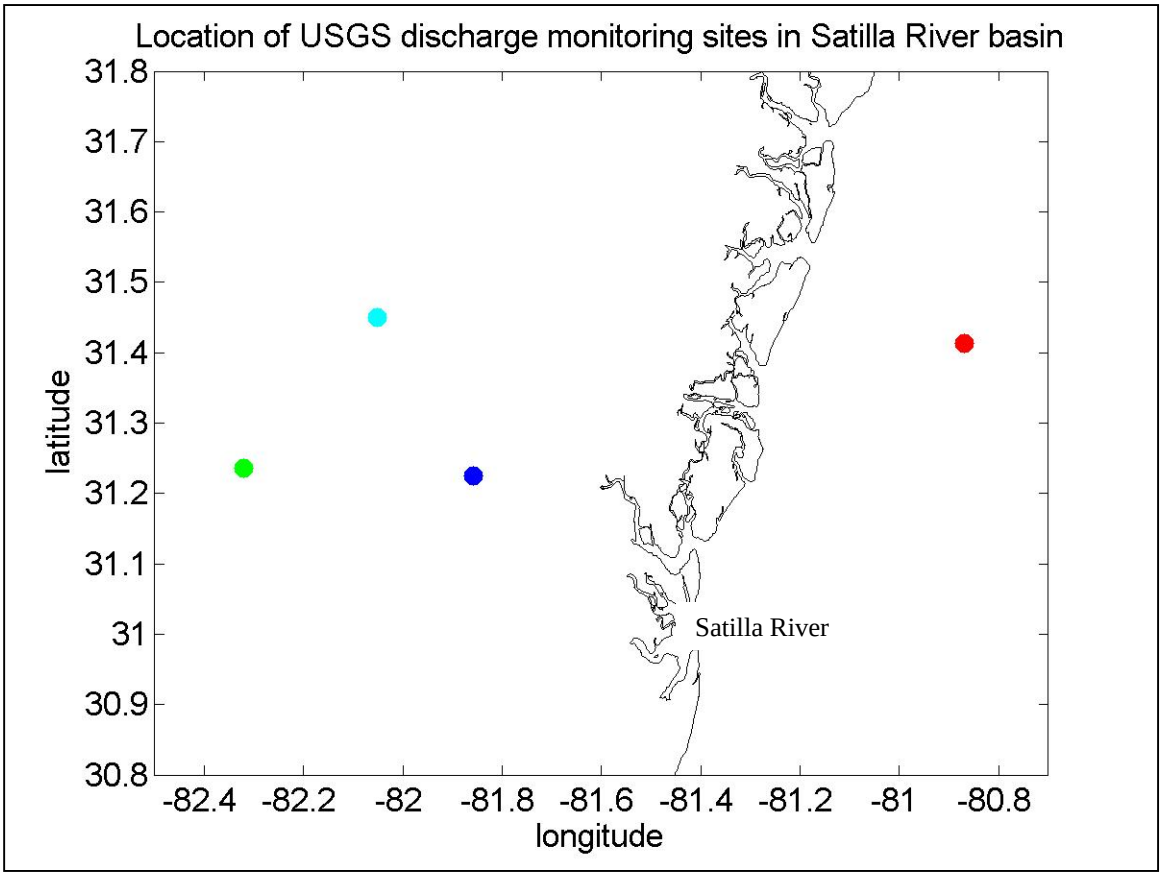

Figure 2.1: Map of study area showing location of upstream USGS monitoring stations on the Little Satilla River, Atkinson, GA (green), Waycross, GA (light blue), and the Satilla River (dark blue) and the NOAA's wind monitoring station at Gray's Reef (red).

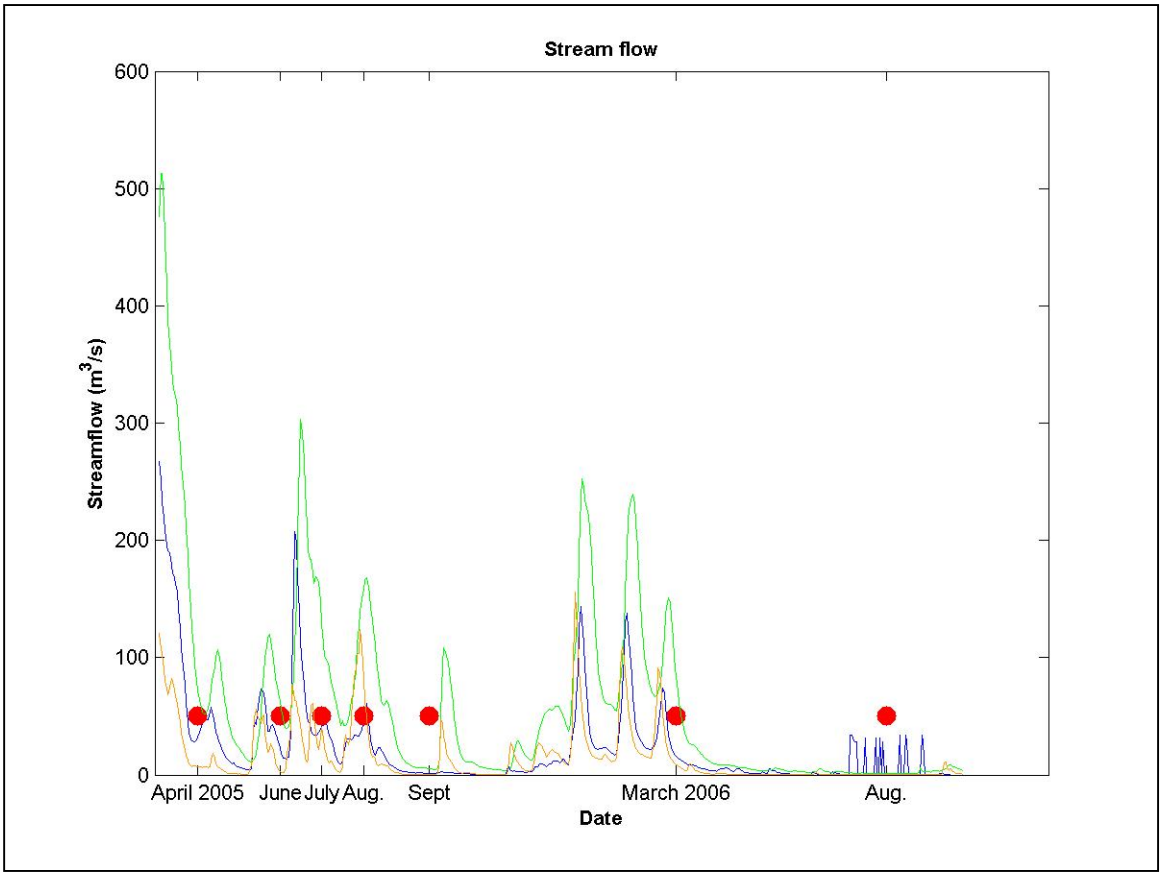

Figure 2.2: Stream flow at two upstream monitoring stations along the Satilla River; Atkinson, GA (green) and Waycross, GA (blue) and at the upstream monitoring stations on the Little Satilla River (orange) along with dates of sampling (red circles).

There is greater river flow past the two Satilla River monitoring stations than the Little Satilla River monitoring station (Fig. 2.2). Mean stream flow past the Atkinson, GA monitoring station for 2005 and 2006 was 60 m^3/s, mean flow at the Waycross, GA station was 24 m^3/s, and mean flow at the Little Satilla River monitoring station was 15 m^3/s. River flow was large in the spring of both 2005 and 2006 as well as in late summer in 2005 in both rivers (Fig 2.2). The flow was drastically reduced in the summer of 2006 at all monitoring stations (Fig. 2.2). Daily precipitation at all three monitoring stations was consistent throughout the two years of this study; however, daily and seasonal variability did occur (Fig 2.3). All three monitoring stations had a daily mean

precipitation of 3 mm/day, which varied from 0 to 63 mm/day at Waycross, GA and the Little Satilla River stations and as much as 0 to 149 mm/day at the Atkinson, GA station (Fig. 2.3).

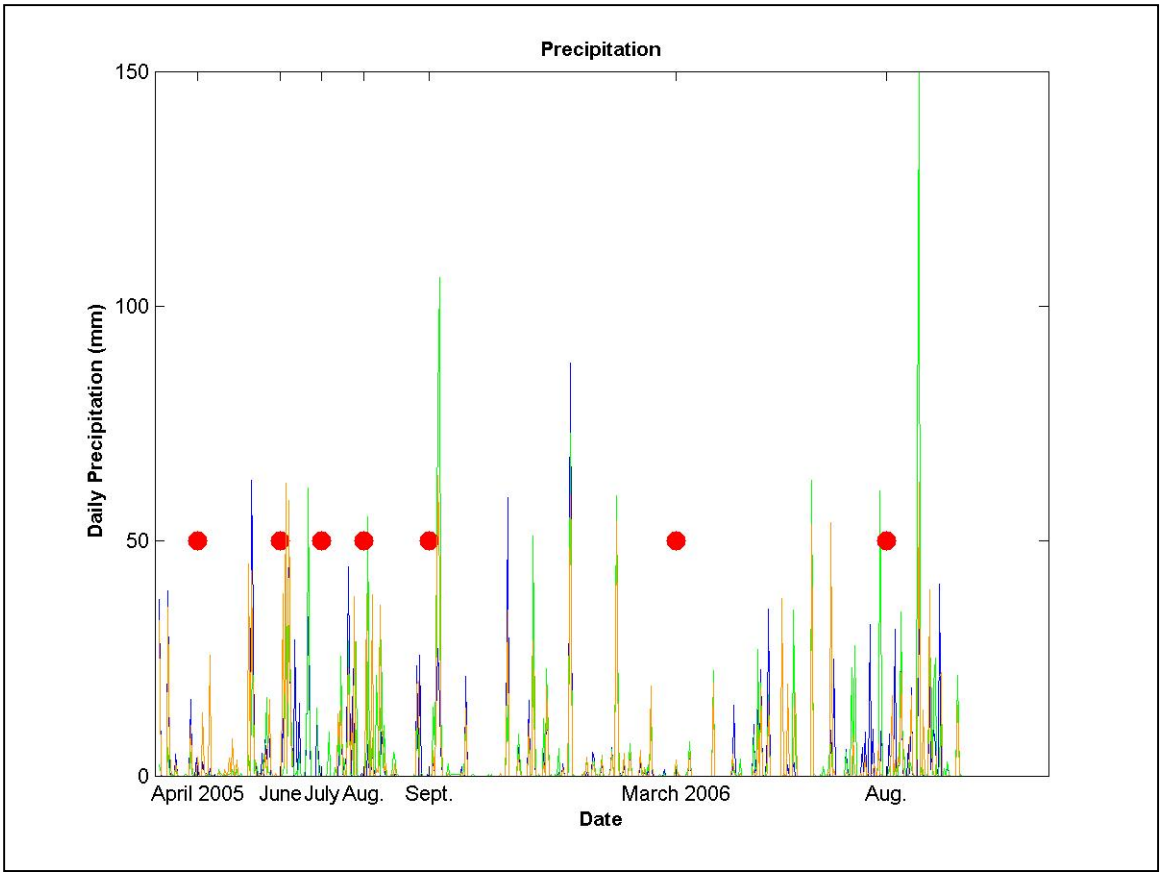

Figure 2.3: Daily precipitation at upstream monitoring stations along the Satilla River; Atkinson, GA (green) and Waycross, GA (blue) and at the upstream monitoring station on the Little Satilla River (orange) along with dates of sampling (red circles).

The wind data show the wind speed as the length of the arrow and direction the wind is heading to by the direction the arrow is pointing. The strength of the wind can affect the water column; a strong wind increases mixing and decreases vertical stratification, while a weak wind will have less effect on the water column. The direction of the wind can also have profound effects on the estuarine flow field. A northward wind, such as seen in April 2005 and March of 2006 would cause a seaward flow of the ocean

(and estuary) surface water, upwelling along the coast, and a decrease in coastal sea level (Fig. 2.4 & 2.5). A southward wind, as seen during the June 2005 sampling, would result in a landward flow of the ocean surface water, downwelling along the coast, and a rise in coastal sea level (Fig. 2.4 & 2.5). A diurnal pattern was seen in August 2005 and 2006 as well as September 2005, where northward winds were present during the daytime hours and the winds speed either slowed or changed direction at night (Fig. 2.4 & 2.5).

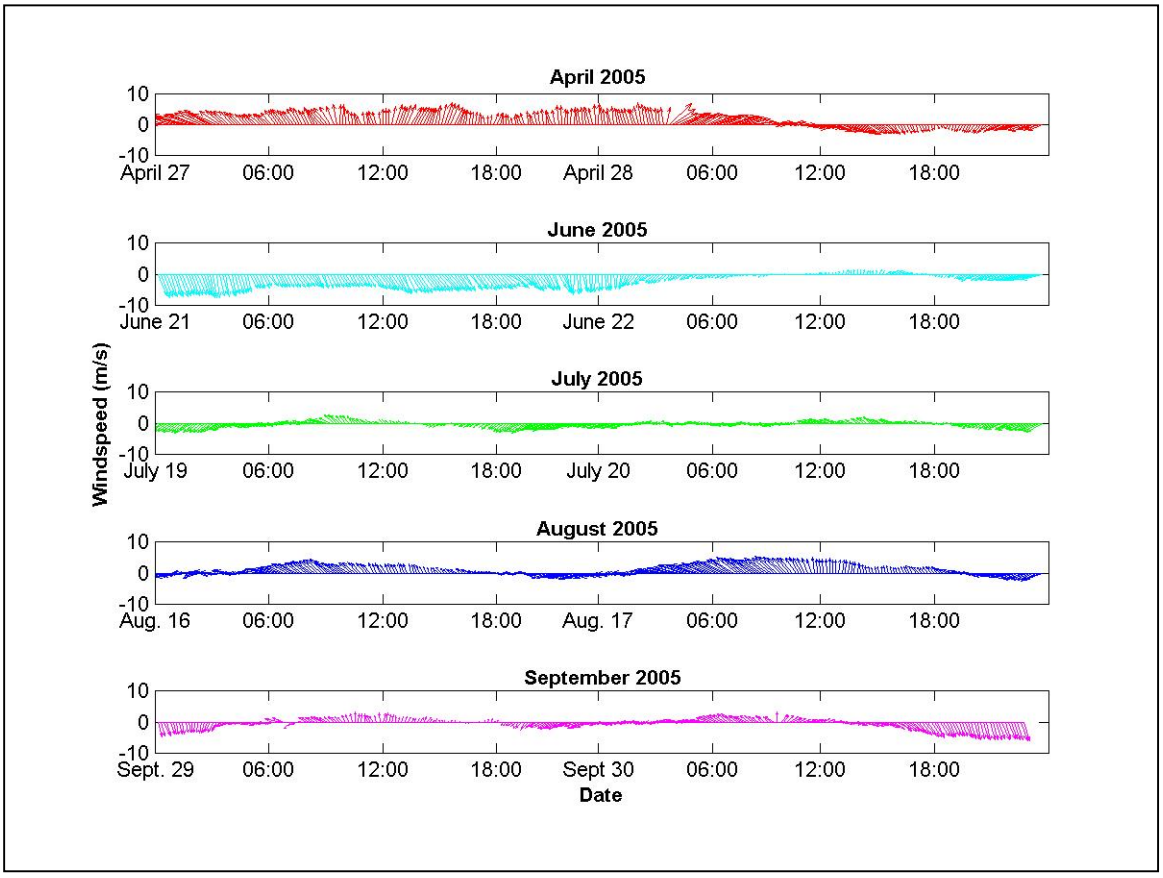

Figure 2.4: Wind speed and direction for Gray's Reef for the dates of 2005 sampling. Arrows depict the direction of the winds and the length of the arrows shows the speed in m/s.

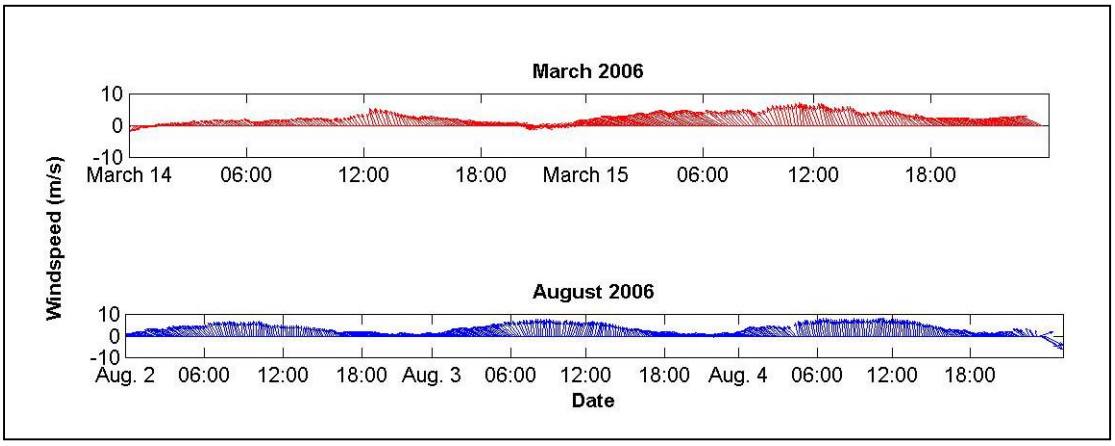

Figure 2.5: Wind speed and direction for Gray's Reef for the dates of 2006 biological sampling. Arrows depict the direction of the winds and the length of the arrows shows the speed in m/s.

Within the estuary proper, velocity data were collected using a RDI 1200 KHz Acoustic Doppler Current Profiler (ADCP) during most of the sampling. However, a number of the sampling periods were plagued by troubles with the ADCP. To provide estimates of the depth-averaged velocities when the ADCP was inoperable, the relationship between sea level at the closest available tide gauge and the measured velocities was examined (Fig. 2.6). The sea surface height is continuously measured at St. Simon's Lighthouse by the National Oceanic and Atmospheric Association (NOAA). Examination of the time series of sea level and the measured velocities reveals that sea level lags the measured velocities by 1.5 hours. The velocities can be related to the sea level by the following equation:

$$v(t) = h(t + \sigma) \cdot A \qquad \textbf{Equation 2.1}$$

where v is the predicted velocity in cm/s,

t is time in hours

h is the measured sea level at St. Simon's Lighthouse in meters,

σ is the lag time,

and A is an assigned constant with units of (cm/(s·m)).

The predicted depth-averaged velocities provided reasonable agreement with actual ADCP measurements (bottom panel of Fig. 2.6) and were used throughout this thesis when the ADCP was not functional.

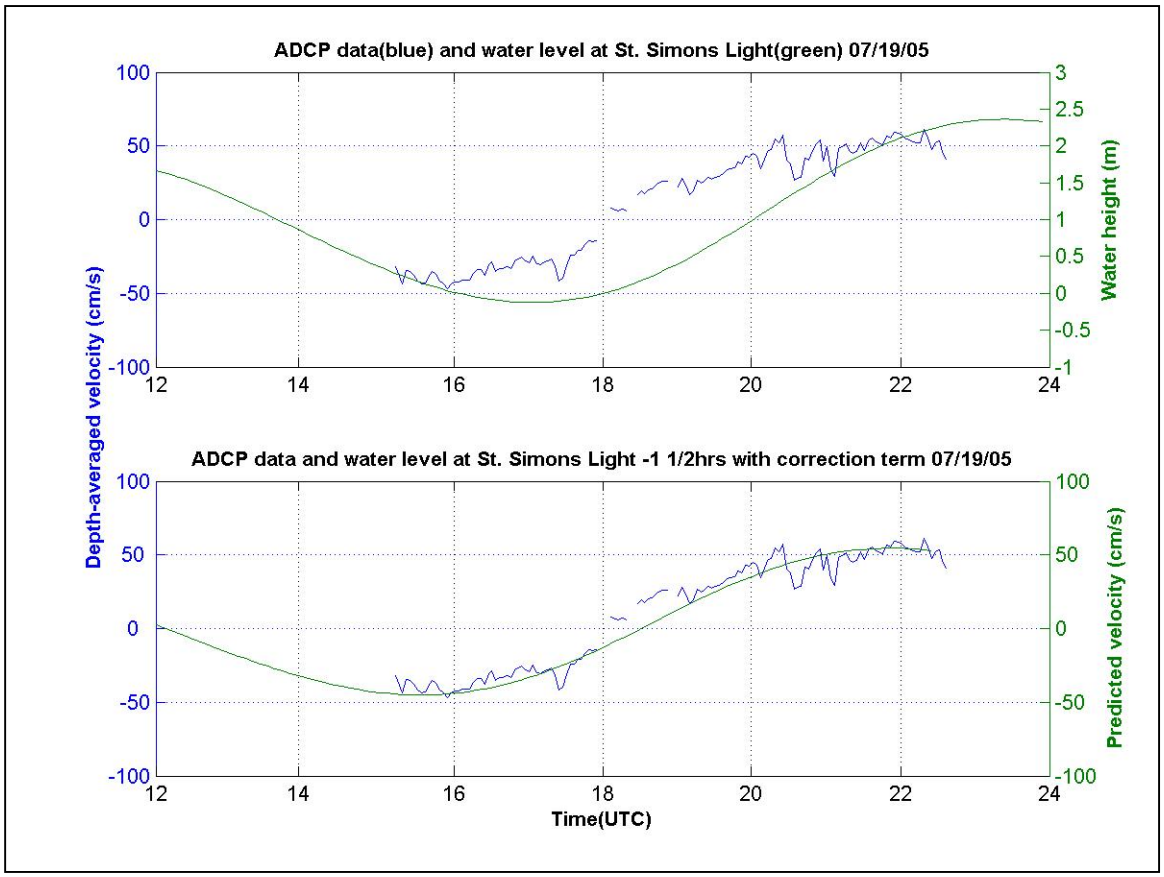

Figure 2.6: Sea Surface height data from St. Simon's Lighthouse and measured depth-averaged velocities (top panel). Measured and predicted depth-averaged velocities (bottom panel). Negative values of water velocity correspond to an ebbing tide while positive values correspond to a flooding tide.

Tributaries

Sampling in 2005 and August 2006 focused on two tributaries, Jointer Creek and the Little Satilla River, located to the north of the main Satilla River. Both tributaries receive small inputs of freshwater from mixing with the Satilla River, and the Little

Satilla River receives some freshwater from upstream sources. They are located toward the mouth of the estuary and are greatly influenced by the ocean water moving into the system, experiencing a tidal amplitude of 1.5 meters (Blanton et al., 2003).

Since the largest differences in the physical parameters measured occurred between the different months of sampling, this section is divided by sampling periods.

April 27 - 28, 2005

Sampling took place in April 2005 during spring tides (there was a full moon on April 24) resulting in strong currents. The winds during this sampling period were strong, reaching almost 8 m/s, and northward until midday on April 28, when they decreased in speed and changed direction (Fig. 2.4). The strong northward winds may have resulted in oceanward flow of surface waters.

Since no measured velocity data were available, velocities were predicted from measured sea surface heights at St. Simon's Lighthouse. A SeaBird SBE-25 CTD was continuously deployed at the surface for the duration of the sampling and recorded salinity and temperature. Complications with the Global Positioning Satellite (GPS) System onboard the research vessel prevented the mapping of the salinity and temperature as functions of location. Instead, surface salinity, temperature, and density are shown as functions of time (Figs. 2.7 & 2.8).

Sampling began during the flooding tide on April 27 and the salinity ranged from 15 PSU to 26 PSU (Fig. 2.7). On April 28, the end of the flood tide and the following ebb tide were sampled and the salinity ranged from 18 PSU to 24 PSU (Fig. 2.8). Temperatures both days ranged from 18 to 21 °C and were slightly higher on April 28 than on April 27 (Figs. 2.7 & 2.8). The measured densities on all sampling days were

strongly correlated with the salinities (r = 0.992) and uncorrelated with the temperatures (r = 0.092), indicating that density changes were controlled by salinity variations as opposed to temperature variations (Figs. 2.7 & 2.8). Consequently, only salinity is shown in all subsequent sections.

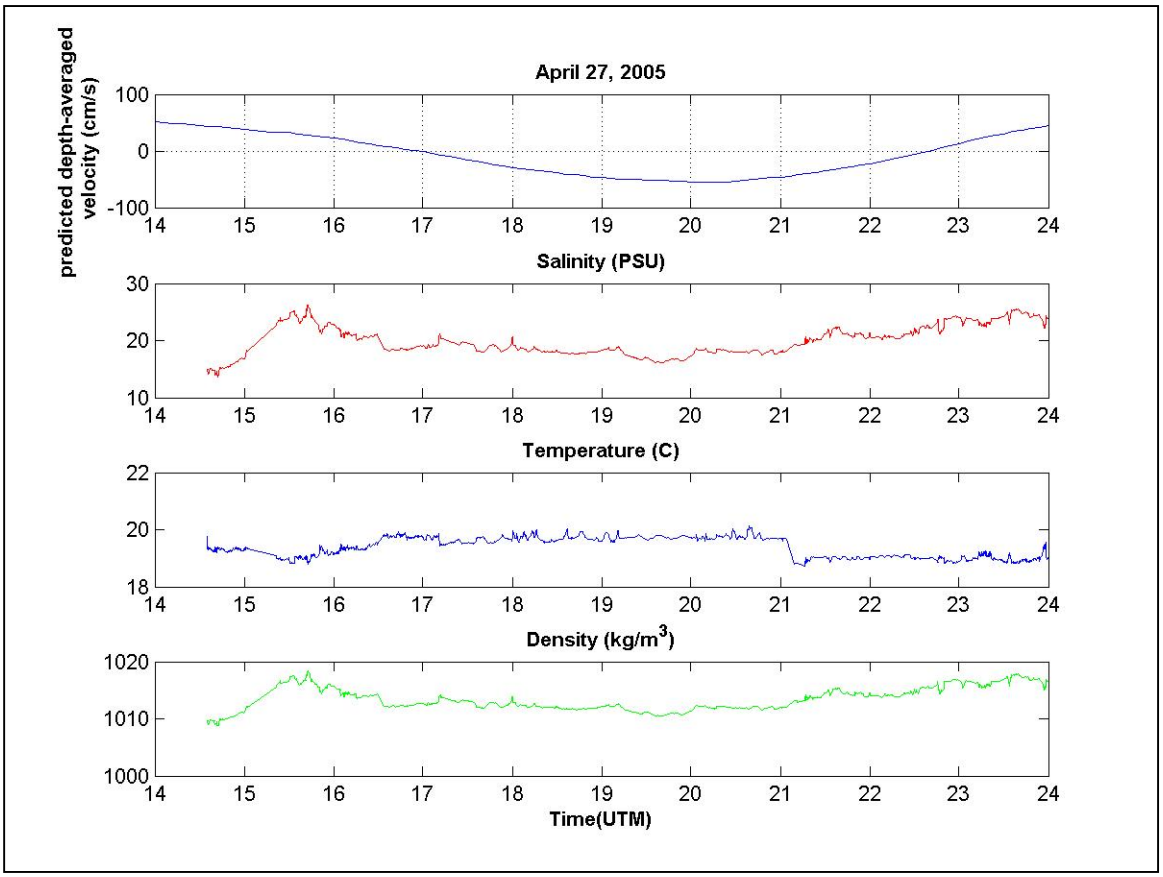

Figure 2.7: Predicted depth-averaged velocity (cm/s), salinity (PSU), temperature (°C), and density (kg/m³) as a function of time on April 27, 2005 in the Little Satilla River and Jointer Creek.

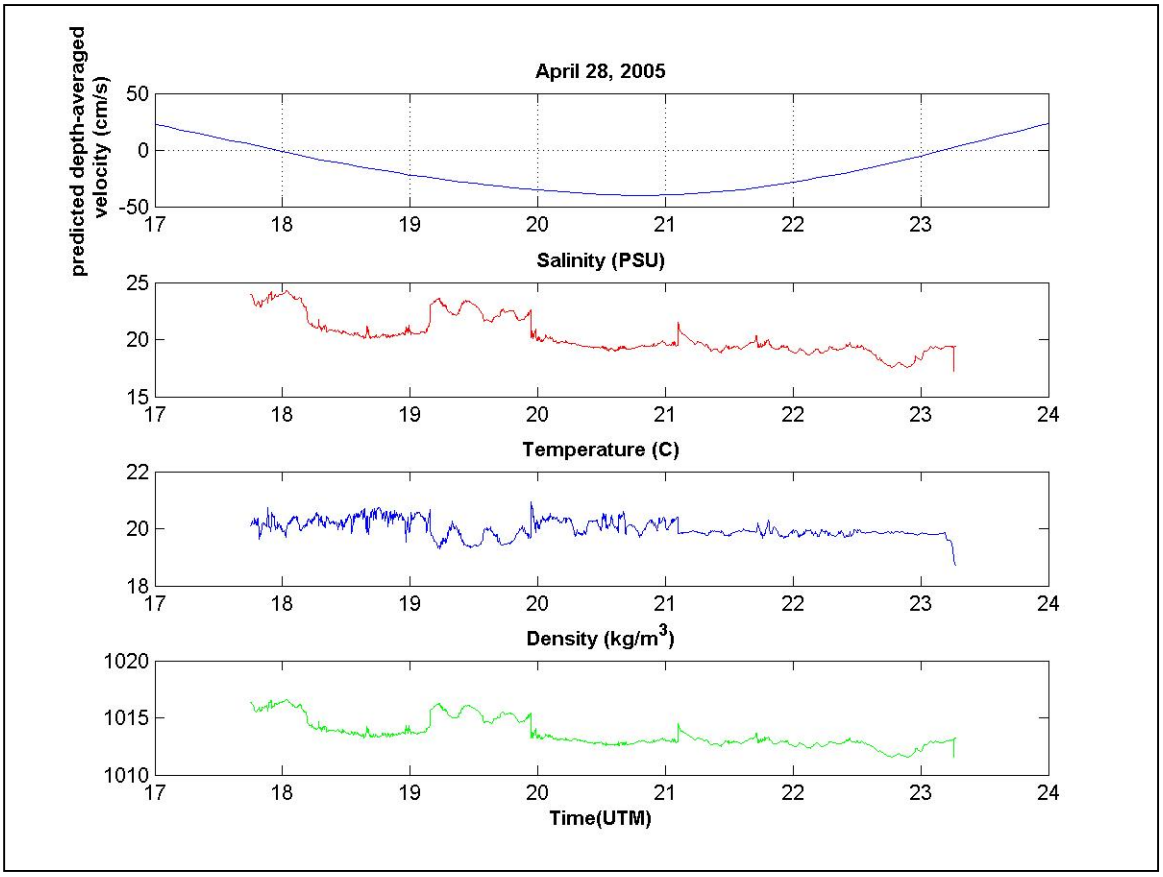

Figure 2.8: Predicted depth-averaged velocity (cm/s), salinity (PSU), temperature (°C), and density (kg/m³) as a function of time on April 28, 2005 in the Little Satilla River and Jointer Creek.

August 16 - 17, 2005

Sampling took place in August 2005 during spring tides (there was a full moon on August 19) resulting in comparable depth-averaged velocities to April (compare Figs. 2.7 & 2.8 to 2.9 & 2.10). The winds during this period were strongly northward and northeastward during the day with wind speeds around 6 to 7 m/s (Fig. 2.4), resulting in oceanward movement of surface water within the estuary. The winds during the night were minimal, less than 1 m/s, and southward (Fig. 2.4).

Vertical profiles of salinity, temperature, and density were taken with a hand-deployed SeaBird SBE-25 CTD at three different stations, A, B, and C in the Little Satilla River and Jointer Creek tributaries (Fig 1.1). The CTD data were used to create a vertical

profile of the measured parameters over time at each station; however, due to the correlation between salinity and density, only salinities are plotted here (Fig. 2.9-2.10). The FSI CT's continually recorded the surface salinity and temperature throughout the sampling (Fig 2.11 & 2.12).

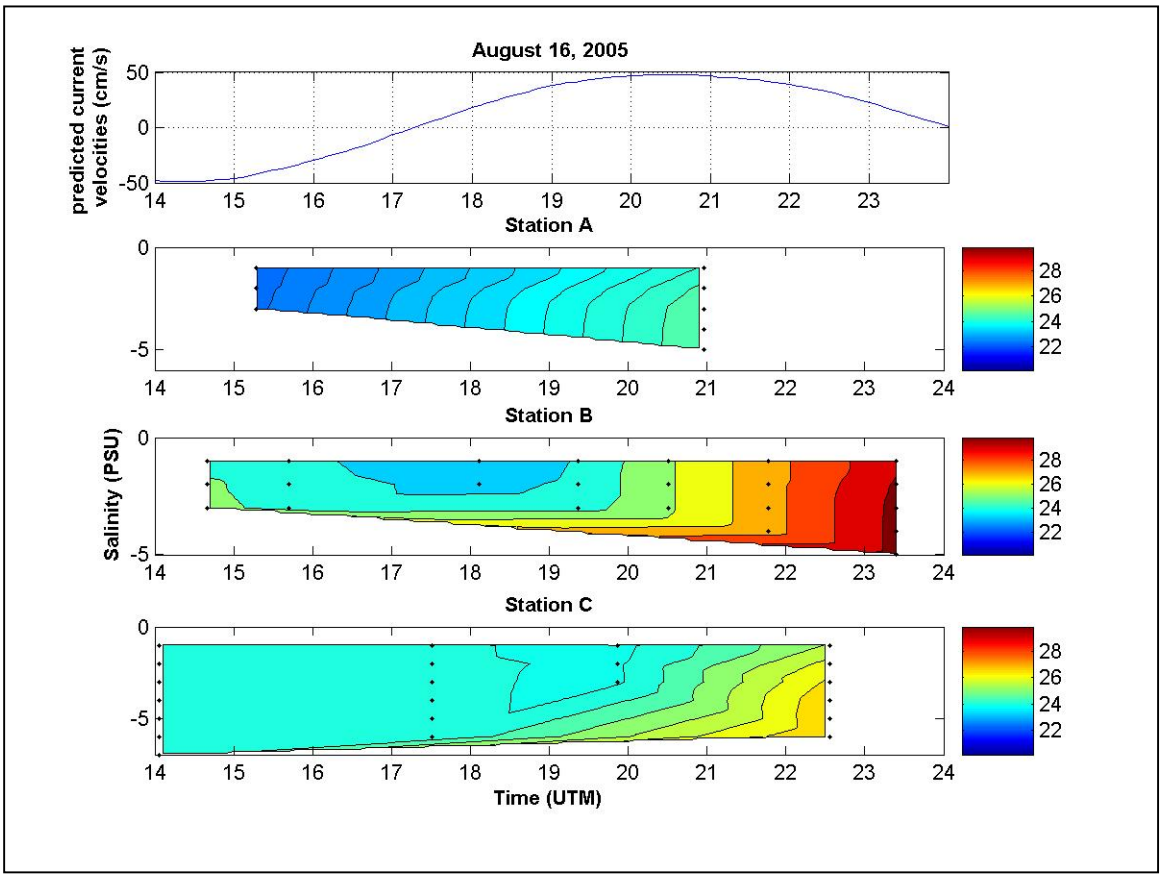

Figure 2.9: Predicted depth-averaged velocities and profiles of salinity (PSU) at stations A, B, and C on August 16, 2005. Black dots indicate time and depth of each CTD cast.

The vertical profiles at all three stations show significant spatial variation. Station B shows the greatest range in salinity, 23 PSU to 29 PSU, and density, 1003 kg/m^3 to 1017 kg/m^3 over the tidal cycle. Station A exhibits the freshest water (Fig. 2.9). A larger range in salinity was seen at Station A on August 17, 2005 than on August 16, 2005 and it was comparable to the salinities seen at Stations B and C (Fig. 2.9 & 2.10). The vertical profiles demonstrated little stratification during ebb tide, around 0.1 PSU/m, but more

stratification during flood tide, 0.2 – 0.3 PSU/m at stations A and C and 0.3 PSU/m at station B (Figs 2.9 & 2.10). Over both days, all three stations displayed higher temperatures in the afternoon and the temperatures were similar, ranging from 30 °C to 32 °C (See Appendix).

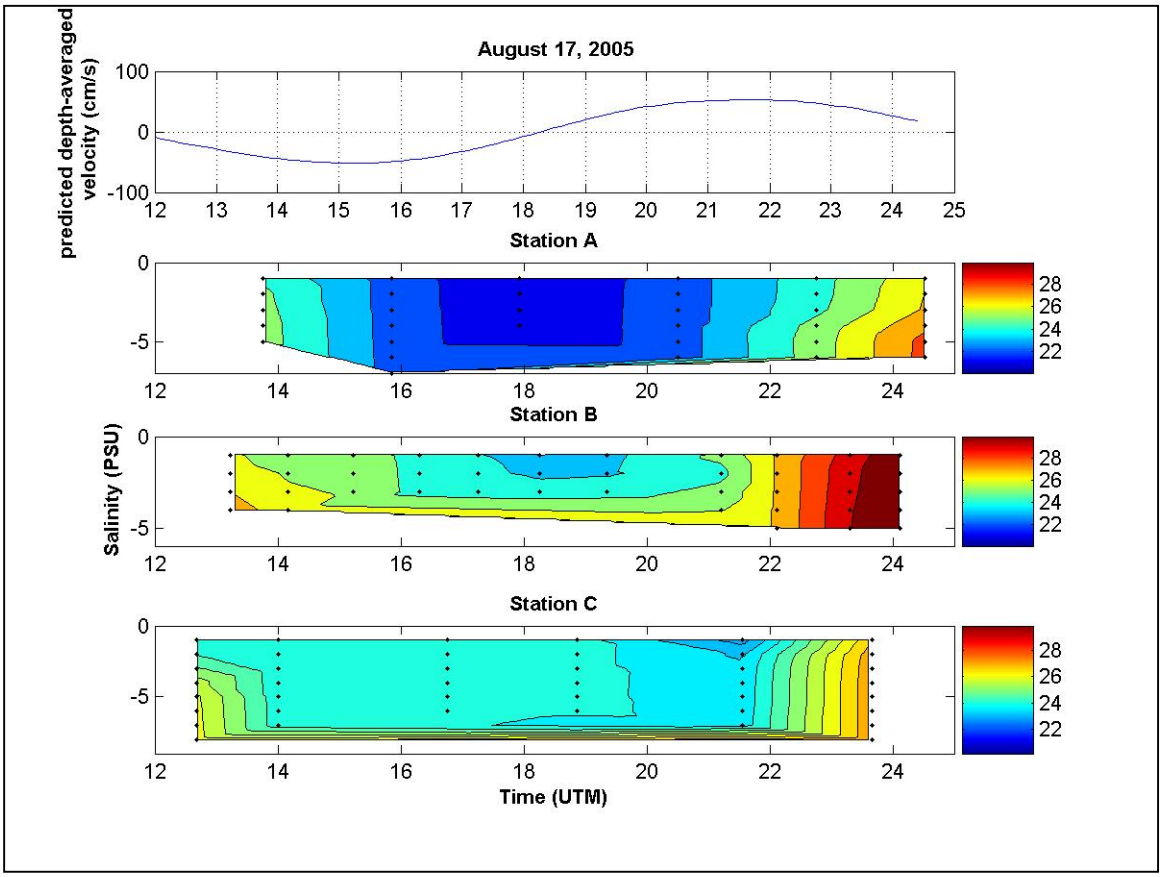

Figure 2.10: Predicted depth-averaged velocities and profiles of salinity (PSU) at stations A, B, and C on August 17, 2005. Black dots indicate time and depth of each CTD cast.

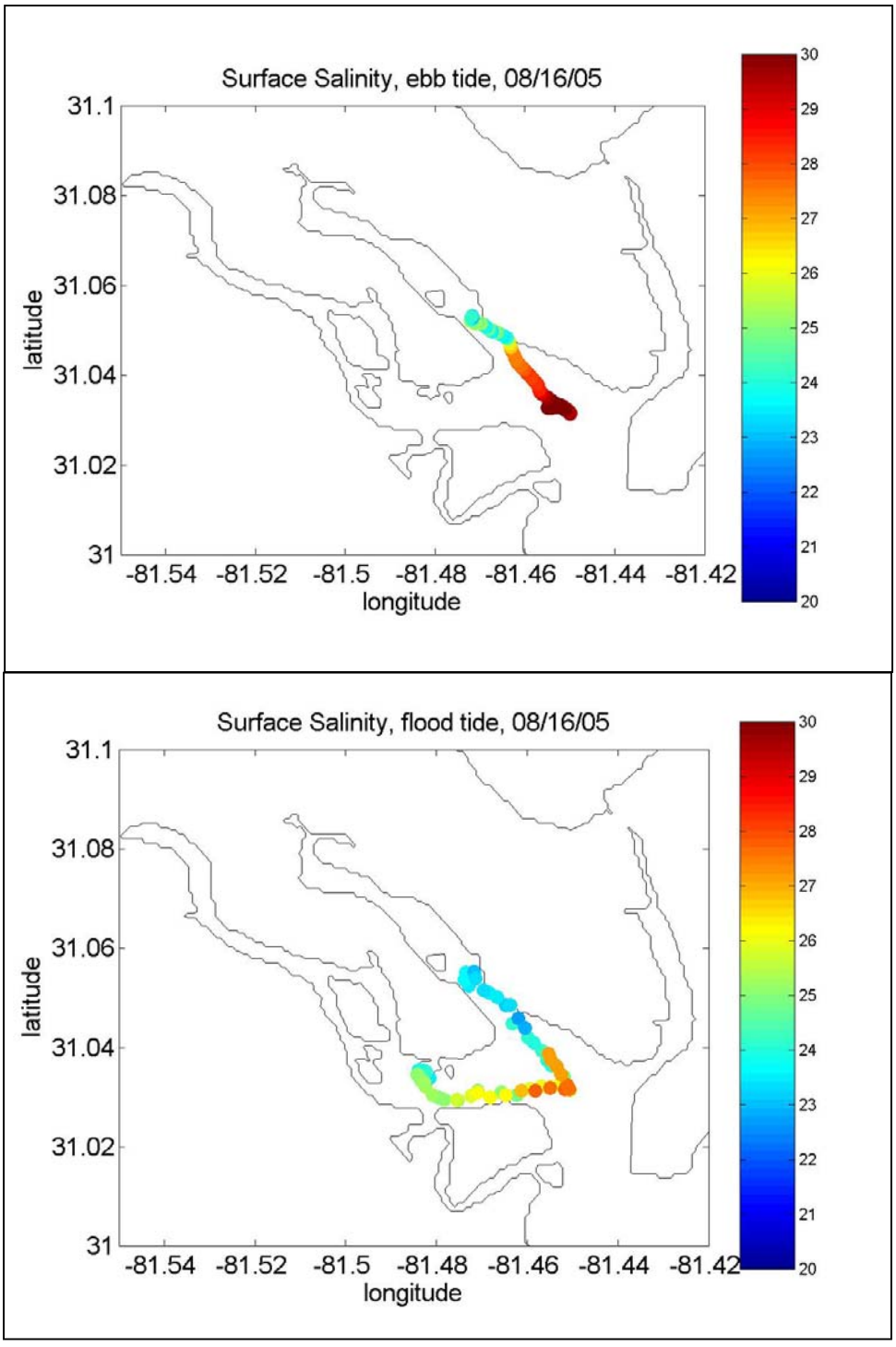

Figure 2.11: Surface salinity during ebb tide (top) and flood tide (bottom) on August 16, 2005.

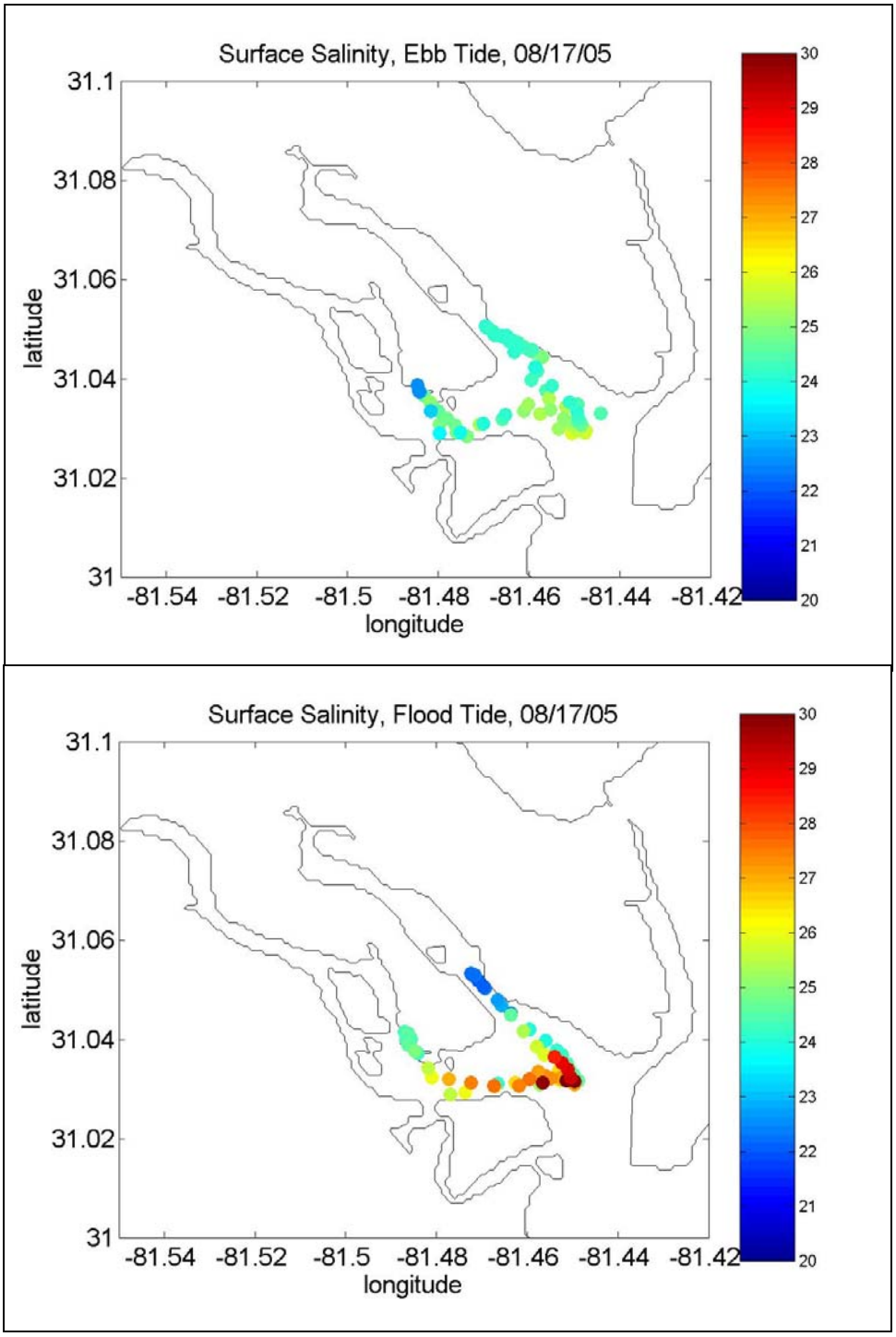

Figure 2.12: Surface salinity during ebb tide (top) and flood tide (bottom) on August 17, 2005.

Surface salinities were similar in Jointer Creek and the Little Satilla River during both days of sampling in August 2005; however, some fresher water was observed in

Jointer Creek during flood tide on both days (Figs. 2.11 & 2.12). The highest surface salinities were measured at station B. Surface temperatures were highest in Jointer creek during both flood and ebb tide on both days of sampling (See Appendix).

September 29 - 30, 2005

Sampling took place in September 2005 during neap tides, due to the quarter moon on September 25, 2005, resulting in weaker currents than April or August (compare Figs. 2.7 - 2.8, 2.9 - 2.10, & 2.13 – 2.14). The winds during this period were sporadic in direction and relatively weak (~ 3 m/s) until the end of the day on September 30 when the wind speed increased to 7 m/s and maintained a southward direction (Fig. 2.4).

The profiles of vertical salinity stratification on September 29-30, 2005 exhibited the same differences in salinity between the Little Satilla River and Jointer Creek as in previous months. Station A showed salinities ranging from 25 PSU to 28 PSU, while Station C exhibited salinities ranging from 27 PSU to 29 PSU (Fig. 2.13 & 2.14). The lowest salinity was seen in the Little Satilla River when the tide changed from ebb to flood (Fig. 2.13 & 2.14). The most saline water, around 30 PSU, was present at station B, again during peak flood tide, when the ocean water reached this station (Fig. 2.13 & 2.14). During both days, the temperature profiles showed slight warming in the afternoon, with temperatures ranging from 27 to 30 °C, but increases were not as extreme as were seen during the summer months (See Appendix). All stations demonstrated a partially mixed system with a maximum vertical salinity gradient of around 0.25 PSU/m with more vertical stratification during the flooding tide than during the ebb tide (Fig. 2.13 & 2.14).

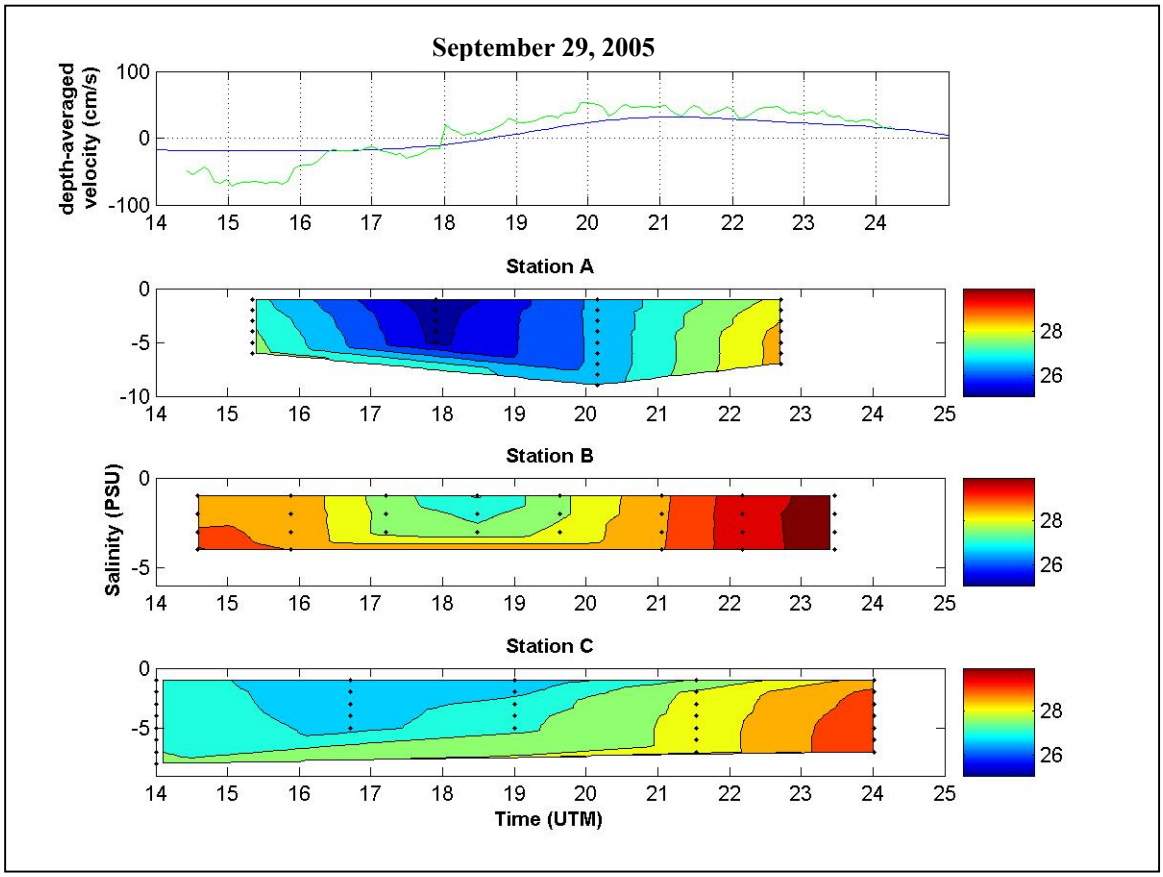

Figure 2.13: Predicted (blue) and actual (green) depth-averaged velocities with profiles of salinity (PSU) Stations A, B, and C on September 29, 2005. Black dots indicate time and depth of each CTD cast.

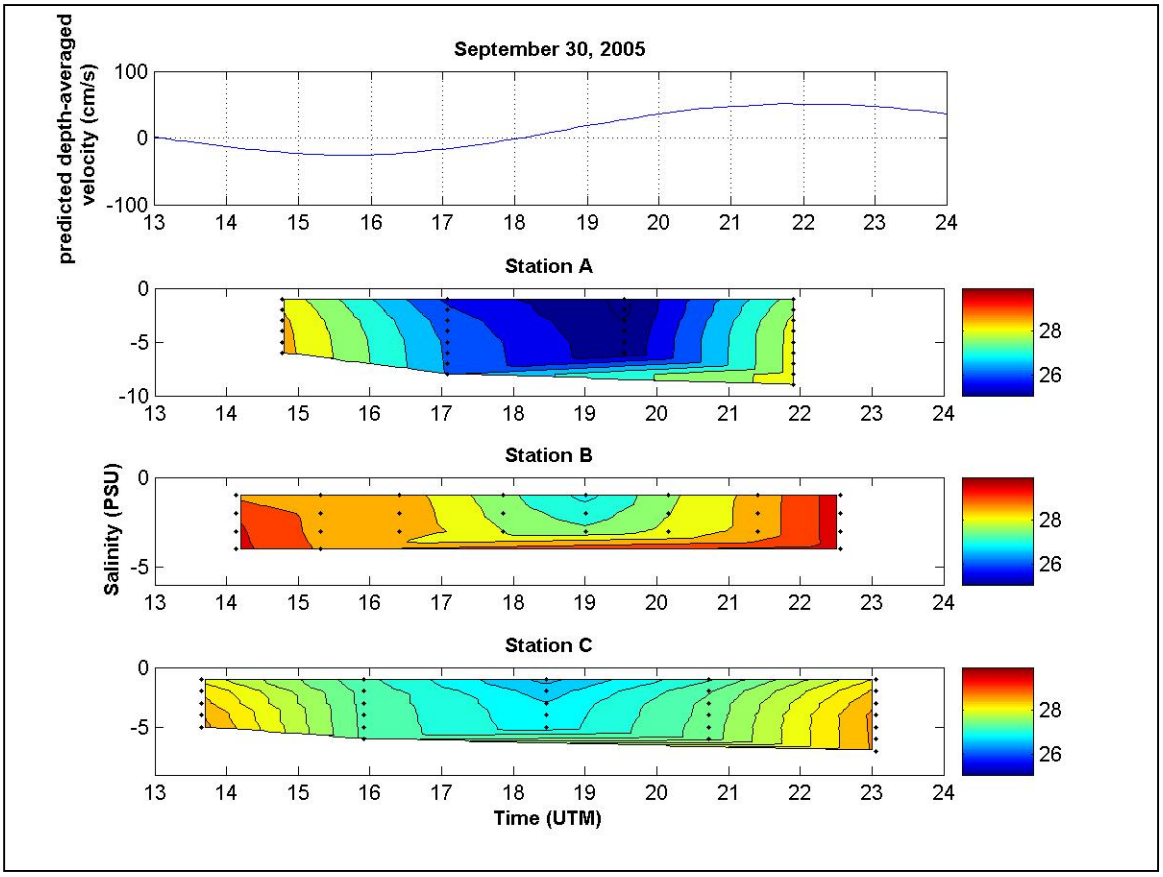

Figure 2.14: Predicted depth-averaged velocities and profiles of salinity (PSU) at stations A, B, and C on September 30, 2005. Black dots indicate time and depth of each CTD cast.

The highest surface salinity was observed where the two tributaries converge near station B, while the lowest surface salinity was seen at the beginning of flood tide in the Little Satilla River (Fig. 2.15 & 2.16). Surface salinities were higher in Jointer Creek than in the Little Satilla River during both phases of the tide on both days of sampling (Fig. 2.15 & 2.16). The highest surface temperatures were recorded in the tributaries during the afternoon on both days of sampling (See Appendix).

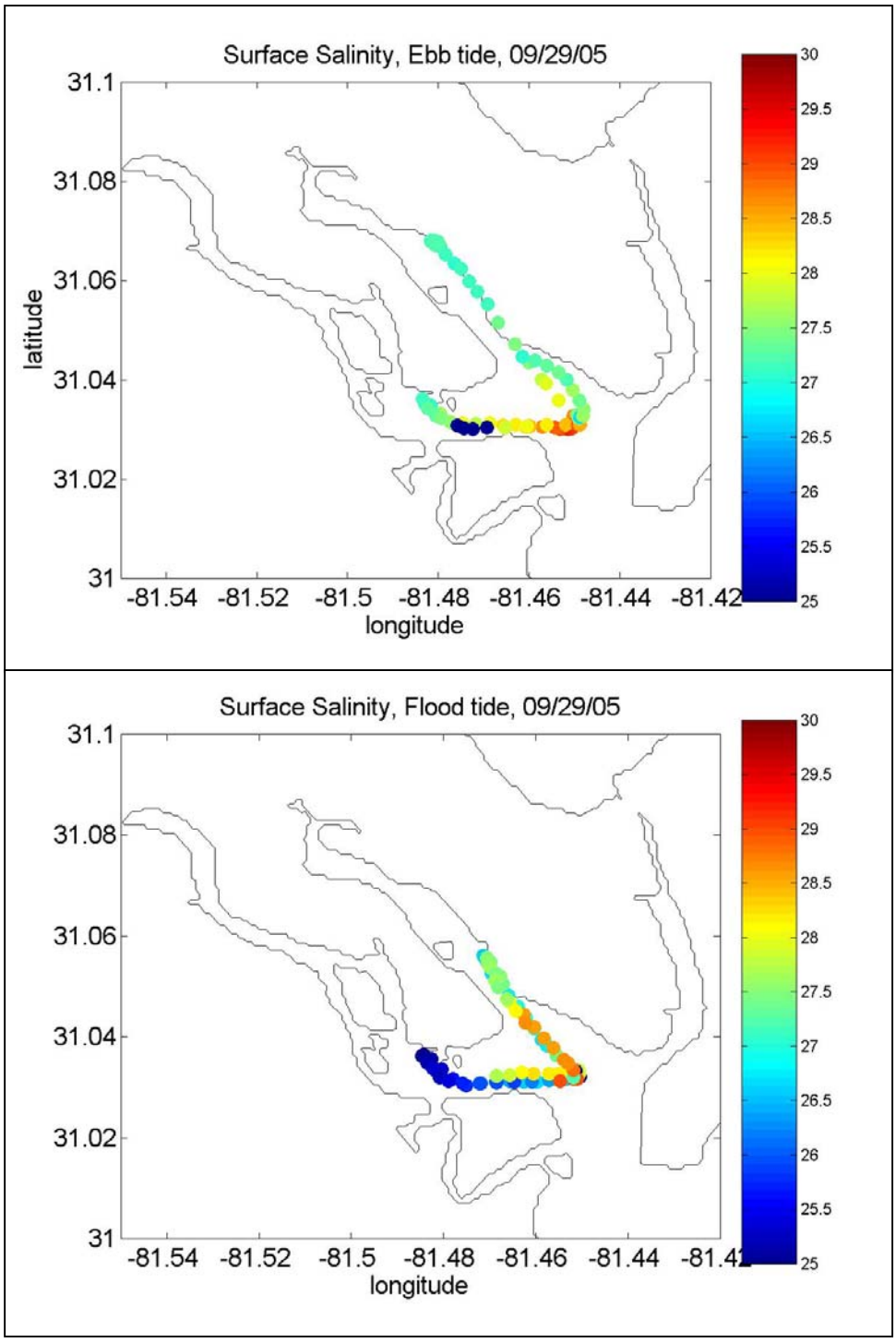

Figure 2.15: Surface salinity (PSU) in the Little Satilla River and Jointer Creek during ebb tide (top) and flood tide (bottom) on September 29, 2005.

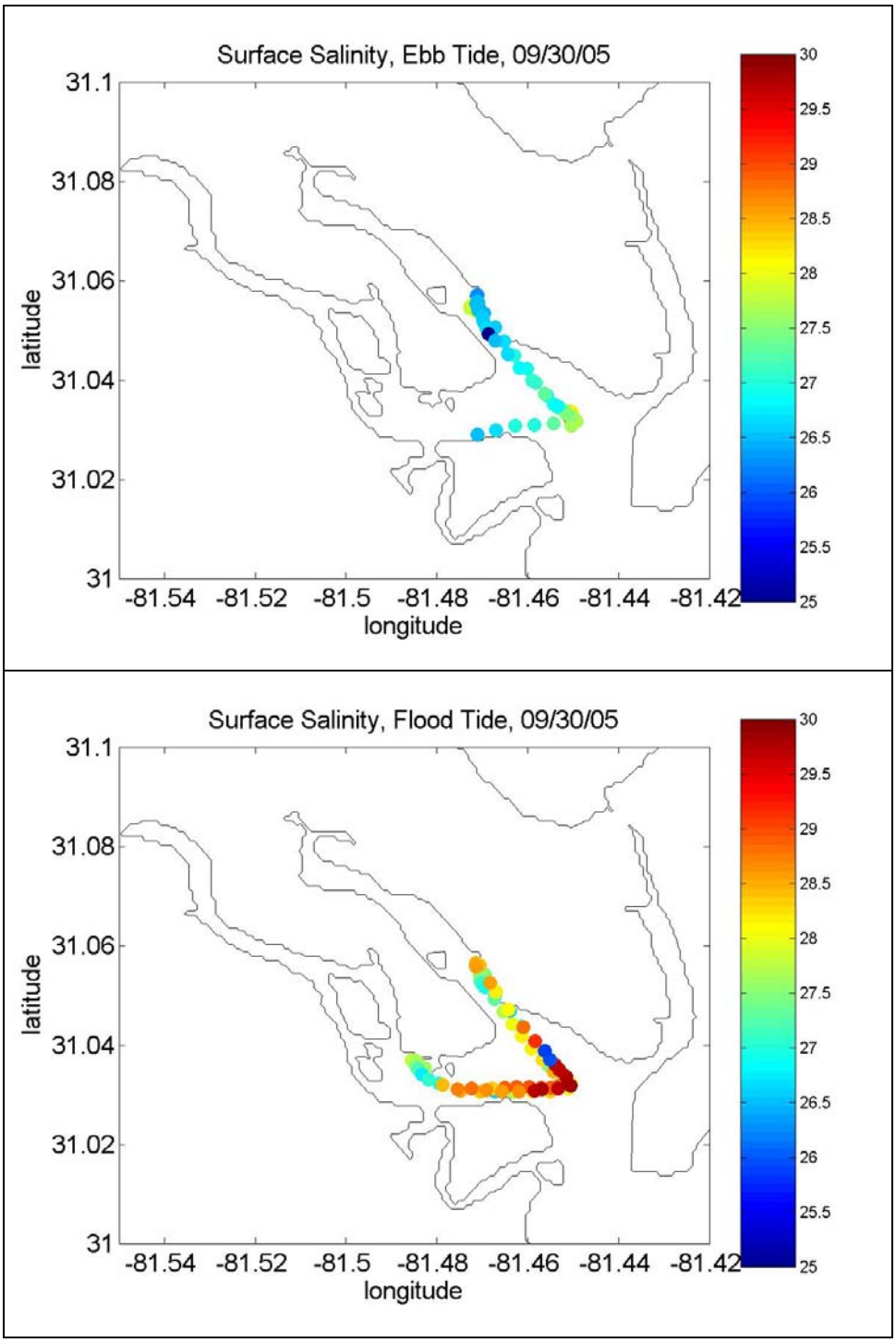

Figure 2.16: Surface salinity (PSU) in the Little Satilla River and Jointer Creek during ebb tide (top) and flood tide (bottom) on September 30, 2005.

August 2, 2006

Sampling took place on August 2, 2006 during neap tides, due to the quarter moon occurring on that date, resulting in comparable currents to the September 2005 sampling dates. The winds during this sampling period were strongly northward, measuring almost 8 m/s during the day (Fig. 2.4), resulting in oceanward movement of surface water within the estuary. The winds during the night were minimal, measuring less than 1 m/s (Fig. 2.4).

A new station in the tributaries was added during the August 2006 sampling dates. Station D (Fig. 1.2) was included in order to examine a more oceanward station and to observe processes occurring between the tributaries and the main Satilla River.

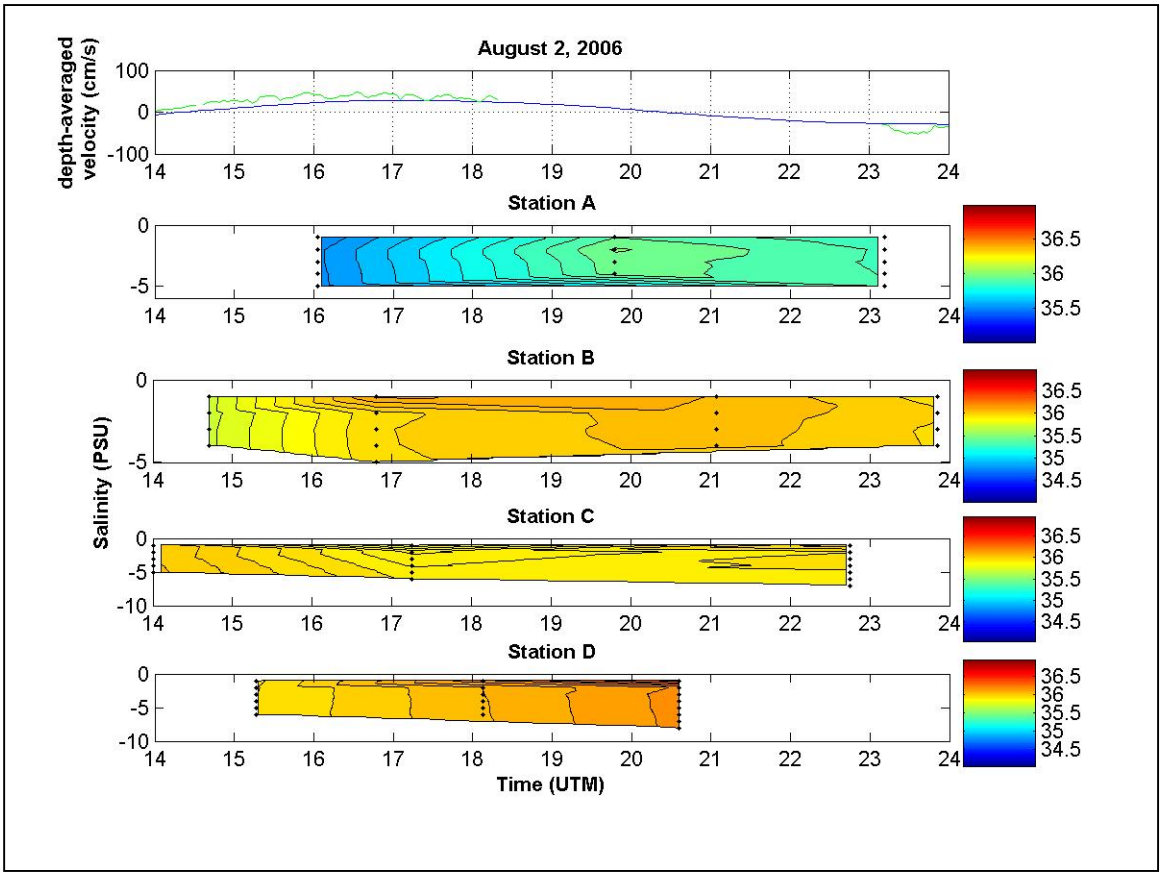

Figure 2.17: Predicted (blue) and actual (green) depth-averaged velocities with profiles of salinity (PSU) over time at stations A, B, C, and D on August 2, 2006. Black dots indicate time and depth of each CTD cast. Note change in salinity scale.

The vertical profiles of salinity for the August 2, 2006 sampling date show much higher salinities in the tributaries than during previous sampling periods (compare Figs. 2.7 – 2.10, 2.13 – 2.14, & 2.17). All the stations within the tributaries exhibited salinities around 36 PSU and the salinities changed little over the entire sampling day. The higher salinities resulted in much higher densities in the estuary and very little vertical stratification: less than 0.1 PSU/m within the tributaries (Fig. 2.17). The temperatures at all four stations varied from 29 - 31 °C and station D exhibited the lowest afternoon temperatures (See Appendix).

While the surface salinities were higher in Jointer Creek than in the Little Satilla, on August 2, 2006, the difference was small (Fig. 2.18). Slightly fresher surface water, 34 – 35.5 PSU, was observed in the Little Satilla River during flood tide (Fig. 2.18). A pulse of fresher water was seen upstream in the Jointer Creek during ebb tide (Fig. 2.18). The ebb tide occurred in the afternoon and resulted in higher surface temperatures during this time (See Appendix).

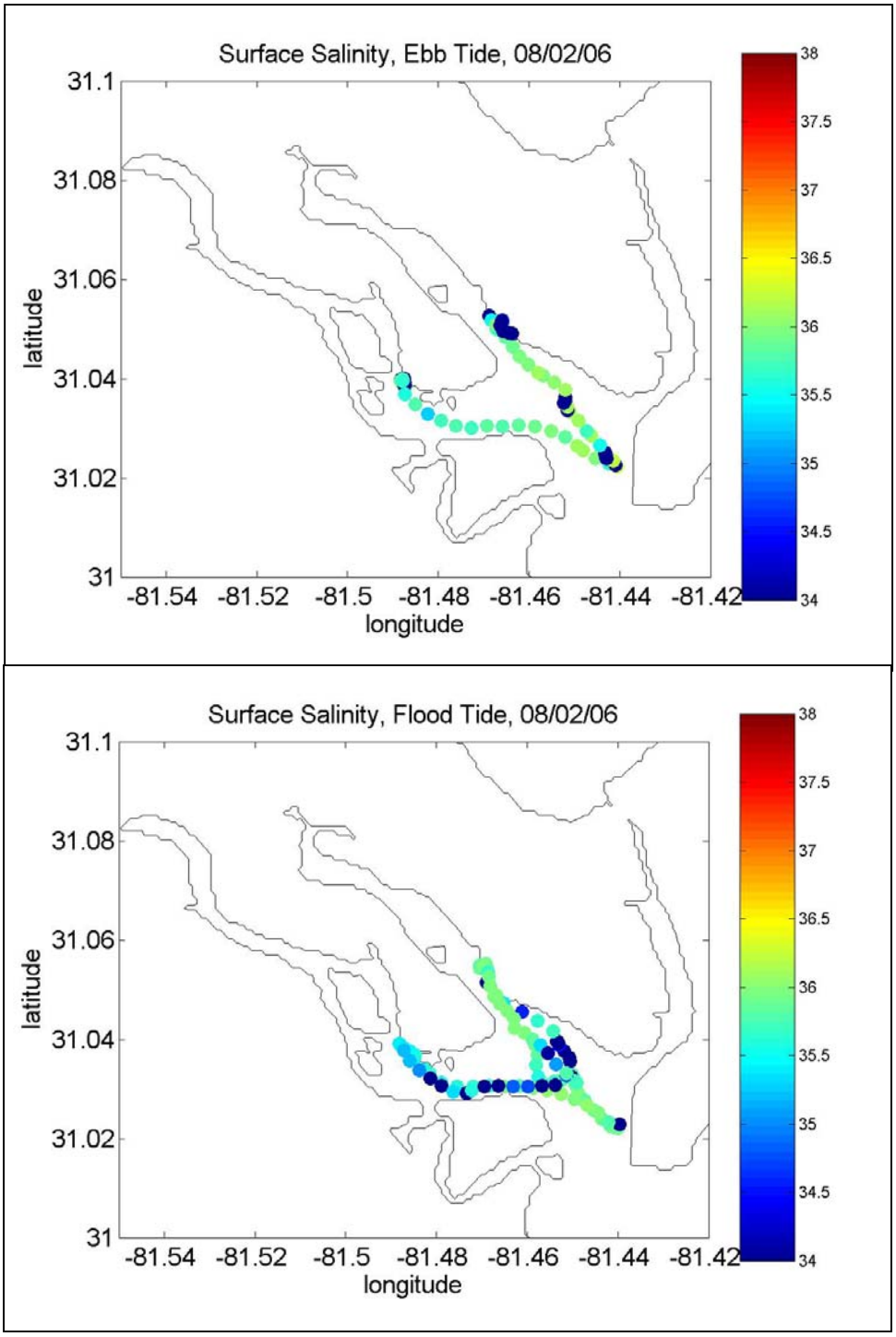

Figure 2.18: Surface salinity (PSU) in the tributaries during ebb tide (top) and flood tide (bottom) on August 2, 2006.

Drifter Results

During June and July of 2005, a number of drifters equipped with GPS trackers were deployed in the tributaries to examine the transport pathways. Additionally, CTD casts were made to measure vertical salinity profiles.

Both June and July 2005 had comparable currents to April and August of 2005 due to the presence of the spring tide. The winds on June 21 were strongly southward, measuring almost 8 m/s (Fig. 2.4), resulting in landward movement of surface water within the estuary. The winds on June 22 were much lighter and varied in their direction throughout the day (Fig. 2.4). Winds during July 19 – 20 oscillated between northward during the middle of the day and southward at night; however, the wind speeds were weaker and only measured 2 to 4 m/s (Fig. 2.4).

All the drifters in this study remained within the tributaries and were not lost to the sound or the coastal ocean over the tidal cycle. The degree of mixing between the tributaries is evident during both time periods (Fig. 2.19 & 2.20) The movement of the drifters in Jointer Creek (top panels of Figs. 2.19 & 2.20) show that little water exits the tributary as none of the drifters released upstream on ebb tide exited Jointer Creek. Instead all returned to the creek on the subsequent flood tide. The movement of water from the Little Satilla River (bottom panel of Figs. 2.19 & 2.20) into Jointer Creek is apparent. During both deployments of drifters into the Little Satilla River, a subset of drifters that were released during ebb tide in the Little Satilla River traveled into and up the Jointer Creek tributary during flood tide (Figs. 2.19 & 2.20). During the June deployment, 1 out of 6 drifters traveled from the Little Satilla River up into Jointer Creek.

During July, 3 out of 6 drifters moved from the Little Satilla River to Jointer Creek (Figs. 2.19 & 2.20).

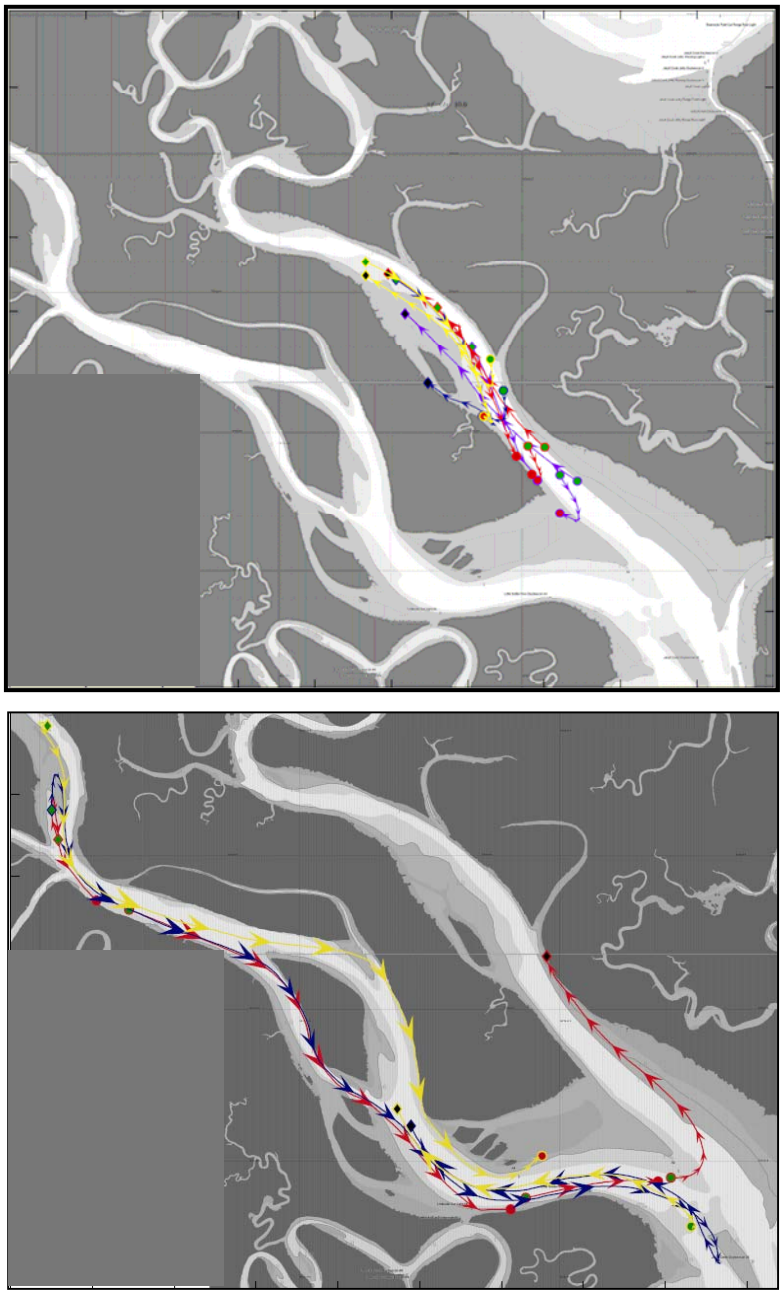

Figure 2.19: Drifter tracks over tidal cycle in Jointer Creek on June 21, 2005 (top) and the Little Satilla River on June 22, 2005 (bottom). The different colors represent the trajectories of different drifters. The arrows show the direction and relative speed of the drifter. The green circles depict where the drifter started, the red circles were it stopped, and the black squares indicate where the drifter was stuck in the marsh.

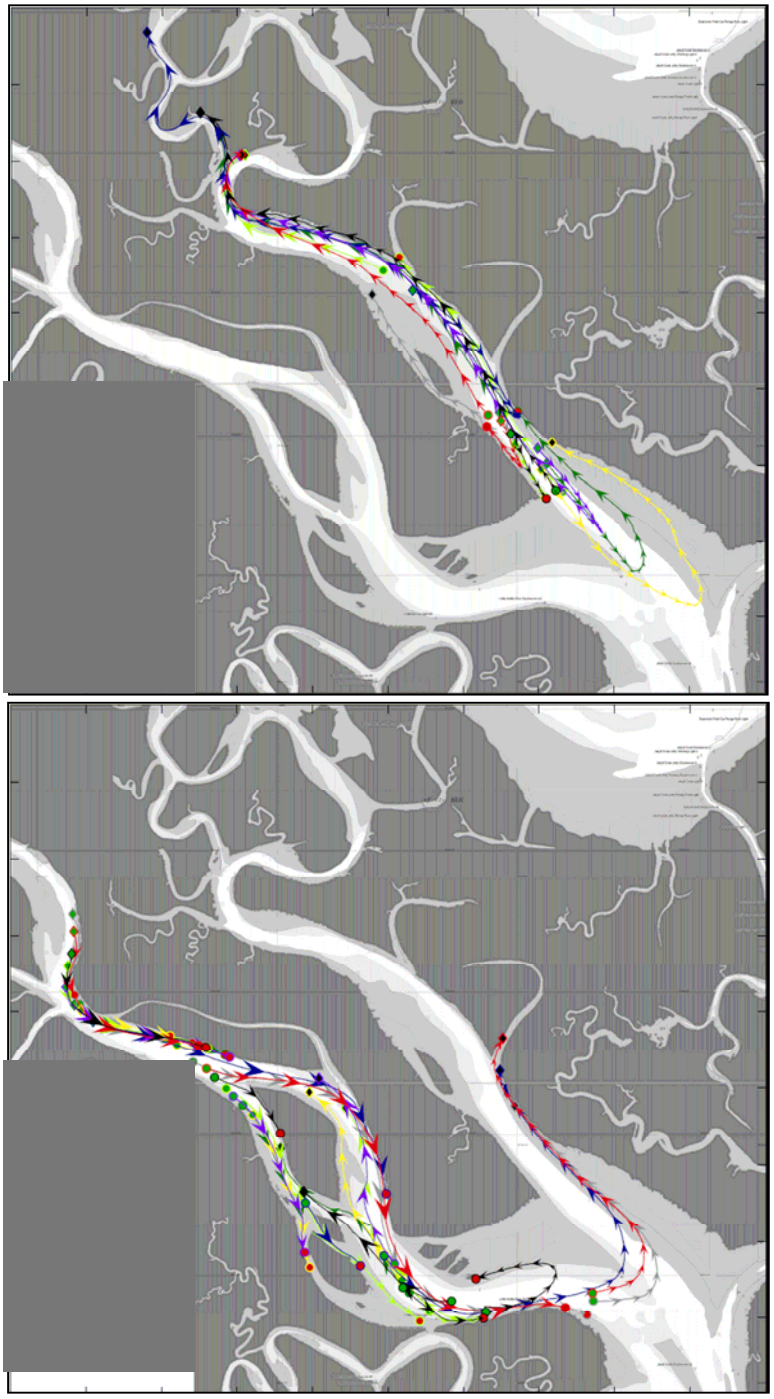

Figure 2.20: Drifter tracks over tidal cycle in Jointer Creek on July 19, 2005 (top) and the Little Satilla River on July 20, 2005 (bottom). The different colors represent the trajectories of different drifters. The arrows show the direction and relative speed of the drifter. The green circles depict where the drifter started, the red circles were it stopped, and the black squares indicate where the drifter was stuck in the marsh.

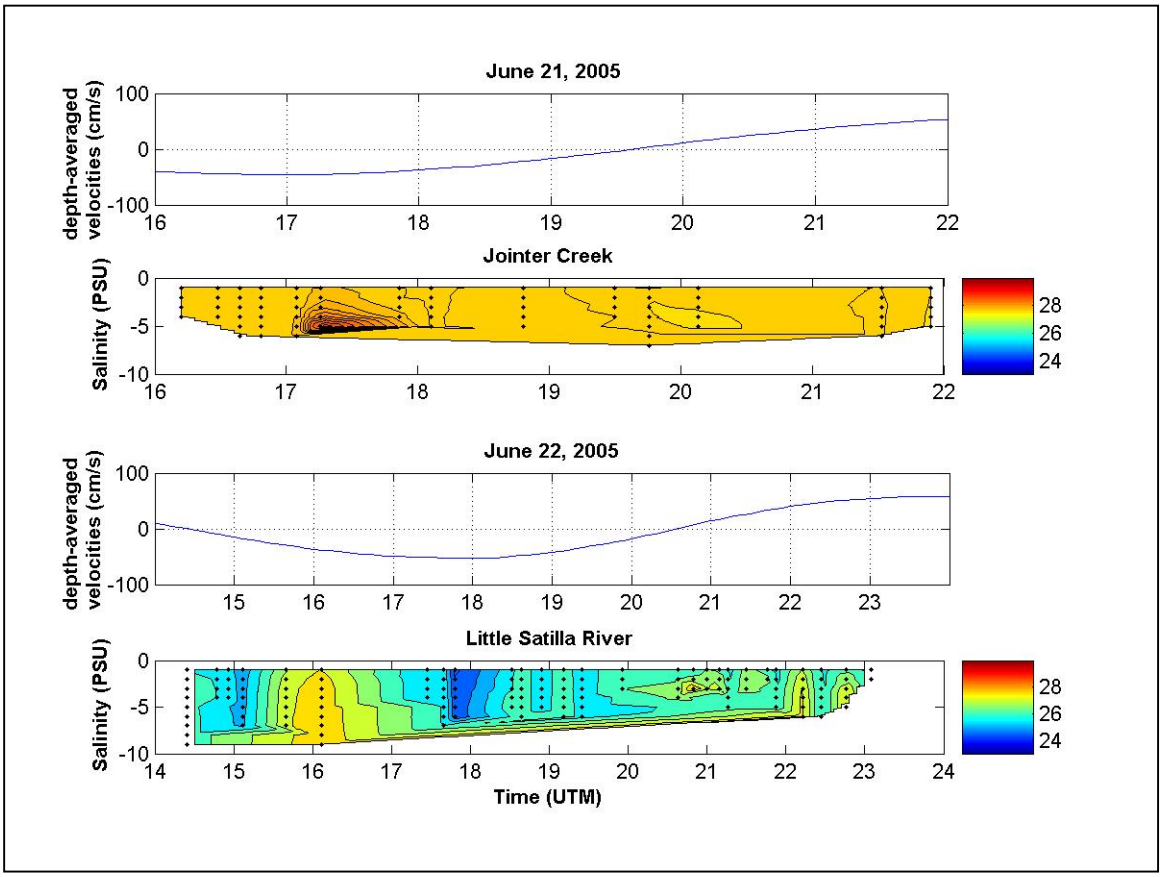

Figure 2.21: Predicted depth-averaged velocities with salinity profiles for June 21, 2005 in Jointer Creek (top 2 panels) and June 22, 2005 in the Little Satilla River (bottom 2 panels). Black dots indicate time and depth of each CTD cast.

The salinity profiles differ greatly between June and July 2005. During June, the salinity in the Little Satilla River varied from 24 to 27 PSU, while the salinity in Jointer Creek remained around 27 to 28 PSU (Figs. 2.21). Jointer Creek showed a vertical stratification of less than 0.1 PSU/m and the Little Satilla River only exhibited vertical stratification of 0.2 PSU/m (Figs. 2.21). The temperature was slightly higher in Jointer Creek than in the Little Satilla River and it increased slightly throughout the day (See Appendix).

The salinities measured in July 2005 were much lower than in June (17 – 23 PSU in July compared to 24 – 28 PSU in June) (compare Figs. 2.21 & 2.22). Jointer Creek exhibited a high salinity of only 23 PSU, while the Little Satilla River reached only 20 PSU (Fig 2.22). The highest temperatures in both tributaries were in the afternoon and the temperatures in both tributaries were equivalent (See Appendix). The salinity profiles for the Little Satilla River and Jointer Creek in July showed more vertical stratification in the tributaries than was seen in the June (Fig. 2.21 & 2.22). In July, Jointer Creek demonstrated vertical stratification of around 0.2 PSU/m, while the Little Satilla River showed vertical stratification of almost 0.3 PSU/m (Figs. 2.22). The presence of little vertical stratification is evidence for a partially mixed system.

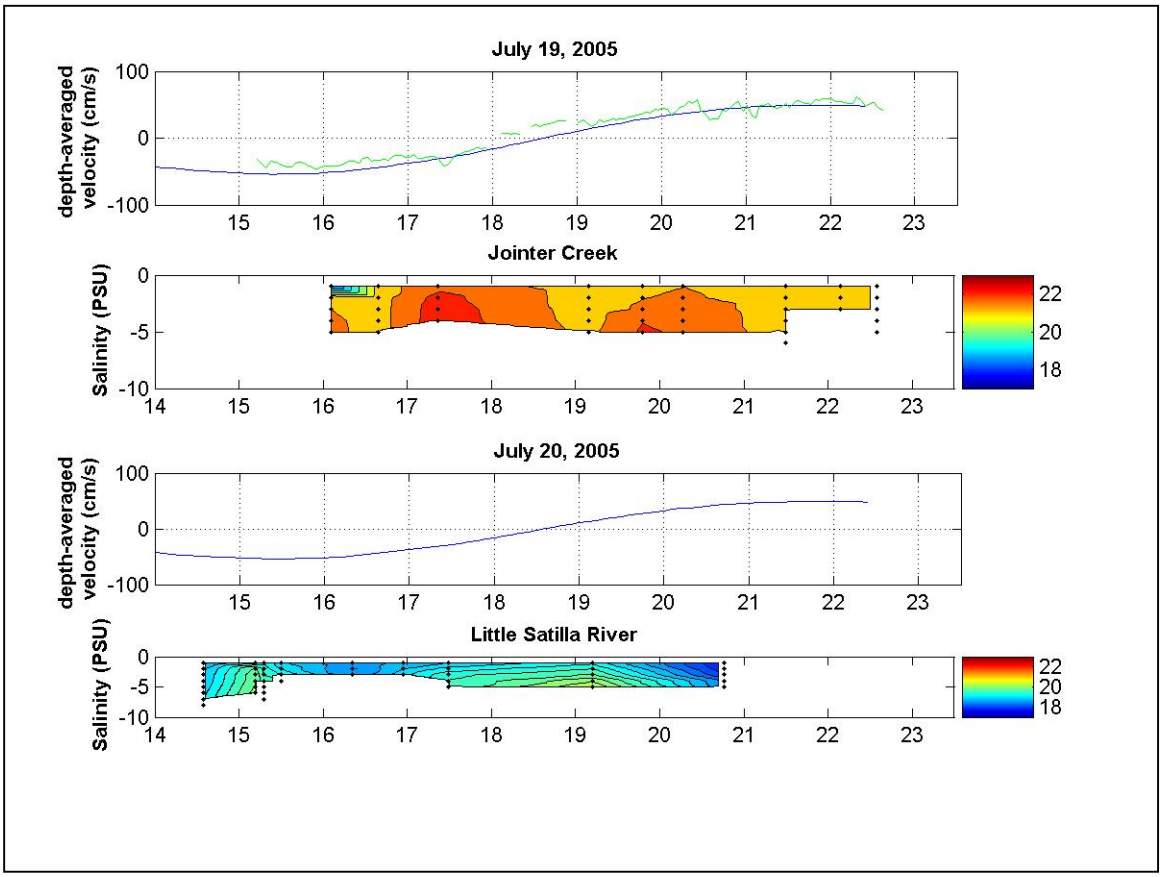

Figure 2.22: Predicted (blue) and actual (green) depth-averaged velocities with salinity profiles for July 19, 2005 in Jointer Creek (top 2 panels) and July 20, 2005 in the Little Satilla River (bottom 2 panels). Black dots indicate time and depth of each CTD cast.

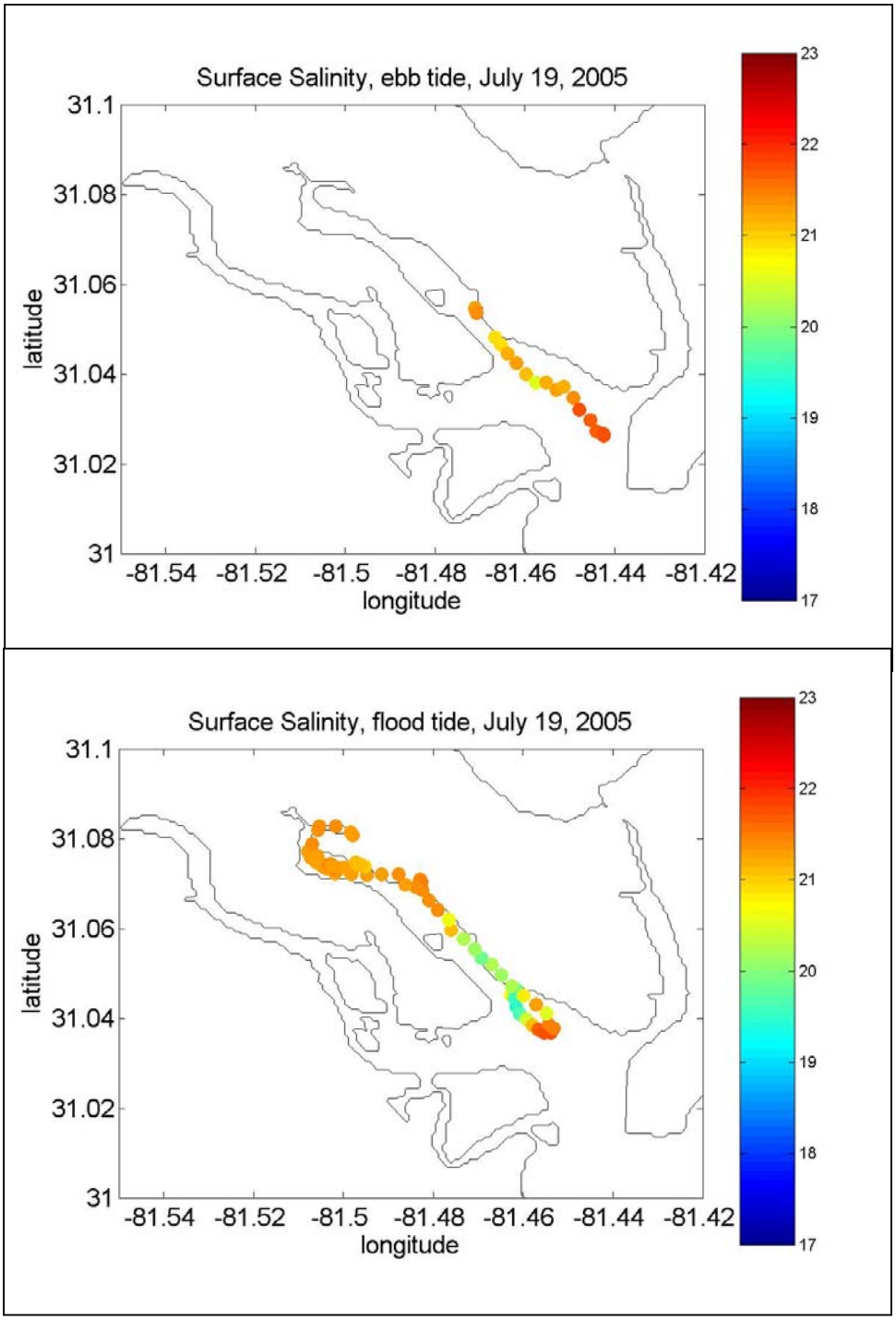

Figure 2.23: Surface salinity (PSU) in Jointer Creek during ebb tide (top) and flood tide (bottom) July 19, 2005.

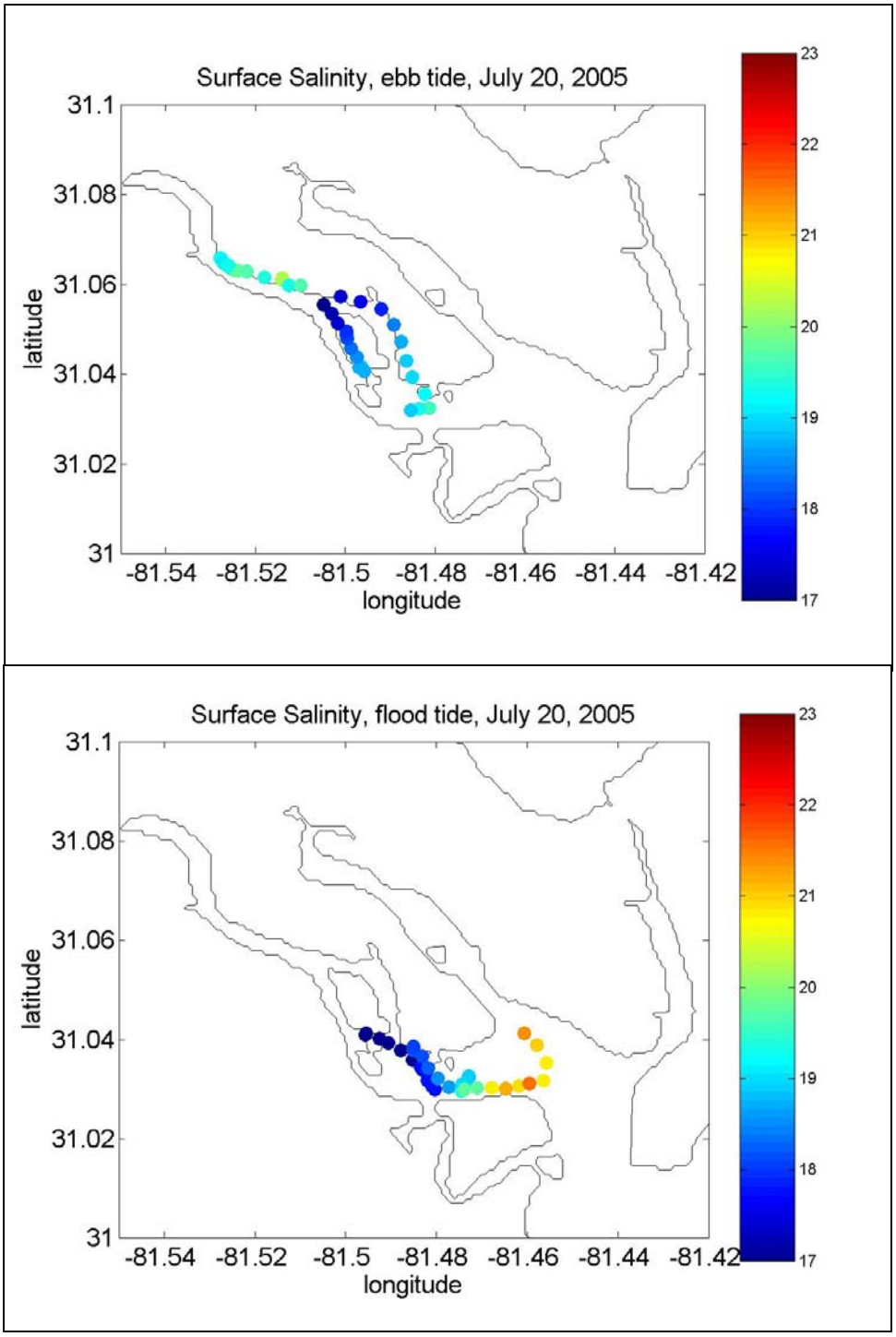

Figure 2.24: Surface salinity (PSU) in the Little Satilla River during ebb tide (top) and flood tide (bottom) on July 20, 2005.

Examination of the surface salinities during July (there were no surface salinity measurements in June) reveals significant differences in the salinity between the two tributaries (Figs. 2.23 & 2.24) that are similar to those in September 2005 and August 2006. The Little Satilla River showed slightly lower salinities than Jointer Creek during July 2005 (compare Figs. 2.15, 2.16, 2.18, & 2.24). The surface salinity in Jointer Creek ranged from 20 PSU to 22 PSU and the lowest salinity was located at the mouth of the creek during flood tide (Fig. 2.24). This pulse of fresher water is likely due to the mixing of ebbing water from the Little Satilla River up into Jointer Creek as was observed by the trajectories of the drifters. The Little Satilla River exhibits fresher water than Jointer Creek with salinities ranging from 17 PSU to 21 PSU (Fig. 2.24). The surface temperature in the Little Satilla River, around 18 °C to 20 °C, is also less than the surface temperature seen in Jointer Creek, around 21 °C to 22 °C (See Appendix).

Satilla River

Sampling in 2006 focused on the main Satilla River. The transect described in figure 1.1 was sampled before and after the tide entered the estuary. Sampling took place in March and August in order to compare the river at different times of the year.

March 14 - 15, 2006

The sampling dates in March 2006 experienced spring tides (due to the full moon on March 14, 2006) resulting in strong currents comparable to those measured in April and August in the tributaries. The winds during this sampling period were mostly northward and reached speeds of 8 m/s during the second day of the sampling (Fig. 2.4), resulting in oceanward transport of surface waters. Ten stations along the transect of the

river were sampled as well as four stations to the south of an island in the middle of the river (Fig. 1.1).

The increased freshwater present in the Satilla River resulted in extremely different salinity profiles from the smaller tributaries. Stations were sampled in the same direction as the tidal currents in the Satilla River, allowing for the sampling of the water returning to the estuary during flood tide and the retreating saltwater originating in the coastal ocean during ebb tide. As a result, the stations and plots of salinity are classified as either (1) after flood tide or (2) after ebb tide. At each station, the physical sampling was similar to that in the tributaries.

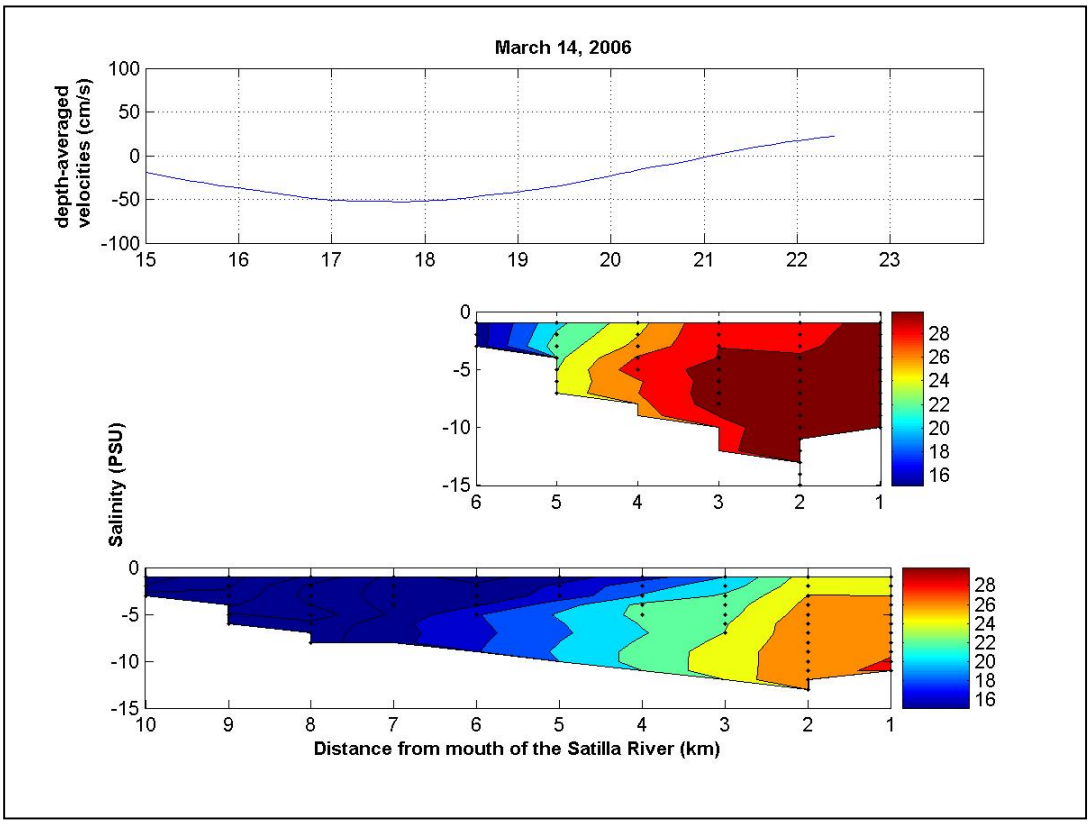

Figure 2.25: Predicted depth-averaged velocity with profiles of salinity (PSU) along transect of the Satilla River after the tide has moved in (middle panel) and after the tide has move out (bottom panel) on March 14, 2006. Black dots show location and depth of CTD casts. Note that the x-axis shows distance away form the mouth of the Satilla River instead of time.

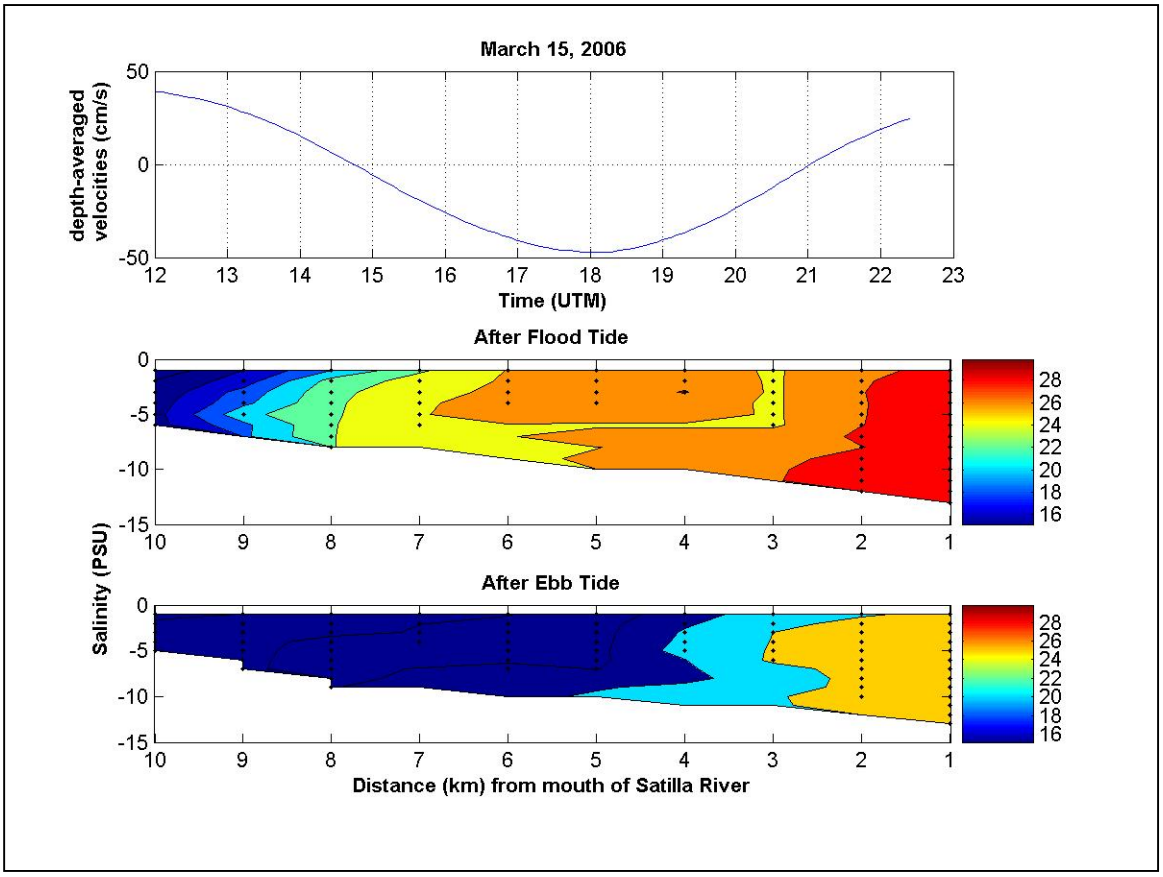

Figure 2.26: Predicted depth-averaged velocity with profiles of salinity (PSU) along transect of the Satilla River after the tide has moved in (middle panel) and after the tide has move out (bottom panel) on March 15, 2006. Black dots show location and depth of CTD casts. Note that the x-axis shows distance away form the mouth of the Satilla River instead of time.

Figures 2.25 and 2.26 show depth-averaged velocity as a function of time (top panel) and salinity as a function of distance away from the mouth of the estuary (bottom panels). The transects are divided between (1) after flood tide or (2) after ebb tide. Salinity profiles reveal a strong horizontal gradient of salinity along the Satilla River after both flood and ebb tide (Fig. 2.25 & 2.26). Salinity ranged from around 30 PSU near the mouth to less than 16 PSU upstream (Figs. 2.25 & 2.26). The flooding and ebbing of the tide plays a large role in the horizontal gradient of salinity within the estuary. After the tide ebbed, the 20 PSU water occurred 4 and 5 km upstream; however after the tide

flooded, the 20 PSU water was found further upriver, around 8 and 9 km upstream (Figs. 2.25 & 2.26). The temperature did not change much over the stations (See Appendix).

The main Satilla River was characterized by greater vertical stratification than the tributaries. The location of the maximum stratification was largely influenced by the tidal phase. After the ebb tide, there was greater vertical stratification downstream, around 0.3 – 0.4 PSU/m at 1 and 2 km from the mouth of the river (Figs. 2.25 & 2.26). After flood tide there was greater vertical stratification upstream, around 0.3 – 0.5 PSU/m at 8 and 9 km upriver (Figs. 2.25 & 2.26). In general the Satilla River experienced greater stratification during ebb tide.

The surface salinities are shown in figures 2.27 and 2.28 and are again divided into (1) after flood tide or (2) after ebb tide. The saltiest water was present after flood tide in the mouth of the estuary, while the freshest water was present upstream (Fig. 2.27 & 2.28). As expected, the effects of the freshwater were seen further downstream after the tide had ebbed and the effects of the freshwater were observed further upstream after the tide had flooded. The surface temperatures varied little throughout both days; however, the highest temperatures were seen in the afternoon (See Appendix).

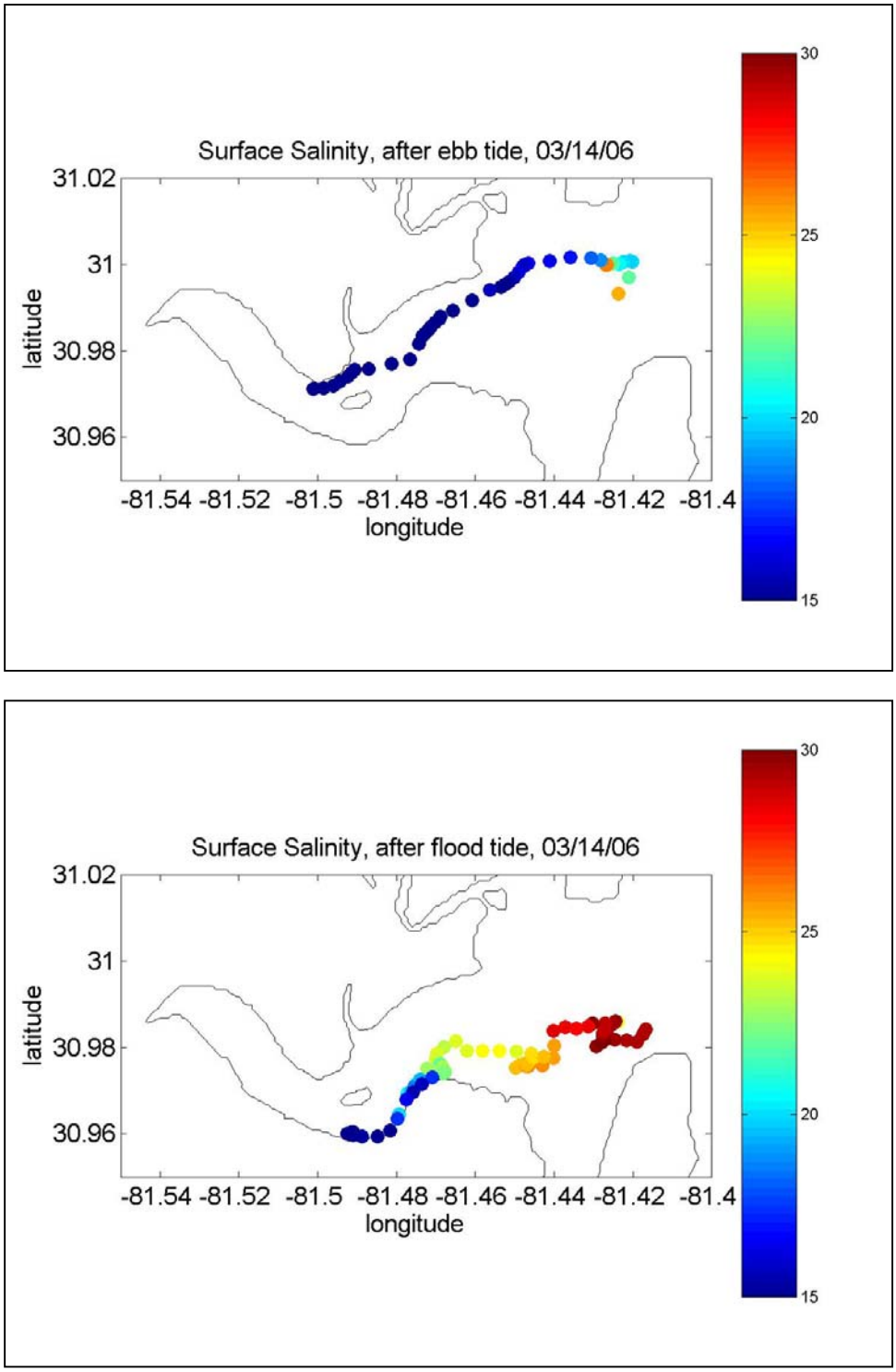

Figure 2.27: Surface salinity (PSU) along the Satilla River after ebb tide (top) and after flood tide (bottom) on March 14, 2006.

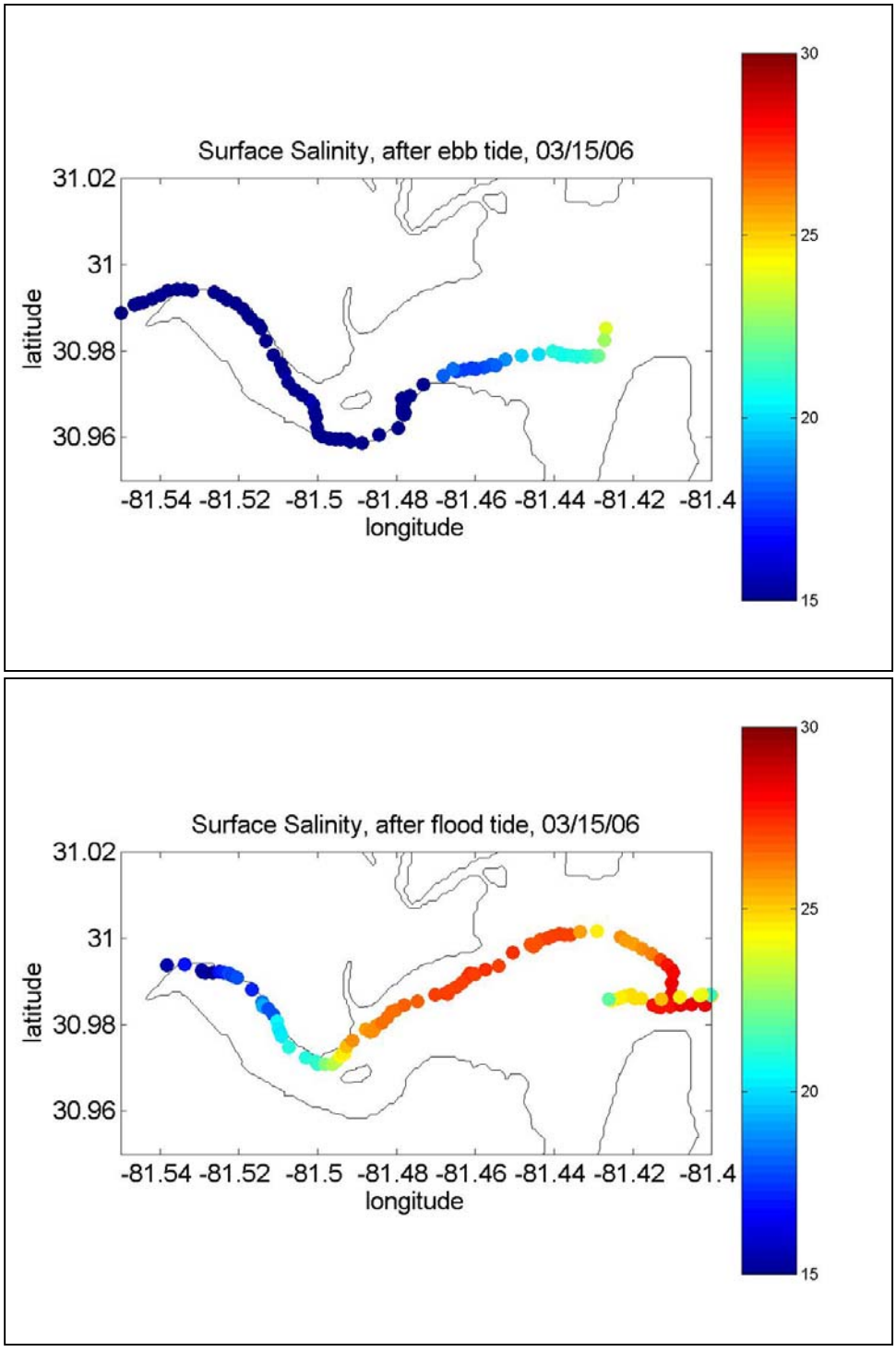

Figure 2.28: Surface salinity (PSU) along transect of the Satilla River after ebb tide (top) and after flood tide (bottom) on March 15, 2006.

August 3 - 4 2006

Sampling in August 2006 took place during the first quarter phase of the moon, resulting in neap tides and weaker currents within the estuary similar to September 2005. The winds during the August 2006 sampling were northward and measured almost 8 m/s during the day for all days of the sampling (Fig. 2.4), resulting in oceanward transport of surface water.

On August 3 and 4, sampling took place along the same transect of the Satilla River as in March 2006. Figures 2.29 and 2.30 show the depth-averaged velocity as a function of time and salinity as a function of distance away from the mouth of the estuary. The salinities along the transect of the river were much higher in August 2006 than they were in March of 2006 and only ranged from 34 PSU to 38 PSU (compare Figs. 2.25 & 2.26 to 2.29 & 2.30). At the mouth of the river, the system showed less than 0.1 PSU/m vertical stratification. Interestingly, the location of vertical stratification did not change with the tides as in March. The greatest vertical stratification was consistently upstream, reaching its largest value of 0.12 PSU/m after the tide had flooded on August 3, 2006 (Fig. 2.29 & 2.30).

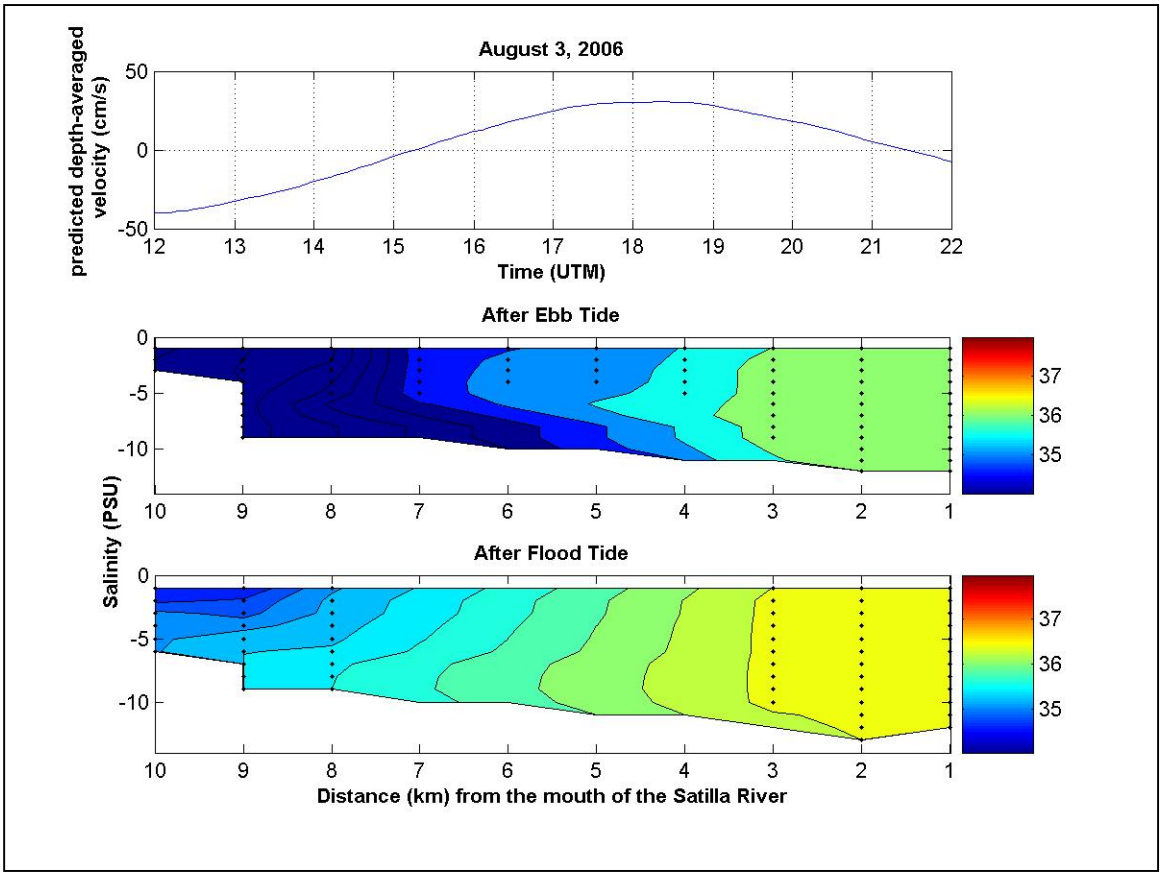

Figure 2.29: Predicted depth-averaged velocities with profiles of salinity (PSU) along the transect of the Satilla River after ebb tide (middle panel) and after flood tide (bottom panel) on August 3, 2006. Black dots show location and depth of each CTD cast. Note that the x-axis shows distance away form the mouth of the Satilla River instead of time.

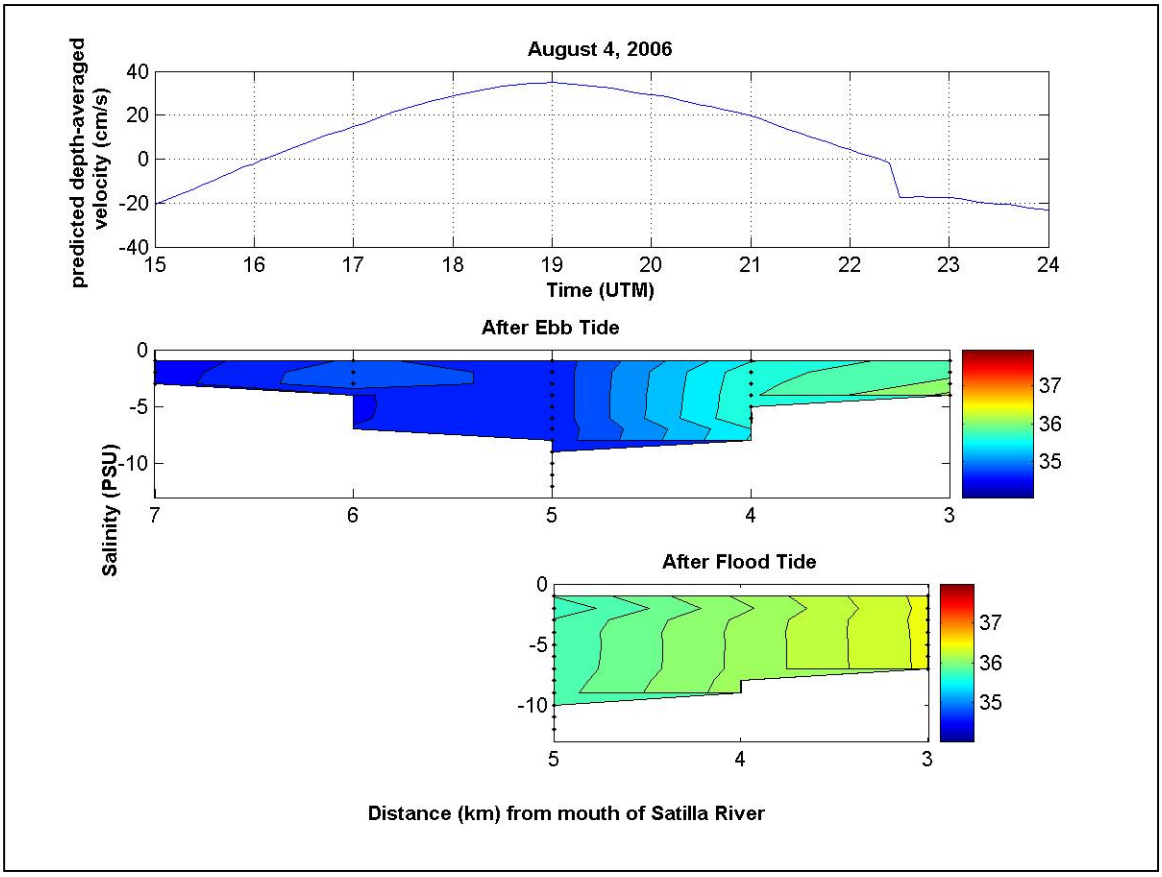

Figure 2.30: Predicted depth-averaged velocities with profiles of salinity (PSU) along the transect of the Satilla River after ebb tide (middle panel) and after flood tide (bottom panel) on August 4, 2006. Black dots show location and depth of each CTD cast. Note that the x-axis shows distance away form the mouth of the Satilla River instead of time.

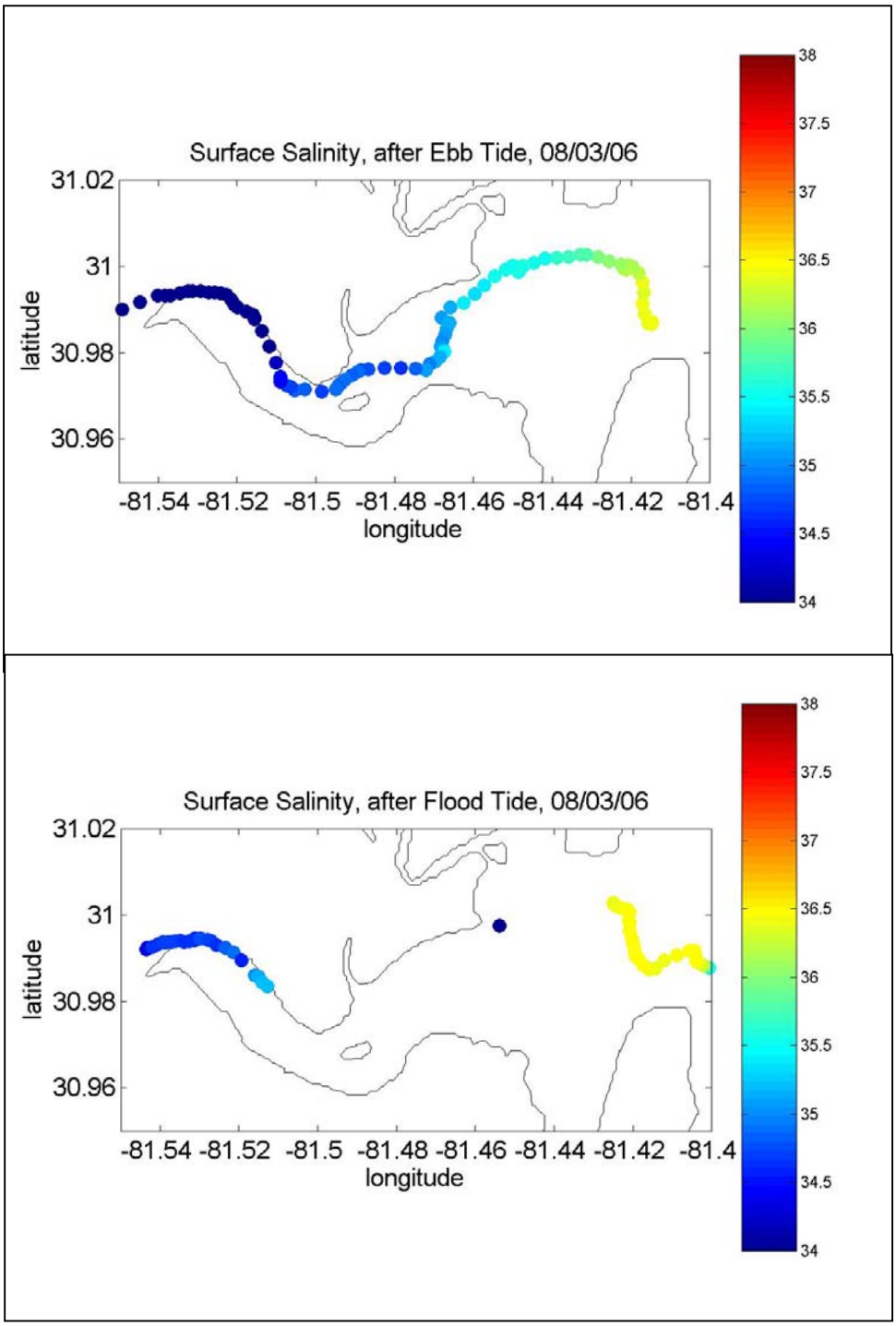

Figure 2.31: Surface salinity (PSU) along Satilla River after ebb tide (top) and after flood tide (bottom) on August 3, 2006.

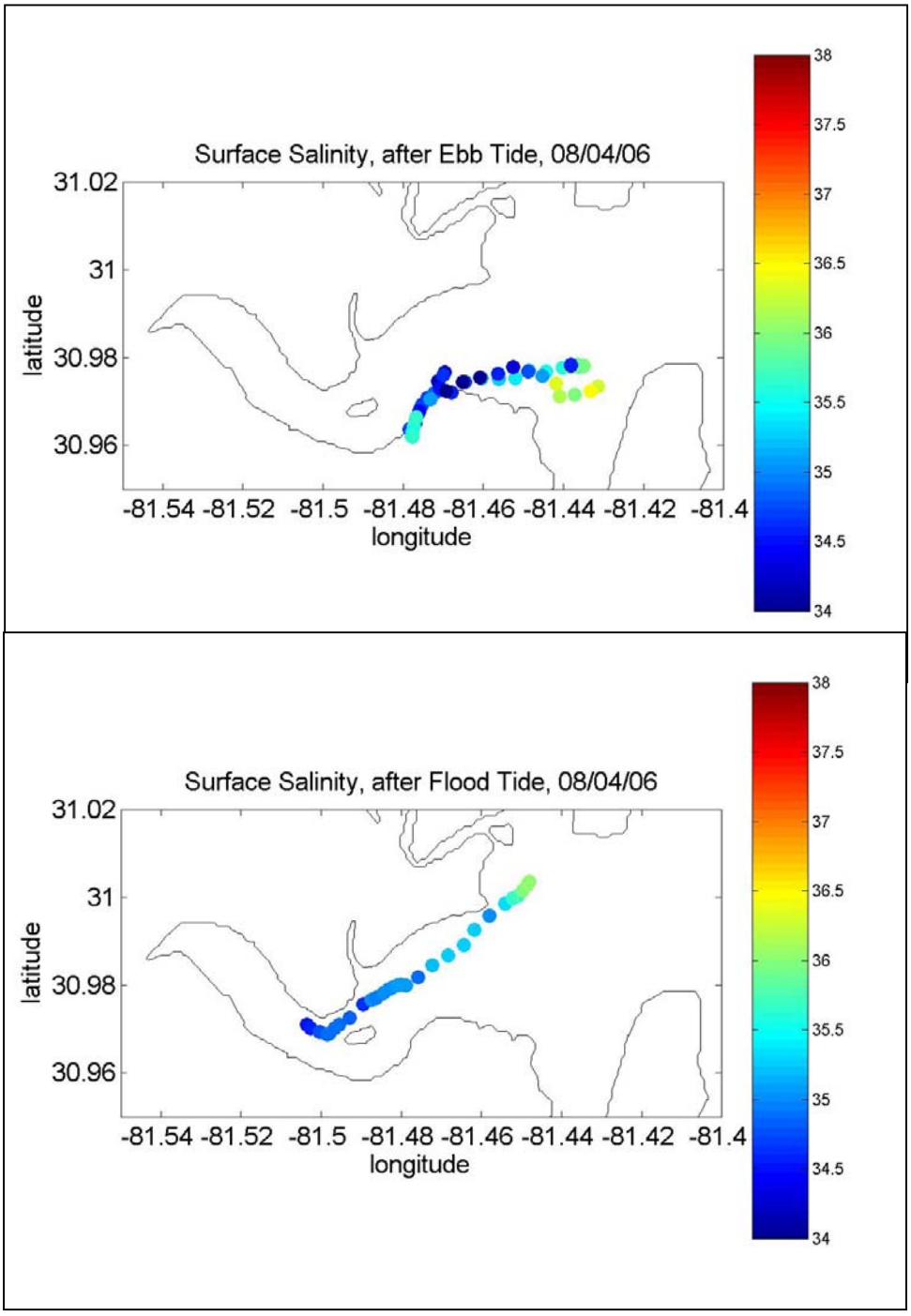

Figure 2.32: Surface salinity (PSU) along Satilla River after ebb tide (top) and after flood tide (bottom) on August 3, 2006.

Surface salinity and temperatures were continuously measured during this sampling period and the results are again grouped as (1) after the tide flooded or (2) after it ebbed on August 3 and 4 (Figs. 2.31 & 2.32). Surface salinity along the transect of the Satilla River increased toward the mouth of the river; however, the salinity was extremely high along the entire transect; only decreasing to 34 PSU (Figs. 2.31 – 2.32). As expected, the presence of the flood tide in the estuary pushed the saltier water further upstream. Warmer water was observed upstream on both days and during both phases of the tide (See Appendix).

Discussion

Seasonal and Inter-annual Variations

The greatest differences in the physical parameters of the Satilla River estuary occurred between the spring and summer and between August 2005 and August 2006. Salinity and temperature varied drastically throughout the spring, summer, and fall in 2005 in the Little Satilla River and Jointer Creek tributaries (Table 2.1). Samples from April 2005 exhibited the lowest salinities in the tributaries, varying between 15 PSU and 26 PSU, while samples from September 2005 exhibited salinities between 25 and 28 PSU (Table 2.1). Seasonally influenced freshwater input affects the salinities seen in the tributaries due to the increased stream flow during the spring months (Fig. 2.2). Temperatures also varied greatly from spring to summer with measured temperatures in April 2005 of 18 – 21°C and in August 2005 of 30 – 32°C (Table 2.1). Density ranges tended to follow salinity patterns and when salinities were higher so were the densities. Vertical stratification did not appear to rely on seasonal variations, but depended more on tidal phases and current strength.

August 2005 and August 2006 show large differences in salinity and density measurements within the tributaries. In August 2005, salinities ranged from 21 – 29 PSU and densities from 1011 – 1017 kg/m³, while in August 2006 salinities ranged from 35.5 – 36 PSU and densities from 1022 – 1023 kg/m³ (Table 2.1). The dramatic increase in salinity (and therefore the density) can be attributed to the lack of upstream freshwater flow from the Satilla and Little Satilla Rivers prior to the August 2006 sampling period (Fig. 2.2). Vertical stratification also differs between August 2005 and August 2006 due to the lack of freshwater in the system in 2006 and may also be compounded by the different tidal regimes under which the tributaries were sampled in 2005 and 2006. August 2005 experienced a spring tide with faster current velocities and exhibited vertical stratification ranging from 0.1 PSU/m to 0.3 PSU/m, while August 2006 experienced a neap tide and relatively weaker currents and showed vertical stratification values around 0.1 PSU/m (Table 2.1).

The Satilla River, where sampling took place in the spring and summer of 2006, exhibits many of the same temporal differences in physical parameters as in the tributaries. The salinity in March 2006 ranged from 15 – 29 PSU and in August 2006 it ranged from 34 – 37 PSU (Table 2.2). Temperatures were much lower in March 2006, 18 – 19.5°C, than in August 2006, 29.5 - 31°C (Table 2.2). Vertical stratification was higher in March 2006, ranging from 0.3 PSU/m to 0.5 PSU/m, than in August 2006, which showed vertical stratification values from less than 0.1 PSU/m to 0.12 PSU/m, possibly due to the increased amount of freshwater input from upstream, when compared to August 2006 (Table 2.2).

Table 2.1: Comparison of salinity, temperature, density, and vertical stratification at stations A, B, and C on all sampling dates in the tributaries.

Cruise Dates (Jointer Creek and Little Satilla)	Tides	Winds	Salinity (PSU)			Temperature (°C)			Density Range (kg/m³)			Vertical Stratification (PSU/m)		
			A	B	C	A	B	C	A	B	C	A	B	C
April 27, 2005	Spring	N,strong	15 - 26			18 - 21			1009 - 1019			ND	ND	ND
April 28, 2005	Spring	N, strong dying off	18 - 24			18 - 21			1011 - 1017			ND	ND	ND
June 21, 2005	Spring	S, strong	ND	ND	27	ND	ND	27-28	ND	ND	1017	ND	ND	0.1
June 22, 2005	Spring	Variable, weak	24-27	ND	ND	27-29	ND	ND	1014-1017	ND	ND	0.2	ND	ND
July 19, 2005	Spring	Variable, weak	ND	ND	21-22	ND	ND	30-32	ND	ND	1011-1012	ND	ND	0.3
July 20, 2005	Spring	Variable, weak	19-20	ND	ND	30-31	ND	ND	1008-1010	ND	ND	0.3	ND	ND
August 16, 2005	Spring	NE, strong	22-24	24-29	22-26	31-32	30-31	30-32	1013-1014	1013-1017	1013-1015	0.2	0.3	0.2
August 17, 2005	Spring	NE, stronger	21-27	24-29	23-27	30-32	30-32	30-32	1011-1015	1013-1017	1013-1015	0.2	0.3	0.2
September 29, 2005	Neap	Variable, weak	25-28	27-30	26-29	29	28-29	28-29	1014-1017	1016-1018	1016-1018	0.2	0.3	0.2
September 30, 2005	Neap	S, pm stronger	25-28	27-30	27-29	28-29	28-29	28-29	1014-1017	1016-1018	1016-1018	0.2	0.4	0.2
August 2, 2006	Neap	N, strong	35.5-36	35.5-36	36	30-31	29.5-31	29.5-31	1022-1022.5	1022-1023	1022-1022.5	0.1	0.1	0.1

Table 2.2: Comparison of salinity, temperature, density, and vertical stratification during all the sampling dates in the Satilla River.

Cruise Dates (Satilla River)	Tides	Winds	Salinity (PSU)	Temperature (°C)	Density Range (kg/m^3)	Vertical Stratification ($\Delta kg/m^3$)
March 14, 2006	Spring	N, strong mid-day, weak rest of day	15-29	18-19.5	1009-1017	0.3 - 0.5
March 15, 2006	Spring	N, strong	15-28	18-18.5	1009-1017	0.3 - 0.5
August 3, 2006	Neap	N, strong during day, weak at night	34-37	29.5-31	1019-1023	0.12
August 4, 2006	Neap	N, strong during day, weak at night	34-36.5	29.5-31	1021-1023	0.12

Spatial Variations

The physical parameters varied significantly by location. Although temperatures varied little within each sampling period and rose throughout the day on all sampling days at all stations, slightly higher temperatures were located up in the tributaries, especially at station C in Jointer Creek (Table 2.1). In contrast, variations in salinity (and therefore density) were large. The salinity and density was always higher in Jointer Creek (station C) than in the Little Satilla (station A) (Table 2.1). Station B demonstrated the highest values of vertical stratification, around 0.2 PSU/m, during most sampling dates (Table 2.1). Station C consistently exhibited the lowest values of vertical stratification, around 0.1 PSU/m vertical salinity change, due to the lack of freshwater input into Jointer Creek (Table 2.1). The values of vertical stratification are low in the tributaries, only a change of 0.1 PSU/m to 0.3 PSU/m, due to the minimal amount of freshwater input in that area.

As expected, salinity and thus density decreased along the transect of the Satilla River as the sampling stations moved further from the mouth of the estuary, ranging from 29 to 15 PSU in March 2006 and from 38 – 34 PSU in August 2006 (Figs 2.25 – 2.32). The vertical stratification along the transect of the estuary was greater than in the tributaries and ranged from 0.3 PSU/m to 0.5 PSU/m in March and from less than 0.1 PSU/m to 0.12 PSU/m in August. The location of the highest vertical stratification was dependent on the tidal phase during March and was found downstream after ebb tide and upstream after flood tide (Figs. 2.25 & 2.26). This movement of the location of the largest vertical stratification is most likely due to the amount of freshwater flowing into

the Satilla River from upstream since the same movement was not seen in August when there was minimal freshwater input.

Transport Pathways

Examination of the trajectories of the deployed drifters allows for a better understanding of the transport pathways of water within the estuary and mixing between the tributaries. The difference in salinity values of Jointer Creek and the Little Satilla River can be attributed to the transport pathways of water between the two tributaries. The movements of the drifters in Jointer Creek suggest that the majority of the water that exits the tributary, returns on the following flood tide, since none of the drifters released upstream on the ebb tide exited the creek during either deployment. Instead all returned on the subsequent flood tide (Fig. 2.19 & 2.20).

Transfer of water from the Little Satilla River to Jointer Creek is apparent, since one drifter that was released during ebb tide in June and three that were released during ebb tide in July in the Little Satilla River traveled into and up the Jointer Creek tributary during the subsequent flood tide (Fig. 2.19 & 2.20). The lower salinity within the Little Satilla River, the greater range of salinities at the junction of the tributaries (station B), and the trajectories of the drifters suggest that water leaving the Little Satilla River on an ebb tide travels up into Jointer Creek on the subsequent flood tide. Interestingly, the strong spring tide experienced during these studies did not result in the loss of drifters from the tributaries. All the drifters in this study remained in the tributaries and were not lost to the sound or the coastal ocean over the tidal cycle (Figs. 2.19 & 2.20), suggesting that mixing between the tributaries and the Satilla River is limited. The pathways taken by the drifters during both June and July were similar even though the salinity ranges

differed drastically between the two months, suggesting that these pathways are representative of typical flow within the tributaries (Figs. 2.19 & 2.20).

Tidal Effects

The tidal regimes, both flood and ebb and neap and spring, greatly affected the salinities, densities, and vertical stratification seen during sampling. The lowest salinities measured at station A on any sampling day were often observed directly after the beginning of the flood tide (Figs 2.13, 2.14, & 2.17) due to the pulse of fresher Satilla River water pushed into the Little Satilla by the incoming tide. Station C, in Jointer Creek, also experienced a pulse of fresher water after the beginning of the flood tide, but at a slight lag behind and slightly higher in salinity than the pulse seen in the Little Satilla River (Figs. 2.9, 2.10, & 2.13). The lowest salinity observed at station B also occurred when the tide changed from ebb to flood, also due to the input of fresher Satilla River water (Figs. 2.9, 2.10 & 2.13).

Vertical stratification was also affected by the tide; greater values of vertical salinity gradients were seen when the tides changed, especially from flood tide to ebb tide, resulting in weaker tidal currents and fresher, less dense river water moving over the saltier, denser ocean water (Figs. 2.9, 2.10 & 2.13). The tide also affected the location of the greatest vertical stratification in the Satilla River during the March 2006 sampling dates.

Differences were also seen between sampling dates that experienced neap tides and those that experienced spring tides. During a neap tide, current velocities are weaker and less mixing is suspected to occur, resulting in greater stratification than during a spring tide when current velocities are stronger. The September 2005 sampling

experienced a neap tide and exhibited more vertical stratification, especially at station B, than the previous sampling dates, which experienced spring tides.

Wind Effects

Wind affects the movement of the surface waters in the coastal ocean and within the estuary and leads to upwelling or downwelling of the water in the coastal ocean. The strength of the wind also affects the mixing that occurs in the water column and, ultimately, the vertical stratification. Stronger wind speeds result in more mixing and a less stratified water column, while weaker wind speeds result in less mixing. Stronger wind speeds were measured at Gray's Reef during the August 2005 sampling dates than during the September 2005 sampling dates and may have aided in the increase in stratification observed from August 2005 to September 2005 (Table 2.1).

Wind direction could have facilitated or hindered the movement of surface water out of the estuary. The presence of northward or southward winds at Gray's Reef did not appear to affect the vertical stratification of the water column within the tributaries but it may aid in transport of larvae entrained in the surface waters.

Conclusions

The Satilla River estuary is a partially mixed estuary that sometimes may approach well-mixed conditions depending on the tide, wind, season, and freshwater input. There is freshwater input from upstream of the Satilla River and the Little Satilla River, which varies seasonally with more discharge in the winter and spring months than in the summer resulting in lower salinities and densities within the estuary.

The salinity, temperature, and density vary, temporally and spatially, with the lowest measurements of all three parameters occurring in the spring of both 2005 and

2006. Since density variations are driven more by salinity than temperature, the vertical density gradients are caused by vertical salinity differences more than vertical temperature differences.

The salinity changed depending on the lateral position within the estuary. The Little Satilla River is always fresher and has a larger range of salinities than Jointer Creek and the salinity of the water decreases along the transect of the Satilla River with distance away from the mouth of the estuary. The freshest water in the Little Satilla River and Jointer Creek occurs at the end of ebb and the beginning of flood and may be due to a pulse of freshwater pushed into the tributary from the main Satilla River at the beginning of the flooding tide. Salinity in the main Satilla River varied, based on the season, however higher salinities were always observed near the mouth of the estuary whereas lower salinities were seen upstream. Salinities in the main Satilla River had a wider range than those in the tributaries.

Vertical stratification is weak in the Satilla River estuary and is dependent on the amount of freshwater in the system. The vertical stratification was greater in the main Satilla River than in the tributaries due to the amount of freshwater flowing down the Satilla River. The occurrence of the slack tide and the neap tide, when the currents were weakest, resulted in the greatest amount of vertical stratification in the tributaries due to decreased mixing.

The tides have a large effect on the salinity, and thus the density, of the Satilla River estuary. The pulse of fresher water seen in the Little Satilla River and Jointer Creek during flood tide suggests that the flood tide brings in denser, more saline water from the coastal ocean and pushes the fresher water in the Satilla River up into the tributaries. The

different velocities present during the spring and neap tides result in different amounts of mixing within the estuary; the stronger currents of the spring tide result in more mixing and less vertical stratification, while the weaker currents of the neap tide result in less mixing and greater vertical stratification.

The winds did not appear to have a large effect on the physical parameters measured in the Satilla River estuary. The strength of the wind could have resulted in increased mixing; however, these results were not clear. Even though the winds did not appear to affect the physics of the estuary, on or offshore transport from upwelling and downwelling winds may have affected the transport of crab larvae.

CHAPTER 3

UCA SPP.

Results

The average densities of larvae collected during this study ranged from 0.8 ± 0.3 *Uca*/m³ in April 2005 to 4,097 ± 2,190 *Uca*/m³ in August 2005 (errors are standard error). The differences in average collected densities occurred due to both spatial and temporal variations during the sampling periods. Densities varied between stations in the tributaries and the main river and among the stations in the river and within the tributaries. Temporally, both the seasons and the tidal phases played roles in the observed densities of *Uca* spp. larvae within the system.

This study spanned April 2005 through August 2006 and encompassed the expected months of larval release by *Uca* spp., as gravid females have been seen as early as April in the southern part of the range, including Georgia (Grimes et al., 1989). The March 2006 sampling found no *Uca* larvae at any station and supported the theory that *Uca* larval release does not occur that early in the year (Grimes et al., 1989). *Uca* spp. larvae, especially early stages, were found during all other sampling dates in April, August and September.

All five zoeal stages of *Uca* spp. as well as megalopae were collected within the estuary during September 2005 and August 2006. The presence and densities of the later zoeal stages also varied spatially and temporally in a similar manner to the total larval densities.

Uca spp. are able to alter their vertical position within the water column (Christy, 1982; Capaldo, 1993; Garrison, 1999); consequently, the sampling in August 2006

involved simultaneous surface and depth larval collections. The densities and zoeal stage composition of larval populations also varied between surface and depth samples based on the phase of the tide.

Spatial Variations

The densities of *Uca* larvae varied horizontally within the estuary, but also varied vertically within the water column. Since sampling in August 2006 included sampling from surface and depth waters in both the main Satilla River and the tributaries, the data from these dates were used to compare spatial distributions of larvae within the estuary. This study investigated both the tributaries of the Little Satilla River and Jointer Creek on August 2, and the main Satilla River on August 3 and 4. Figure 3.1 shows the average larval densities from all stations in the tributaries and the main river during the August 2006 sampling dates. There was no significant difference between samples from the surface in the tributaries and the main Satilla River during either ebb tide (*p*-value = 0.486) or flood tide (p-value = 0.598) (Fig. 3.1). At depth, the total densities of *Uca* larvae are higher during flood tide in the tributaries than in the main river (*p*-value = 0.007) (Fig. 3.1). The densities in the tributaries and the main river at depth during ebb tide are not significantly different (*p*-value = 0.112) (Fig. 3.1).

During ebb tide, surface waters at the stations in the tributaries had extremely high average larval densities, (~ 200 zoea/m^3), whereas along the Satilla River transect, only four of the nine stations had high average larval densities at the surface (Fig 3.2). One station along the transect of the Satilla River, located near the mouth of the river, had an extremely low average larval density, around 20 zoea/m^3, in surface waters during ebb tide (Fig. 3.2). The highest larval density seen during flood tide, 246 *Uca* larvae/m^3, was

collected in the main Satilla River directly to the west of the tributaries at the beginning of flood tide (Fig. 3.2). All other stations showed lower average densities during flood tide than during ebb tide (Fig. 3.2).

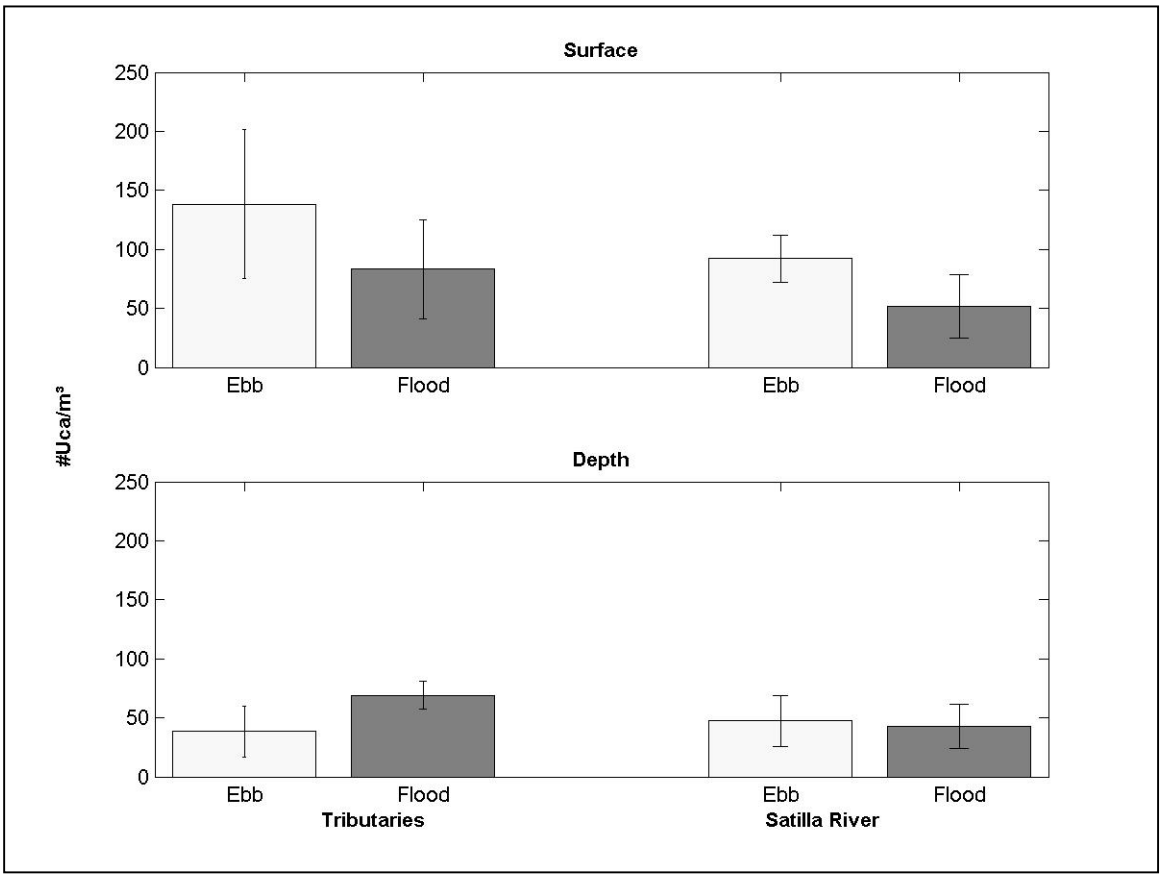

Figure 3.1: Comparison of total *Uca* densities at the surface and at depth during ebb and flood tide in August 2006. Error bars are based on standard error.

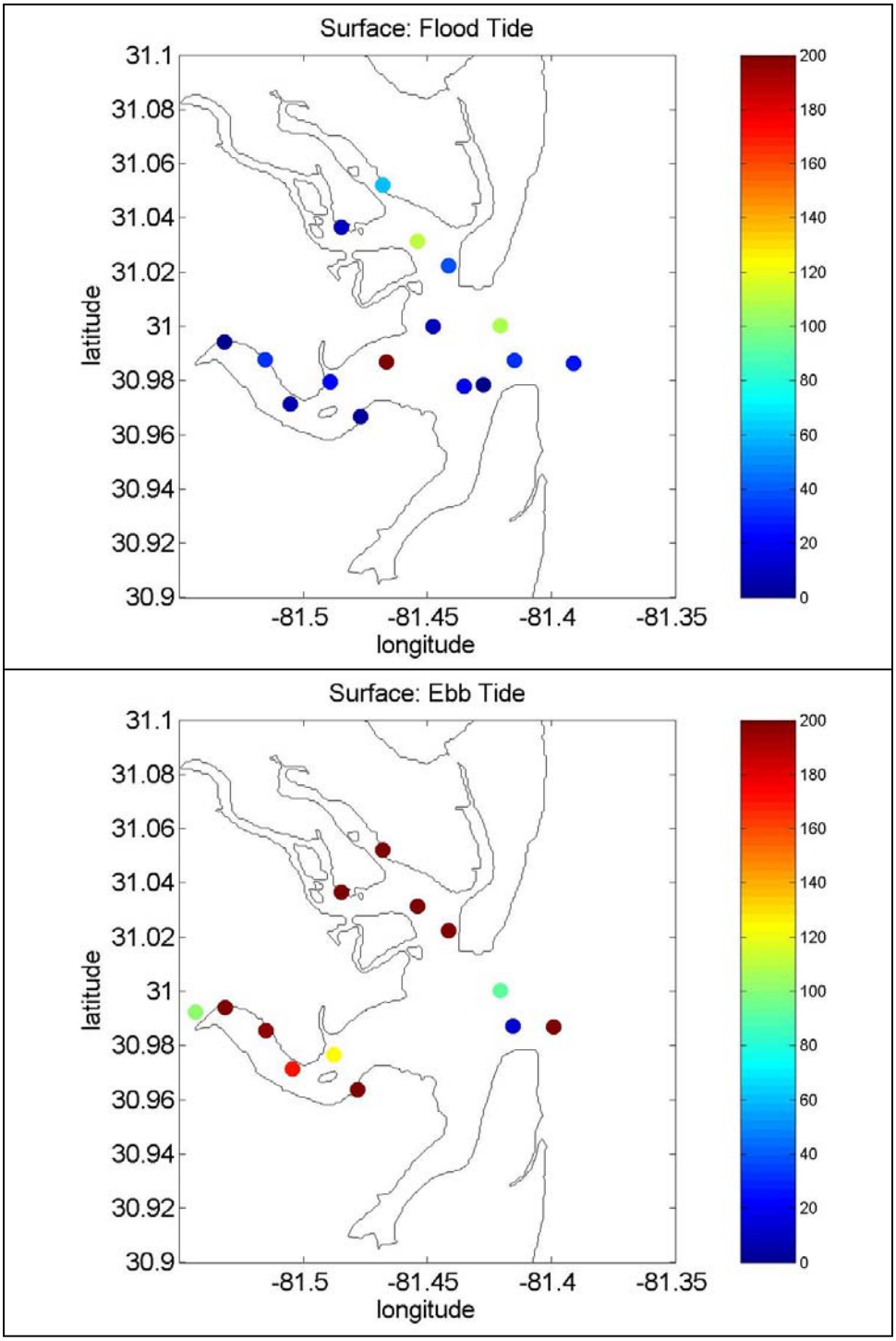

Figure 3.2: Average *Uca* larval densities in the surface waters at all stations during flood tide (top) and ebb tide (bottom) during August 2006.

Table 3.1: Comparison of mean *Uca* larval densities during flood and ebb tides on all sampling dates during August 2006, with *p*-values from t-tests to determine significant difference between the means from surface samples vs. depth samples. The means showing significant difference at *p*-value ≤ 0.05 are in bold.

Sampling Date	Tide	Density at surface	Density at depth	p-value from t-test
August 2, 2006 (tributaries)	Flood	83	73	0.909
August 2, 2006 (tributaries)	Ebb	**178**	**38**	**0.028**
August 3, 2006 (Satilla River)	Flood	53	30	0.598
August 3, 2006 (Satilla River)	Ebb	72	64	0.773
August 4, 2006 (Satilla River)	Flood	**2.4**	**22**	**0.022**
August 4, 2006 (Satilla River)	Ebb	75	37	0.357

Differences in average larval densities were observed between the surface samples and the samples at depth, especially in the tributaries. The surface samples taken in the tributaries during ebb tide are significantly greater, averaging 178 ± 43 *Uca*/m³, than the depth samples taken in the tributaries during ebb tide, averaging 38 ± 15 *Uca*/m³ (*p*-value = 0.028) (Fig. 3.1; Table 3.1). The samples taken at the surface and at depth during flood tide in the tributaries are not significantly different (*p*-value = 0.909) (Fig. 3.1; Table 3.1). The samples taken in the main Satilla River on August 3, 2006 show no significant difference between the samples at the surface and at depth during ebb tide (*p*-value = 0.773) or flood tide (*p*-value = 0.598) (Fig. 3.1). However, on August 4, 2006, significantly higher densities occurred at depth than at the surface during the flood tide (*p*-value = 0.022) (Table 3.1).

All five zoeal stages and the megalopal stage were collected in the tributaries and the main Satilla River in August 2006. Zoea I and zoea II comprise the majority of all

samples from the tributaries and the river at flood and ebb tides (Fig. 3.3). The densities of zoea I in the creeks were similar to those found in the main Satilla River (p-value = 0.486); however the densities of zoea II are greater in the surface waters of the tributaries than in the surface waters of the main river, especially during ebb tide (*p*-value = 0.021) (Fig. 3.3). The later stage larvae were present at depth during both phases of the tide and in both the tributaries and the main Satilla River; however, there were no significant differences between surface and depth densities of zoea III or zoea IV-V during flood or ebb tide in the creeks or the main river (Fig. 3.3). Densities of *Uca* megalopae are greater at depth in the main river during both phases of the tide (*p*-value = 0.009). In the tributaries, megalopae are significantly more common at depth than at the surface during flood tide (*p*-value = 0.007), but not during ebb tide (*p*-value = 0.769) (Fig. 3.3).

Within the tributaries, *Uca* larvae were collected at three different stations. Average larval densities were always higher at station A (located in the Little Satilla River) during ebb tide than during flood tide on all sampling dates (*p*-values = 0.001) (Fig. 3.4). Station A showed higher average densities during ebb tide than station B, located where the two tributaries converge and station C, located in Jointer Creek on both sampling dates in April 2005, these differences were significantly higher on April 28, 2005 (*p*-value = 0.041) (Fig. 3.4). There is no significant difference between stations A and C in September 2005 or August 2006 during ebb tide (Fig. 3.4). Sampling in September 2005 and on August 17, 2005 exhibited higher average densities at station B, where the tributaries converge, during flood tide than at the stations up in the tributaries, however these differences were not significant (Fig. 3.4).

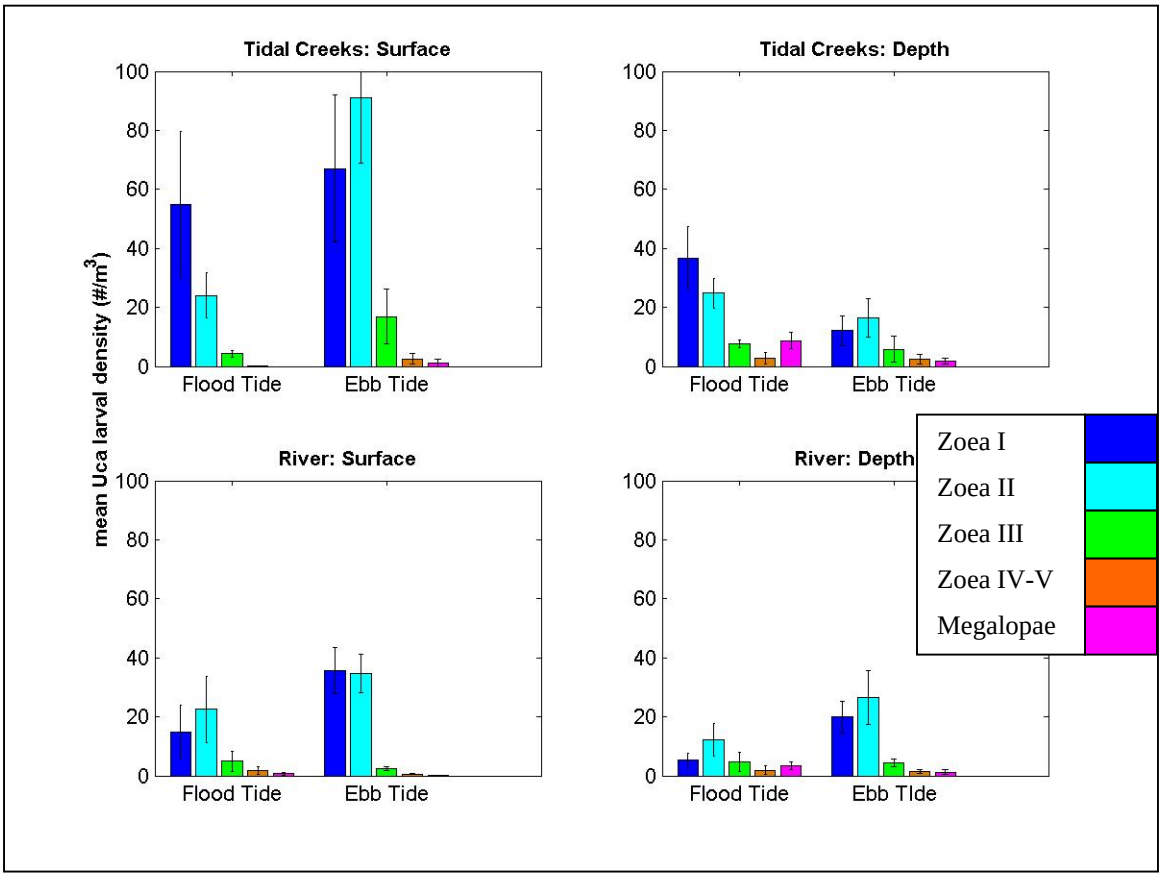

Figure 3.3: Comparison of *Uca* larval stages from surface and depth samples within the tributaries and the main Satilla River in August, 2006. Error bars are based on standard error.

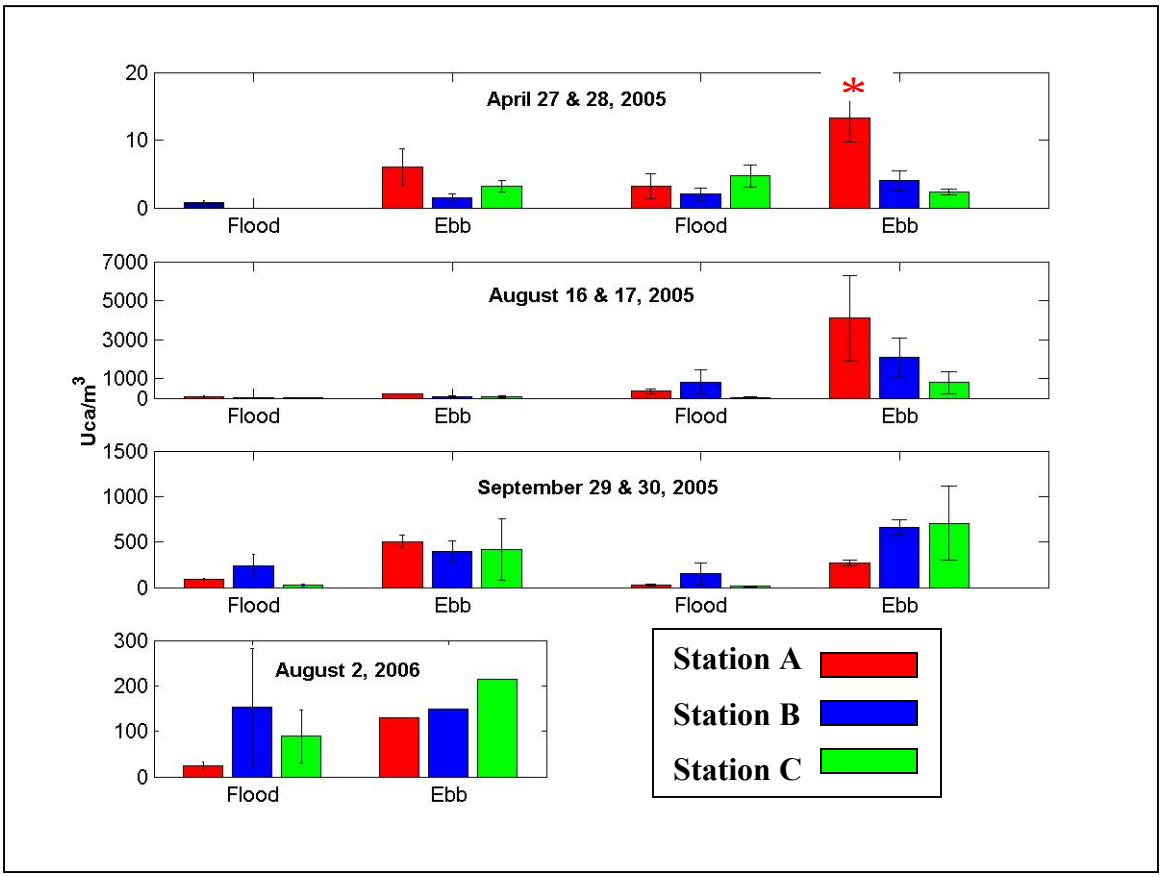

Figure 3.4: Comparison of average *Uca* larval densities at stations A, B, and C during ebb and flood tides on all sampling dates. Note difference in y-axis values. Error bars are based on standard error. (* shows statistical significance between stations A and C with p-value ≤ 0.05). Ebb tide on August 2, 2006 lacks errorbars due to the lack of data collected on that date.

Temporal Variations

Differences in larval densities also occurred due to the season and the phase of the tide in which the sampling took place. Higher densities of larvae were collected during the months of August and September than during April (Fig. 3.5). The highest densities of larvae in the surface water of the tributaries were collected during ebb tide on August 17, 2005 and averaged 2,278 *Uca*/m³ (Fig. 3.5). August 17, 2005 and both sampling dates in September 2005 exhibited higher average larval densities during ebb tide than were

observed during ebb tide in August 2006 (p-value = 0.022 for August 2005 and August 2006 and p-value = 0.044 for September 2005 and August 2006) (Fig. 3.5).

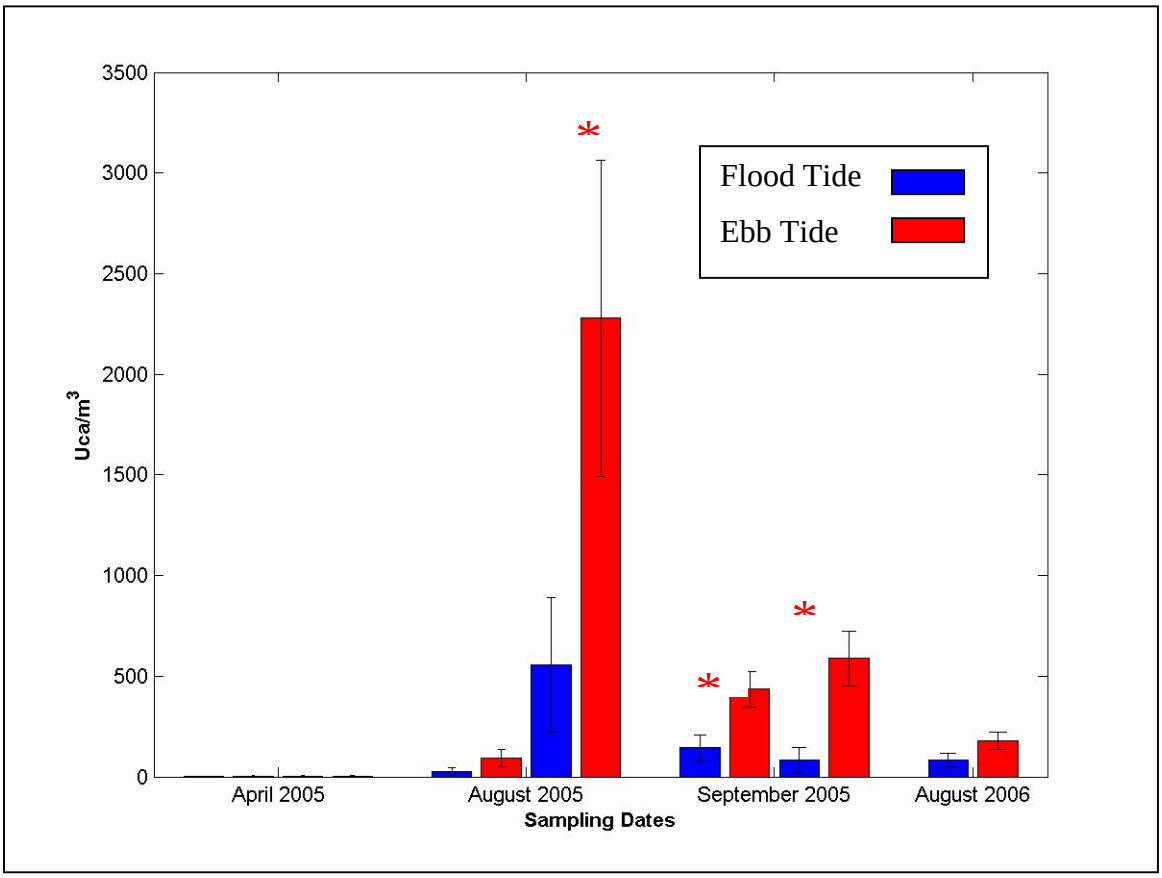

Figure 3.5: Comparison of average larval densities during flood (blue) and ebb (red) tides during the two sampling dates for April 2005, August 2005, September 2005 and the one sampling date for August 2006. Error bars are based on standard error. (* shows statistical significance between flood and ebb tides with p-value ≤ 0.05).

March 2006 is not included in figure 3.5 because no *Uca* larvae were found during that sampling period. Since April 2005 larval densities were small compared to the other sampling dates, figure 3.6 shows the comparison of the average larval densities during flood and ebb tides during the April 2005 sampling dates. Averages of *Uca* densities during ebb tide on April 27 were significantly higher than densities during flood tide (p-value=0.03) (Fig. 3.6).

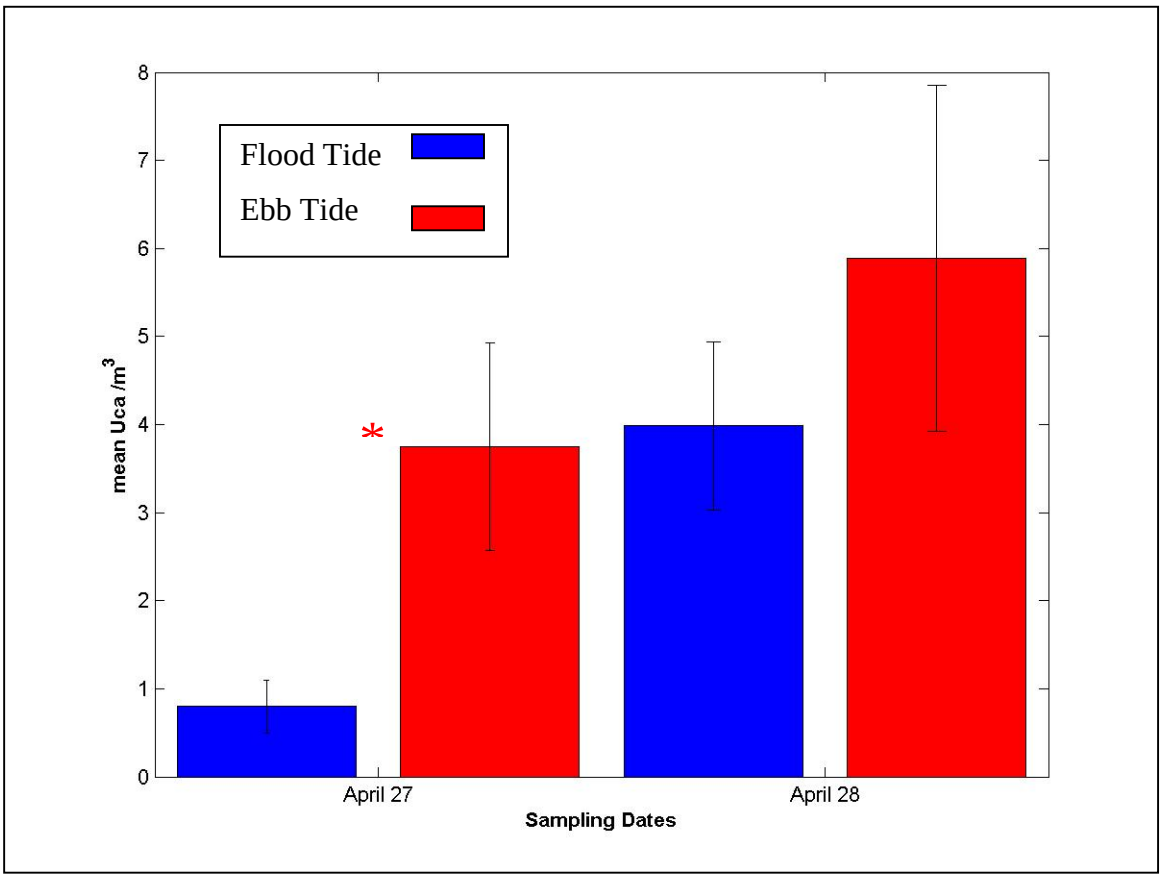

Figure 3.6: Comparison of average *Uca* larval densities during flood (blue) and ebb (red) tide during the two April 2005 sampling dates. Error bars are based on standard error. (* shows statistical significance between flood and ebb tide with p-value ≤ 0.05).

The presence of the five different larval stages also varied seasonally. Only zoea I were collected in the April 2005 samples, while zoea I – III were collected in August 2005, and all 5 zoeal stages were collected in September 2005 and August 2006 (Fig. 3.7 & Table 3.3). Megalopae were collected in small numbers in August 2005, September 2005, and August 2006 (Fig. 3.7 & Tables 3.3 & 3.4). All the sampling periods in 2005 exhibited much higher zoea I densities than zoea II densities, while August 2006 shows similar densities of zoea I and zoea II (Fig. 3.7). Greater amounts of later stage zoea were collected during the August 2006 sampling period than during previous sampling dates (Fig. 3.7 & Table 3.4).

Table 3.2: Comparison of mean *Uca* larval densities during flood and ebb tides on all sampling dates with p-values from t-tests to determine significant difference between the means. The means showing significant difference at p-value ≤ 0.05 are in bold. The dates shaded in grey indicate samples taken in surface water of the Satilla River. All other samples were taken in the surface water of the tributaries.

Sampling date (Surface only)	**Mean Flood density**	**Mean Ebb density**	***p*-value from t-test**
April 27, 2005	**0.8**	**3.4**	**0.030**
April 28, 2005	3.3	5.9	0.196
August 16, 2005	25.2	93.1	0.127
August 17, 2005	**554.5**	**2278.0**	**0.050**
September 29, 2005	**143.3**	**435.2**	**0.017**
September 30, 2005	**84.4**	**587.8**	**0.006**
August 02, 2006	83.2	178.6	0.106
August 03, 2006	53.2	72.2	0.604
August 04, 2006	2.5	75.3	0.055

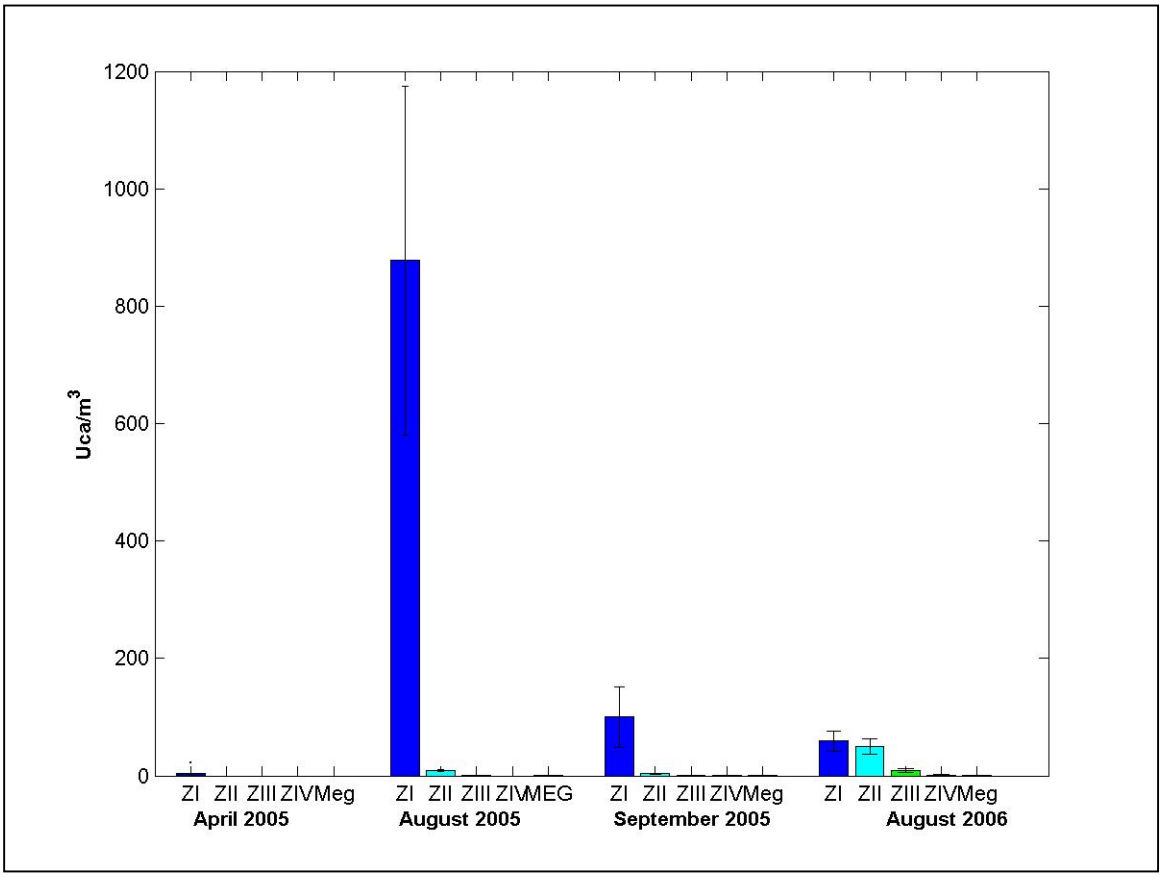

Figure 3.7: Comparison of average densities of zoeal stages collected from the surface waters in the tributaries during each sampling period. Error bars are based on standard error.

The phase of the tide also affected the densities of larvae collected. Four out of seven of the sampling days show significant difference between the densities of larvae collected during flood and ebb tides, and all sampling days exhibited higher average densities during ebb tide than during flood tide (Figs. 3.5 & 3.6 & Table 3.2). When examining the difference between samples from the surface and those from depth on August 2006, there were significantly higher larval densities at the surface than at depth during ebb tide in the tributaries (*p*-value = 0.028) (Fig. 3.1). In the tributaries at the surface, the ebb tide average larval densities were greater than the flood tide larval densities, while at depth, the flood tide densities were greater than the ebb tide densities, although neither difference was significant (*p*-value = 0.106 for surface and *p*-value = 0.067 for depth) (Fig. 3.1). In the main Satilla River, the densities at depth did not show a discernable difference between flood and ebb tides (Fig. 3.1).

The tidal phase also affected the larval stages collected at depth in August 2006. In the tributaries, zoea stage II showed significantly higher average densities in the surface samples than in the depth samples during ebb tide (*p*-value = 0.023), but exhibited no significant difference in surface and depth samples during flood tide (*p*-value = 0.925) (Fig. 3.8). In the main Satilla River, zoea stage I exhibited slightly higher densities in the surface samples than the depth samples during ebb tide (Fig. 3.9). Zoeal stages III through megalopae show no discernable difference between surface and depth during ebb tide in the tributaries; however, they all show slightly higher average densities at depth than at the surface during flood tide (Fig. 3.3 & 3.8). Megalopae densities are significantly greater during flood tide than during ebb tide at depth (*p*-value = 0.007) (Fig. 3.9). The densities of later stage larvae were similar in both the tributaries and the

main Satilla River during both ebb and flood tides, while the densities of zoea I and II were higher in the tributaries, especially during ebb tide (Figs. 3.8 & 3.9).

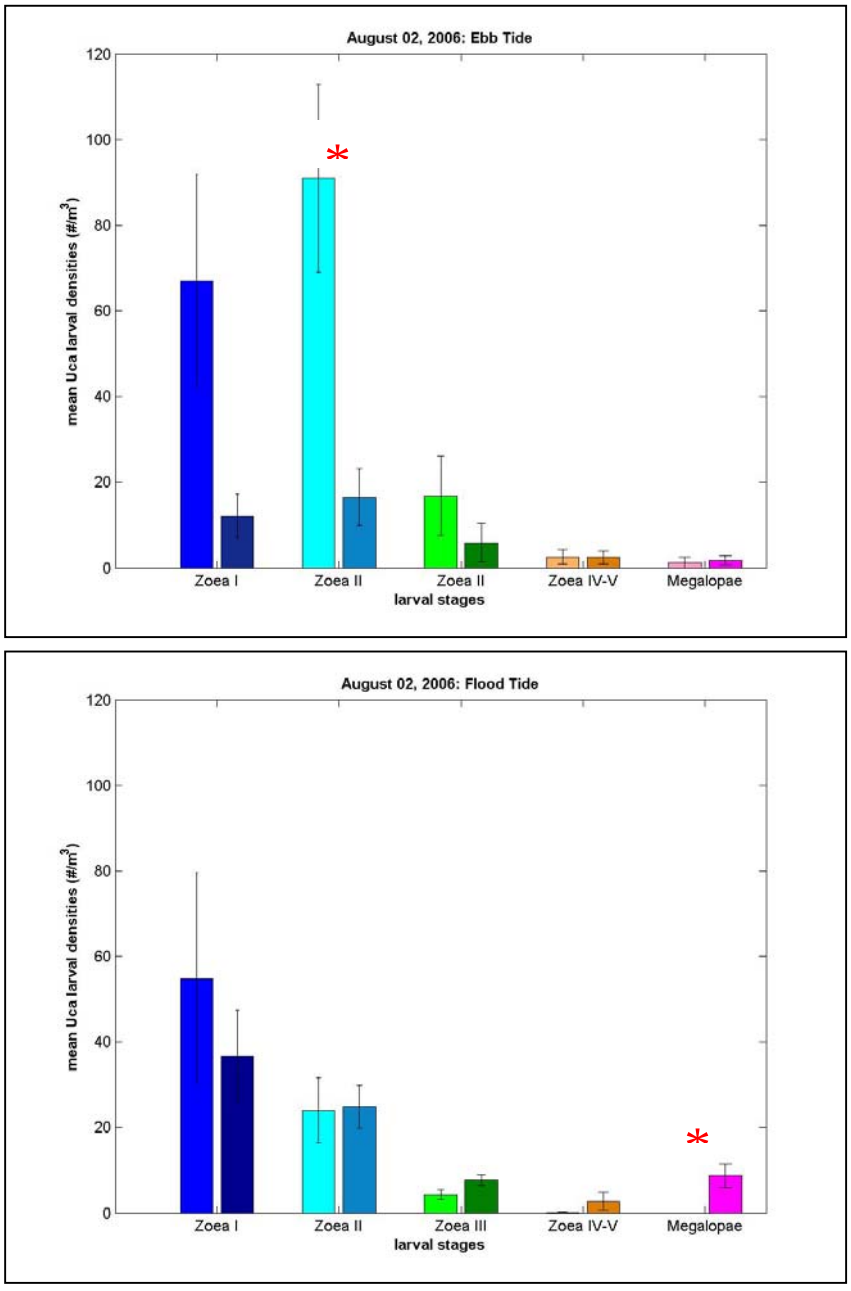

Figure 3.8: Comparison of *Uca* larval stages collected at the surface (lighter color) and at depth (darker color) during ebb tide (top panel) and flood tide (bottom panel in the tributaries on August 2, 2006. Error bars are based on standard error.
(* shows statistical significance between surface and depth densities with p-value ≤ 0.05).

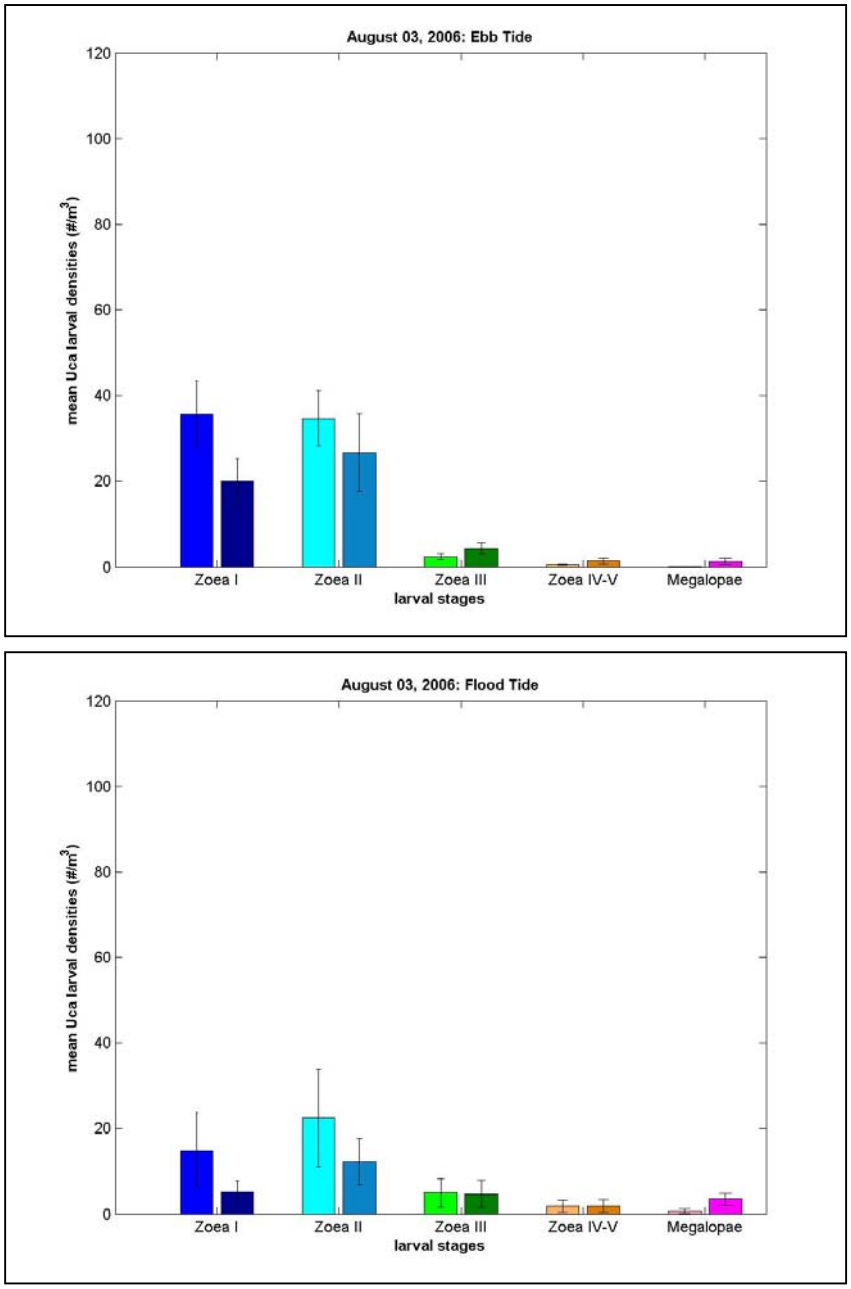

Figure 3.9: Comparison of *Uca* larval stages collected at the surface (lighter color) and at depth (darker color) during ebb tide (top panel) and flood tide (bottom panel) in the Satilla River on August 3, 2006. Error bars are based on standard error.

Table 3.3: Comparison of *Uca* larval densities and zoeal stages at all stations during 2005 sampling. (ND means No Data is available).

Sampling Dates and Physical parameters	Station	Tide	Average *Uca* larval density (#/m³)					
			ZI	ZII	ZIII	ZIV-V	Meg	Total
April 27,2005	A	Flood	0.8	0	0	0	0	0.8 ± 0.3
Tides: Spring		Ebb	6.0	0	0	0	0	6.0 ± 2.7
Winds: N, strong	B	Flood	ND	ND	ND	ND	ND	ND
Salinity: 15 - 26		Ebb	1.5	0	0	0	0	1.5 ± 0.6
Temp: 18 – 21 ° C	C	Flood	ND	ND	ND	ND	ND	ND
Stratification: ND		Ebb	3.2	0	0	0	0	3.2 ± 0.8
April 28,2005	A	Flood	3.2	0	0	0	0	3.2 ± 1.9
Tides: Spring		Ebb	13.2	0	0	0	0	13.2 ± 3.5
Winds: N, strong	B	Flood	2.0	0	0	0	0	2.0 ± 0.9
Salinity: 18 – 24		Ebb	4.0	0	0	0	0	4.0 ± 1.5
Temp: 18 – 21 °C	C	Flood	4.7	0	0	0	0	4.7 ± 1.6
Stratification: ND		Ebb	2.3	0	0	0	0	2.3 ± 0.4
Aug. 16, 2005	A	Flood	68.1	9.3	0.04	0	0.004	78.2 ± 67.7
Tides: Spring		Ebb	206.7	17.0	0	0	0	223.7 ± ND
Winds: NE, strong	B	Flood	8.4	2.2	0.01	0	0.002	10.9 ± 5.9
Salinity: 22 – 29		Ebb	70.2	7.9	0.02	0	0	78.6 ± 67.2
Temp: 30 – 32 ° C	C	Flood	0.7	0.05	0	0	0	0.7 ± 0.5
Stratification: 0.2 – 0.3 PSU/m		Ebb	46.6	2.9	0	0	0	49.5 ± 49.3
Aug. 17, 2005	A	Flood	339.4	9.2	0.006	0	0	348.9 ± 114.2
Tides: Spring		Ebb	4077.1	20.9	0	0	0	4097.9 ± 2190.1
Winds: NE, stronger	B	Flood	811.9	13.9	0.001	0	0	826.1 ± 609.6
Salinity: 21 – 29		Ebb	2064.0	13.1	0.001	0	0	2077.2 ± 1012.9
Temp: 30 – 32 ° C	C	Flood	47.6	0.2	0.005	0	0	48.2 ± 34.1
Stratification: 0.2 – 0.3 PSU/m		Ebb	790.5	2.3	0	0	0	792.7 ± 585.3
Sept. 29, 2005	A	Flood	88.2	5.2	0.3	0.3	0	94.2 ± 11.2
Tides: Neap		Ebb	494.0	10.8	1.2	0.6	0	506.7 ± 64.6
Winds: variable, weak	B	Flood	226.8	6.9	1.2	0.1	0.8	235.9 ± 123.6
Salinity: 25 – 30		Ebb	391.3	7.7	1.1	0.4	0	400.5 ± 111.7
Temp: 28 – 29 °C	C	Flood	21.1	0.6	0	0	0	21.7 ± 13.9
Stratification: 0.2 – 0.3 PSU/m		Ebb	411.6	4.0	0	0	0	415.6 ± 336.5
Sept 30, 2005	A	Flood	25.1	3.9	0.1	0	0	29.2 ± 12.6
Tides: Neap		Ebb	258.4	12.2	1.1	0	0	271.7 ± 34.3
Winds: S, stronger in pm	B	Flood	130.7	17.7	0	0	0	148.5 ± 126.0
Salinity: 25 – 30		Ebb	628.1	28.2	0	0	0	656.2 ± 84.5
Temp: 28 – 29 °C	C	Flood	8.6	2.7	0	0	0	11.4 ± 5.7
Stratification: 0.2 – 0.4 PSU/m		Ebb	689.9	17.2	0	0	0	707.1 ± 406.8

Table 3.4: Comparison of *Uca* larval densities and zoeal stages at surface and depth at all stations during August 2, 2006 sampling. (ND means No Data is available).

Sampling Dates and Physical Parameters	Station	Tide	Average *Uca* larval densities #/m³					
			ZI	ZII	ZIII	ZIV-V	Meg	Total
August 2, 2006	**A (Surface)**	Flood	11.1	10.9	2.3	0.1	0	24.5 ± 9.1
Tides: Neap Winds: N, strong Salinity: 35.5 - 36 Temp: 29.5 – 31 °C Stratification: < .1 PSU/m		Ebb	51.2	67.3	10.5	0	0	129.1 ± ND
	A (Depth)	Flood	32.0	25.3	10.5	2.85	6.68	77.4 ± 14.5
		Ebb	23.7	31.6	18.9	6.3	0	80.6 ± ND
	B (Surface)	Flood	109.5	36.7	6.2	0	0	152.5 ± 129.7
		Ebb	74.7	66.9	5.9	1.5	0	149.2 ± 114.9
	B (Depth)	Flood	35.7	33.3	5.1	0.2	9.6	84.1 ± 32.6
		Ebb	9.8	11.7	0	0	2.2	23.7 ± 16.0
	C (Surface)	Flood	59.7	24.8	4.3	0.2	0	89.3 ± 57.9
		Ebb	106.1	98.7	8.4	0.6	0	213.8 ± ND
	C (Depth)	Flood	71.4	19.7	5.2	0	11.5	107.8 ± 11.8
		Ebb	ND	ND	ND	ND	ND	ND
	D (Surface)	Flood	38.3	23.7	4.5	0	0	66.6 ± 46.4
		Ebb	28.4	154.6	53.4	9.2	6.2	251.7 ± ND
	D (Depth)	Flood	7.9	14.3	9.9	7.9	6.9	47.2 ± 17.8
		Ebb	4.9	11.2	4.4	3.7	2.4	26.7 ± ND

Discussion

Spatial Variations

There was no difference between the average densities of *Uca* larvae found at the surface or at depth in the main Satilla River and the tributaries of the Little Satilla River and Jointer Creek during either phase of the tide (Fig. 3.1); however, the highest individual densities were collected within the tributaries (Fig. 3.2). When each station was examined individually, all the stations within the tributaries showed extremely high average densities during ebb tide, while only some stations along the transect of the Satilla River showed equally high densities (Fig. 3.2). The occurrence of high larval densities at stations within the tributaries was most likely due to the origin of the larvae themselves. Since female *Uca* release their larvae from the creek bank (Grimes et al., 1989), it is expected that more larvae would be more concentrated in the tributaries,

where the winding tributaries are exposed to more creek bank area. The stations along the transect of the Satilla River where higher densities occurred may be areas of convergence or locations where smaller tributaries enter the main body of the river (Fig. 3.2). The highest density of larvae seen during flood tide was collected just to the west of where the Little Satilla River and Jointer Creek meet the main Satilla River (Fig. 3.2). Larvae exiting the tributaries with the ebbing tide were possibly pushed upriver with the incoming flood tide, which created a higher larval density at that station, as that sample was collected at the beginning of flood tide. Other locations of higher larval density during flood tide were station B, located where the Little Satilla River and Jointer Creek converge, and the station at the entrance to the Satilla River estuary (Fig. 3.2). High larval densities at both these stations can be attributed to the convergence of the larvae during the previous ebb tide and demonstrate that it takes many tidal cycles for the larvae to move out of the estuary (Petrone et al., 2005).

Within the tributaries, spatial variation occurred between the stations. Station A, located in the Little Satilla River, typically had lower salinities (Table 2.1) and showed higher average larval densities during ebb tide than station C, located in Jointer Creek, during spring tide sampling in April 2005 and August 2005 (Fig. 3.4). The difference between stations A and C may be attributed to the adult spawning population located in these two tributaries or could be due to the higher salinities at station C. Capaldo (1993) found that *Uca* zoea preferentially move to areas of lower salinity to facilitate seaward movement with the less saline surface water. Station B, located where the Little Satilla River and Jointer Creek converge, exhibited higher average densities during flood tides of the late summer months due to the previous ebbing tide moving larvae out of the two

tributaries and congregating them at station B. This convergence of larvae at station B during flood tide was not seen during April 2005 and its absence was most likely due to the lack of large densities of larvae during that time.

The different stages of larvae also demonstrated some spatial variation. During the 2005 sampling dates, later stage larvae were only collected at stations A and B (Table 3.1). The occurrence of later stage larvae at stations A and B may be due to the method of reentry into the estuary and result from the mixing of water from the main Satilla River into the Little Satilla River. Since salinities at all stations were similar and high numbers of all zoeal stages were collected during August 2006, little difference was seen between the stations (Table 3.2). However, the highest densities of later stage larvae were collected at stations B and D (Table 3.2), the most oceanward stations, possibly demonstrating the reentry of later stage zoea into the estuary.

Vertical spatial variations were also detected during sampling in August 2006. In the tributaries, the densities of *Uca* larvae at the surface were much higher than densities at depth during ebb tide (Fig. 3.1). During flood tide, the larval densities at depth were greater than the larval densities at the surface (Fig. 3.1). August 2006 experienced little stream flow from upstream and high salinities were measured throughout the estuary resulting in vertical salinity stratification of less than 0.1 PSU/m (Table 2.1). Even though salinity (and density) stratification was minimal during this sampling period, the *Uca* larvae in the tributaries appeared to be stratified based on the tide. In the main Satilla River, the same stratification of larvae was not as evident, possibly resulting from the swifter currents and increased mixing occurring there (Table 2.2).

Temporal Variations

The average densities of *Uca* larvae were greater in the late summer and early fall than in the spring. The lack of larvae collected during March 2006, demonstrates that *Uca* larvae were not released that early in the year, or were present at such low densities as to be undetectable by the sampling methods used in this study. This lack of *Uca* larvae is consistent with findings from Grimes et al. (1989). The presence of small densities of *Uca* larvae in April 2005 indicate that the beginning of spawning occurs between mid-March and late April. August 2005, September 2005 and August 2006 all had much higher average larval densities due to the progression of larval release throughout the late spring and summer months (Fig. 3.5). The highest average larval density was collected on August 17, 2005 during the ebb tide and it coincided with the impending spring tide that occurred on August 19, 2005 (Table 2.1), which is consistent with the thought that *Uca* larval release is timed with spring ebb tides (Wheeler, 1978; Christy, 1982; Salmon et al., 1986; Forward, 1987).

The presence of different larval stages also changed throughout the year (Fig. 3.7). Since April is early in the spawning season, samples collected during this sampling period contained only stage I zoea (Table 3.1). August 2005 samples contained zoeal stages I – III and small numbers of megalopae. September 2005 and August 2006 samples contained all five larval stages as well as megalopae (Table 3.1 & 3.2). The presence of more later stage larvae during September 2005 and August 2006 may be due to the higher salinities measured during these periods. Higher salinities within the estuary may have caused larvae to molt into later stages due to salinity cues while still within the confines of the estuary (O'Connor & Epifanio, 1985). These sampling dates also

experienced neap tides and weaker currents, which would not expel the larvae out of the estuary as quickly as the stronger currents of the spring tide, which occurred during the August 2005 sampling dates.

The tidal phases appeared to play the largest role in determining the density of *Uca* larvae in the surface waters. With the exception of April 28, 2005 (in which larval densities were extremely low), all sampling dates exhibited higher larval densities during ebb tide than during flood tide (Fig. 3.5). *Uca* larvae travel out to the coastal ocean in order to develop (Wheeler, 1978; Christy, 1982; Salmon et al., 1986; Forward, 1987). Being entrained in the surface waters during the ebbing tide facilitates the movement of the *Uca* larvae out of the estuary and to the coastal ocean. The presence of higher numbers of larvae, especially zoeal stages I and II, in the surface waters during ebb tide than during flood tide is consistent with *Uca* larval development occurring in the coastal ocean. When examining the vertical spatial variations from August 2006, it was also evident that there are higher densities of larvae at depth during flood tide than during ebb tide (Fig. 3.1). By being located at depth during the flood tide, the larvae may deter their movement back into the estuary with the incoming waters.

The composition of zoeal stages of the samples taken at the surface and at depth also varies with the tides. During ebb tide in the tributaries, the presence of zoea stage I and II were much greater in the surface than at depth while the later stages showed similar densities at the surface and at depth, illustrating that earlier stage larvae tend to leave the tributaries for development in the coastal ocean (Fig. 3.8). During flood tide in the tributaries, the difference between the surface and depth samples of stage I and stage II zoea was negligible, while the densities of later stage zoea and megalopae at depth are

much greater than at the surface (Fig. 3.9). A similar response to the tides was seen in the main Satilla River, but the differences were not as significant (Fig. 3.9). Although change is seen in the average densities of stage I larvae from surface to depth both in the tributaries and in the main river, the largest increase in average densities is observed in stage II larvae, especially in the tributaries during ebb tide (Fig. 3.8). This large change could result from the ability of the larger stage II larvae to alter their vertical position within the water column to facilitate their export to the coastal ocean. Since larval swimming speeds range from 3 to 12 mm/s and increase with larval stage, stage I larvae may not be strong enough to overcome the vertical currents and mixing to change their vertical position (Garrison, 1999). The difference between the observed vertical spatial variations of later stage zoea may be due to settlement cues present in the tributaries and the need of the later stage zoea to reach appropriate settlement habitats (Epifanio et al., 1988; O'Connor, 1993).

Environmental Effects

The winds in April 2005 and August 2005 were northward and strong, measuring 8 m/s, and resulted in surface water movement out of the estuary possibly expulsing larvae from the estuary (Fig. 2.6). The effect of the winds may have resulted in fewer later stage larvae within the estuary during these sampling periods. The winds measured in September 2005 were variable in direction and much weaker than previous dates and would not have had much effect on the surface water movement. Winds during August 2006 were northward and strong, measuring almost 8 m/s. However, since all stages of larvae were collected within the estuary, the winds do not seem to affect the larval transportation as data from April 2005 and August 2005 might suggest. The winds in

August 2006 may have resulted in increased mixing of the water column leading to decreased vertical density stratification.

However, the wind variations do not appear to determine the distribution or transport of the larvae as much as the spatial and temporal variations examined earlier.

The vertical stratification within the water column differs only slightly throughout this study. The largest difference in vertical density seen during this study was 0.4 PSU/m and the smallest difference seen was a change of less than 0.1 PSU/m. September 2005, which experienced neap tides but very high salinity due to the lack of freshwater discharge upstream, showed the least amount of stratification (Table 2.1). Since vertical stratification of larvae was observed during August 2006 even when little vertical density stratification was evident it appears that vertical density stratification is not the cue that larvae use in determining their depth within the water column.

Conclusions

Both spatial and temporal variations affect the distribution and transport of *Uca* larvae within the Satilla River estuarine system. While there is little difference between average *Uca* larval densities in the main Satilla River and the tributaries, differences between stations appear to be determined by proximity to spawning locations and convergence zones. The difference between surface and depth samples was more pronounced in the tributaries than in the main Satilla River and can be attributed to the swifter currents in the main river and to the larvae moving out of or into the tributaries.

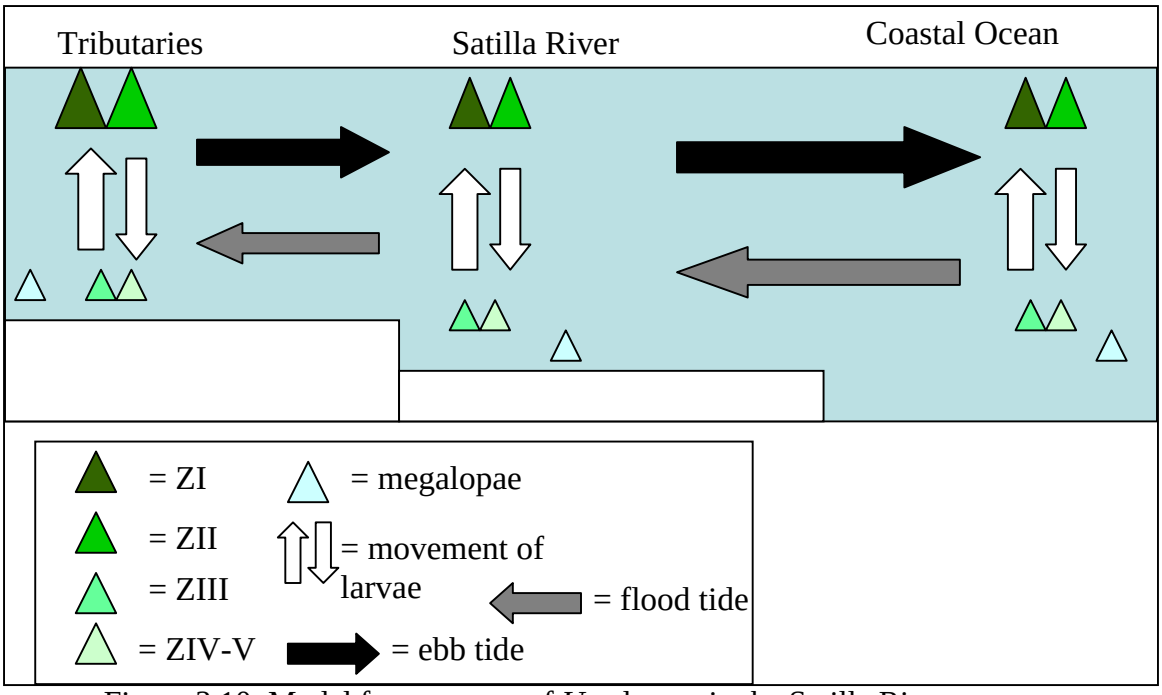

Figure 3.10: Model for transport of *Uca* larvae in the Satilla River estuary.

The changing of seasons played a major role in determining the total average larval density collected as well as the zoeal stage composition of each sample period. The highest densities of *Uca* larvae, averaging 2,278 *Uca*/m³, were found on August 17, 2005 and may have resulted from its proximity to the full moon and spring tides. The tidal phases appeared to have the greatest effects on the densities of larvae collected, as more *Uca* larvae were collected during ebb tide than during flood tide in all seasons. Since the majority of the *Uca* larvae sampled in the estuary on all sampling dates consisted of earlier stages, the higher densities in the surface waters during ebb tide would result in larval movement out of the estuary for development in the coastal ocean.

The seasons and tides also determined which larval stages were present. Later stage zoea were more common later in the summer and early fall during times which would facilitate their movement to settlement habitats, while earlier stages of larvae were

present throughout the spawning season and were associated with tides which aided in their expulsion from the estuary.

Both environmental influences as well as biological responses from the larvae affect the distribution and transport of *Uca* larvae in the Satilla River estuary. Figure 3.10 shows a conceptual model for the movement of *Uca* larvae through the estuarine system. It describes the overall distribution and transport of the different stages of larvae. Vertical stratification of the larvae is evident in the model as zoea I and II are located in surface waters, whereas zoea III are in both surface and depth showing no significant difference in their vertical location, and zoea IV-V and megalopae are shown at higher densities at depth (Fig. 3.10). Vertical migration (depicted by vertical white arrows) of zoea I – V occurs in the tributaries, the main Satilla River and in the coastal ocean (Fig. 3.10). Similar to the study by Brookins and Epifanio (1985), megalopae were found in significantly greater numbers at depth in the tributaries and in the main Satilla River and may maintain this position due to stronger swimming ability; consequently, the model shows them only at depth and not participating in the vertical migration within the estuary (Fig. 3.10). By responding to environmental changes and cues, the larvae are able to be released by females at the edge of the marsh, travel out to the coastal ocean for development, and return to the marsh as juvenile crabs ready to settle into the adult habitat (Fig. 3.10).

CHAPTER 4

PETROLISTHES ARMATUS

Results

The distribution of *P. armatus* larvae in the Satilla River estuarine system varied spatially between the tributaries and the main Satilla River as well as among the different stations sampled. The larval densities were similar at the surface and at depth in the tributaries; however, more larvae were collected at depth than at the surface in the main river. Temporally, the changing of the seasons also appears to play a role in the presence of *P. armatus* larvae in the Satilla River estuary, as more larvae were collected in the late summer and fall while no larvae were collected during the spring. The largest difference in average *P. armatus* larval densities, however, was seen between samples taken in 2005 and those in 2006.

P. armatus undergoes only two larval stages and completes development in 17 to 49 days (Gore, 1969). Both larval stages were found within the estuary during this study suggesting that *P. armatus*, which have long spines making them harder for predators to catch and maneuver, may remain in the estuary for the entire larval cycle (Bishop, personal communication). No megalopae of *P. armatus* were collected during this study.

Samples collected during spring, summer, and fall in 2005 and 2006 in the Satilla River estuary show that no *P. armatus* larvae were found in April 2005 or March 2006. While *P. armatus* larvae were found during August 2005, the average densities (0.02 – 0.79 larvae/m^3) were low when compared to the numbers of larvae collected during September 2005 (0.1 – 4.0 larvae/m^3) and August 2006 (19.6 – 33.1 larvae/m^3), and the largest increase was observed from 2005 to 2006.

Spatial Variations

Since sampling during August 2006 involved surface and deep samples in the tributaries and the main river, spatial differences in *P. armatus* larval distribution were examined for this period. The average density of *P. armatus* in the surface waters was significantly greater in the tributaries than in the main river during ebb tide (*p*-value = 0.016) (Fig. 4.1). During flood tide, the densities in the surface waters of the tributaries were greater than those in the main river, but the difference was not significant (*p*-value = 0.059) (Fig. 4.1). The average larval density at depth in the tributaries was greater than those in the main river; however, the difference is not significant (*p*-value = 0.053) (Fig. 4.1). The densities at depth in the tributaries and the main river are similar during ebb tide (Fig. 4.1).

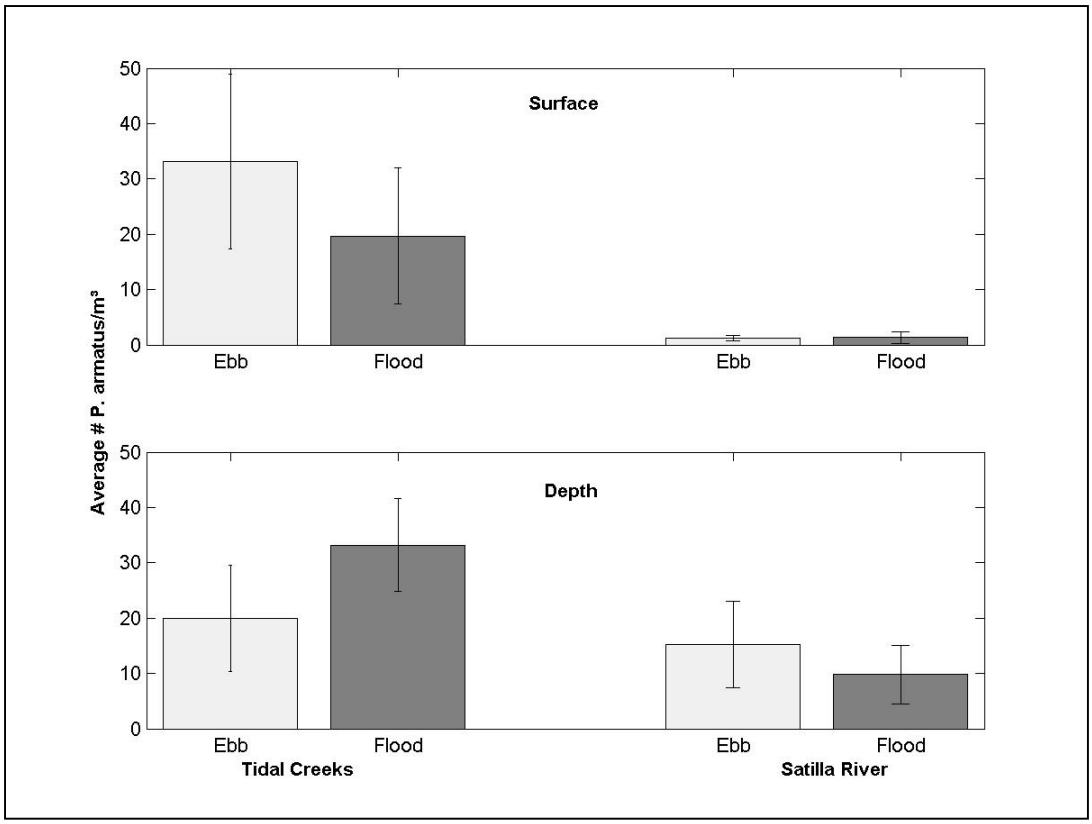

Figure 4.1: Comparison of *P. armatus* larval densities in the surface (top) and depth (bottom) samples during flood and ebb tide in the tributaries and the main Satilla River.

Table 4.1: Comparison of mean *P. armatus* larval densities during flood and ebb tides on all sampling dates during August 2006 with *p*-values from t-tests to determine significant difference between the means from surface samples vs. depth samples.

Sampling Date	Tide	Density at surface	Density at depth	p-value from t-test
August 2, 2006 (tributaries)	Flood	19	33	0.380
August 2, 2006 (tributaries)	Ebb	33	20	0.528
August 3, 2006 (Satilla River)	Flood	0.1	8	0.598
August 3, 2006 (Satilla River)	Ebb	1	18	0.104
August 4, 2006 (Satilla River)	Flood	5	14	0.399
August 4, 2006 (Satilla River)	Ebb	1	11	0.103

When all the stations sampled in the tributaries and the main Satilla River in August 2006 were compared, the highest larval densities were collected from the surface waters in the tributaries, especially at station C, in Jointer Creek, and at station B, where the two tributaries converge (Fig. 4.2). Station C exhibited higher *P. armatus* larval densities at the surface than station A during both ebb and flood tides (*p*-value = 0.034) (Fig. 4.2). The stations sampled from the transect of the Satilla River show higher densities at depth than at the surface during ebb tide (*p*-value = 0.029) and during flood tide (*p*-value = 0.043) (*p*-values are a combination of all samples collected on August 3 and August 4, 2006 and are shown separately in Table 4.1) (Fig. 4.2). The highest density sampled from the main river was collected at depth at the mouth of the river during ebb tide (Fig. 4.2).

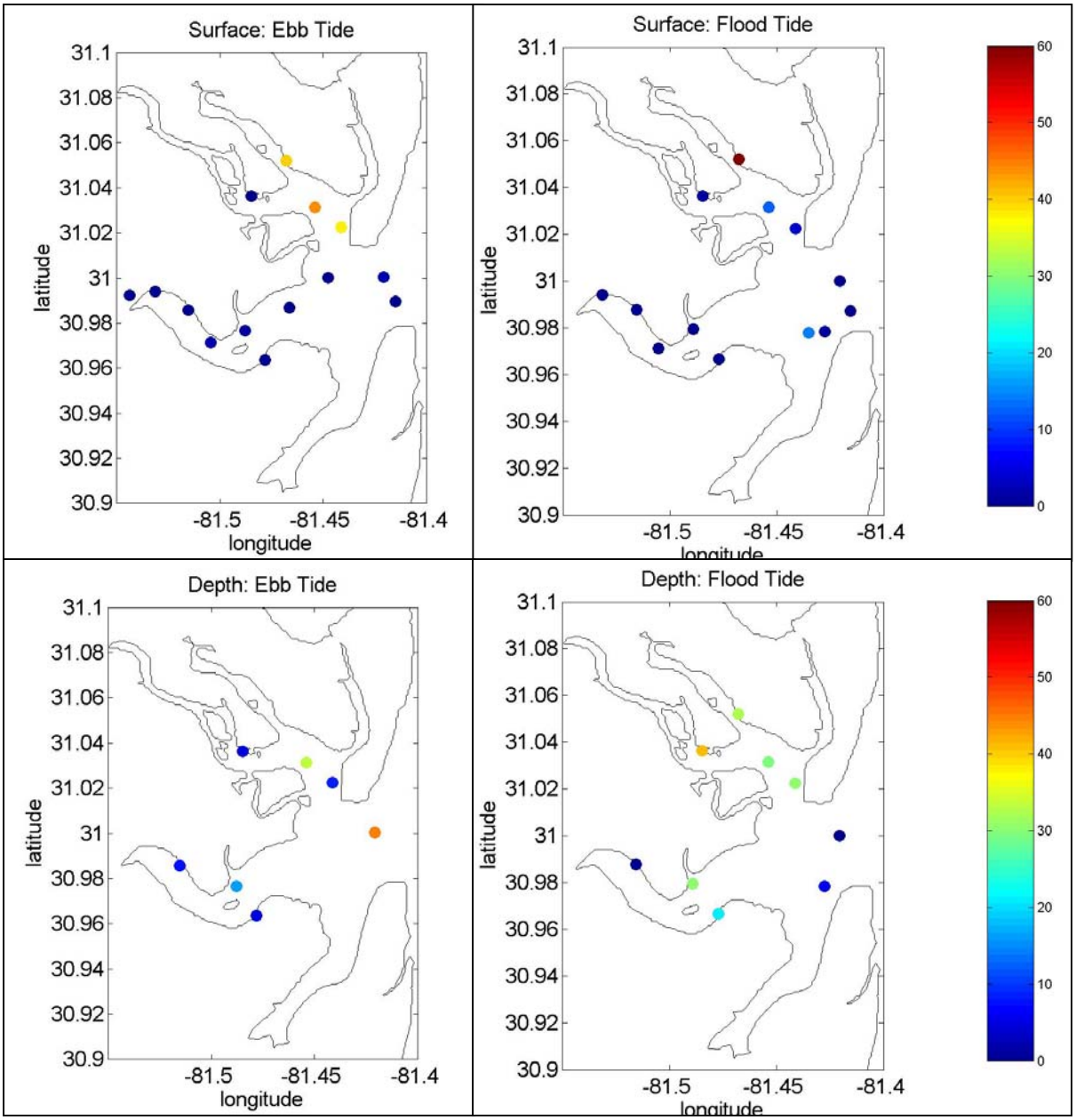

Figure 4.2: Average *P. armatus* larval densities in the surface (top) and depth (bottom) samples from all stations during ebb tide (left) and flood tide (right) during all sampling days in August 2006. Stations showing no data point at depth were only sampled at the surface.

Another spatial variation examined in August 2006 involved the vertical distribution of *P. armatus* larvae within the water column. Within the tributaries there was no significant difference between surface and depth samples during flood or ebb tide (Table 4.1). Two stations upriver exhibited higher average densities at depth during flood

tide and all stations within the tributaries showed higher densities at depth during flood tide (Fig. 4.2)

Two stages of *P. armatus* larvae were collected within the Satilla River estuarine system during this study. No significant difference was observed in the horizontal or vertical spatial location of the two different stages, however only 2 of 34 samples contained zoea II during 2005, while 9 of 34 samples contained zoea I (Table 4.2).

Temporal Variations

The largest increase in *P. armatus* larvae in the Satilla River estuary was seen between August 2005 and August 2006. Samples from the tributaries in August 2005 showed the presence of *P. armatus* in the system, but only exhibited densities of 0.02 to 0.79 larvae/m^3, while samples from the tributaries on August 2, 2006 showed average larval densities around 33 larvae/m^3 (Fig. 4.3).

Seasonally, *P. armatus* larvae showed a higher propensity for the late summer and early fall months as no larvae were collected during March 2006 or April 2005. *P. armatus* larvae were collected during all other sampling periods and more larvae were collected in September 2005 than in August 2005 (p-value = 0.036).

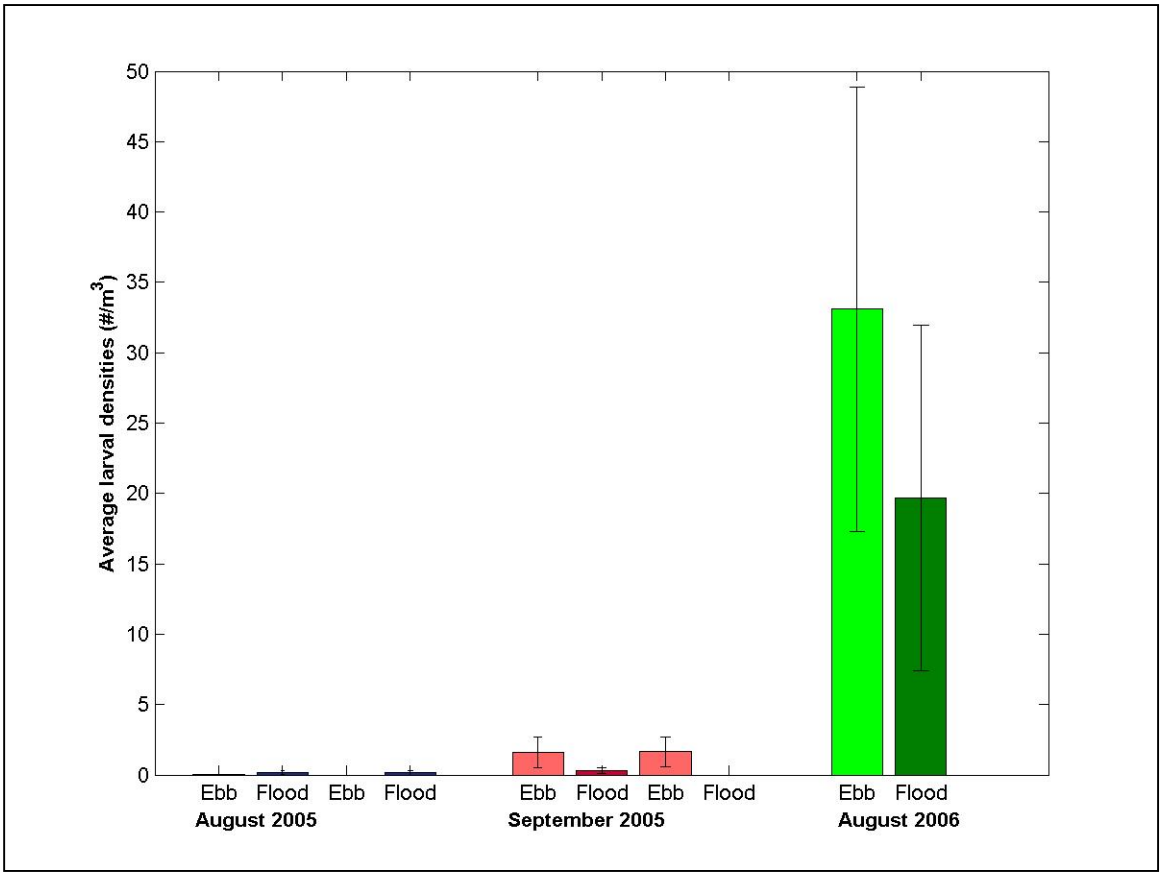

Figure 4.3: Comparison of *P. armatus* larval densities in the surface samples from the tributaries during ebb and flood tides for the two days of sampling in August 2005 and September 2005 and for the one day of sampling in August 2006.

Table 4.2: Comparison of *P. armatus* larval densities and zoeal stages at all stations during 2005 sampling. (ND means No Data is available).

Sampling Dates and Physical Parameters	**Stations**	**Tides**	**Average *P. armatus* larval density (#/m³)**		
			ZI	**ZII**	**Total**
August 16, 2005	**A**	Ebb	0	0	0
Tides: Spring		Flood	0.47	0.32	0.79 ± ND
Winds: NE, strong	**B**	Ebb	0	0	0
Salinity: 22 – 29		Flood	0.04	0	0.04 ± 0.04
Temp: 30 – 32 ° C	**C**	Ebb	0.09	0	0.09 ± 0.09
Stratification: 0.2 – 0.3 PSU/m		Flood	0	0	0
August 17, 2005	**A**	Ebb	0	0	0
Tides: Spring		Flood	0.4	0	0.4 ± 0.4
Winds: NE, stronger	**B**	Ebb	0	0	0
Salinity: 21 – 29		Flood	0	0	0
Temp: 30 – 32 ° C	**C**	Ebb	0	0	0
Stratification: 0.2 – 0.3 PSU/m		Flood	0	0	0
September 29, 2005	**A**	Ebb	1.6	0	1.6 ± 1.6
Tides: Neap		Flood	0	0	0
Winds: variable, weak	**B**	Ebb	1.7	0.8	2.5 ± 2.5
Salinity: 25 – 30		Flood	0.5	0	0.5 ± 0.4
Temp: 28 – 29 °C	**C**	Ebb	0.15	0	0.15 ± 0.15
Stratification: 0.2 – 0.3 PSU/m		Flood	0.1	0	0.1 ± 0.1
September 30, 2005	**A**	Ebb	3.27	0.72	4.0 ± 4.0
Tides: Neap		Flood	0	0	0
Winds: S, stronger in pm	**B**	Ebb	1.49	0	1.49 ± 1.49
Salinity: 25 – 30		Flood	0	0	0
Temp: 28 – 29 °C	**C**	Ebb	0.26	0	0.26 ± 0.26
Stratification: 0.2 – 0.4 PSU/m		Flood	0	0	0

The abundance of *P. armatus* larvae was not based on the phase of the tide as was seen with the *Uca* larval densities. Samples from the tributaries showed similar densities at the surface and at depth during both ebb and flood tide, so vertical stratification of the larvae did not occur in the tributaries at any time (Fig. 4.1). The samples from the main river exhibited vertical stratification with higher densities at depth than at the surface, during both flood tide (p-value = 0.043) and ebb tide (p-value = 0.029) (Fig. 4.1).

Table 4.3: Comparison of *P. armatus* larval densities and zoeal stages at all stations during August 2, 2006 sampling. (ND means No Data was collected).

Sampling Dates and Physical Parameters	**Stations**	**Tides**	**Average *P. armatus* larval density (#/m³)**		
			ZI	**ZII**	**Total**
August 2, 2006	**A (Surface)**	Ebb	0	0	0
Tides: Neap Winds: N, strong Salinity: 35.5 - 36 Temp: 29.5 – 31 °C Stratification: < .1 PSU/m		Flood	0.7	0.5	1.7 ± 0.6
	A (Depth)	Ebb	3.2	1.6	4.7 ± ND
		Flood	20.6	19.9	40.45 ± 28.8
	B (Surface)	Ebb	25.0	18.8	43.5 ± 42.3
		Flood	6.8	6.0	12.8 ± 9.3
	B (Depth)	Ebb	19.5	13.7	33.2 ± 13.8
		Flood	28.3	1.1	29.3 ± 24.54
	C (Surface)	Ebb	29.6	10.0	39.6 ± ND
		Flood	39.2	21.8	60.9 ± 42.3
	C (Depth)	Ebb	ND	ND	ND
		Flood	21.4	10.9	32.3 ± 21.4
	D (Surface)	Ebb	13.3	22.0	38.3 ± ND
		Flood	1.3	2.6	3.8 ± 0.9
	D (Depth)	Ebb	2.5	6.2	8.7 ± ND
		Flood	18.9	11.6	30.5 ± 3.6

Discussion

Spatial Variations

The average larval densities of *P. armatus* from the surface water in the tributaries were significantly higher than those in the main Satilla River during ebb tide (*p*-value = 0.016) and flood tide (but not significant, *p*-value = 0.059). At depth, the densities in the tributaries and the river are similar during ebb tide, but show some variation during flood tide (*p*-value = 0.053) with more larvae in the tributaries than in the main river. This distribution is consistent with the retention of *P. armatus* larvae in the estuary for the duration of development.

The larvae are vertically stratified in the main Satilla River with more larvae at depth than at the surface, while there is no such vertical stratification observed in the tributaries. By not being stratified within the water column in the tributaries, the larvae

are able to move back and forth with the tides to facilitate their dispersal around the estuary as well as hinder their expulsion from it. Once the larvae are in the main river, however, they are located in the deeper, higher saline, water, to prevent being washed out of the estuary. By remaining at depth while in the main river, especially during ebb tide, *P. armatus* larvae hinder their movement out of the estuary with the outgoing water.

During August 2006, the highest densities of larvae were collected in Jointer Creek (station C). The greater number of larvae found at this station are consistent with the flow patterns seen during drifter deployment in the area. Since water from the Little Satilla River (station A) flows into Jointer Creek (station C), but very little water from Jointer Creek flows into the Little Satilla River, larvae from the Little Satilla River may have been advected into Jointer Creek where they remained (Fig. 2.19 & 2.20). Additionally, Jointer Creek (station C) is characterized by higher salinities than the Little Satilla River (station A) (Table 2.1), which are preferred by adult *P. armatus* (Gore, 1969). The potentially larger adult populations in Jointer Creek could have resulted in the presence of more larvae being released into Jointer Creek than other areas, however, more work on the adult populations needs to be completed in order to test this prediction.

Temporal Variations

The drastic interannual increase in densities of *P. armatus* from 2005 to 2006 might have been due to the higher salinities observed in 2006 (Table 2.1) or the establishment of a successful breeding population within the Satilla River estuary. The quantity of *P. armatus* larvae collected in the estuary appeared to be slightly correlated to the salinity ($r = 0.573$). The lowest densities were collected in August 2005 when salinities ranged from 21 – 29 PSU (Fig. 4.3 & Table 2.1). September 2005 exhibited

salinities ranging from 25 – 30 PSU and had higher average *P. armatus* larval densities than in August 2005 (Fig. 4.3 & Table 2.1). August 2006 showed the highest salinities, ranging from 35.5 – 36 PSU, and the highest larval densities (Fig. 4.3 & Table 2.1). The difference in salinities from August 2005 to August 2006 may explain the large increase in *P. armatus* larvae present within the Satilla River estuary because the higher salinities may cause the adults, which show affinities for higher salinities, to reproduce or release larvae at higher rates. The large increase of larvae may also have been due to the predicted increasing adult population of *P. armatus* inhabiting the Satilla River estuarine system. *P. armatus* populations have been increasing in Georgia since their initial invasion in 1994 and the densities of larvae collected in 2006 may have reflected their established breeding population (Knott et al., 1999; Hollebone, 2006).

The changing of the seasons appeared to play a role in the timing of larval release by *P. armatus*. No samples from the April 2005 or the March 2006 sampling dates contained any *P. armatus*, suggesting that the spawning season of the green porcelain crab occurs after these months. The timing of spawning may be a function of temperature since these crabs have moved into the area from warmer climates (Knott et al., 1999; Coen & McAlister, 2001). Hollebone (2006) also found an increase in gravid female P. armatus along the Georgia coast during warmer months. The temperatures in March and April are much lower than in August and September and may have hindered spawning (Table 2.1).

In contrast to *Uca* larvae, the distribution of *P. armatus* larvae was largely unaffected by the tides. *Uca* larvae use the tides to move out of the estuary for development in the coastal ocean (Wheeler, 1978; Christy, 1982; Salmon et al., 1986;

Forward, 1987); however, *P. armatus* larvae remain in the estuary and their lack of movement due to the tides supports this idea.

Environmental effects

Since wind speed and direction can cause movement of the surface water and result in mixing of the water column, it is important to examine the wind during the sampling periods to determine if it affected the observed distribution of *P. armatus* larvae. The measured winds during both August 2005 and August 2006 were strong, almost 8 m/s, and towards the north (Table 2.1). Since the larval densities and distributions from August 2005 and August 2006 are drastically different, it is clear that wind effects were not the primary cause for the difference in the overall larval densities. The sampling dates in September 2005 experienced variable winds that were relatively weak, 3 – 5 m/s (Fig. 2.4). These weaker winds would not have affected the surface waters like the winds from August 2005 or August 2006 would and so they were most likely not responsible for the observed *P. armatus* larval densities and distribution.

Sampling in August 2005 took place during a spring tide and resulted in stronger currents than the neap tides in which the September 2005 and August 2006 sampling took place. The presence of stronger currents in August 2005 resulted in higher velocities, increased mixing (Table 2.1) and strong tidal flushing which would have caused *P. armatus* larvae to be expelled from the estuary more quickly. The lack of *P. armatus* larvae during this sampling period may be the result of preferential larval release during the weaker velocities of the neap tides as seen in September 2005 and August 2006. Just as *Uca* are expected to release larvae during the spring ebb tide to facilitate export from

the estuary, *P. armatus* may release larvae during neap tide to aid retention within the estuary.

Conclusions

P. armatus larvae are highly dependent on the physical parameters of the estuary. When the salinity is high, as in August 2006, *P. armatus* larvae are extremely abundant in the estuary. They also appear to survive better at higher temperatures as seen in August and September of 2005 and August 2006 rather than at the cooler temperatures of the spring months of April 2005 and March 2006.

P. armatus were more abundant in the tributaries than in the main river in August 2006 and their vertical distribution differed between the two locations. *P. armatus* were found at depth when in the main river; however, stratification did not occur within the tributaries and there was no significant difference between densities from surface or depth samples. The highest densities of larvae at the surface were seen within the tributaries during both ebb and flood tides during the August 2006 sampling dates (Fig. 4.2).

Figure 4.4 shows the schematic model of transport for *P. armatus* larvae within the Satilla River estuary. Movement of larvae in the tributaries results in relatively equal densities of larvae at the surface and at depth during both ebb and flood tide (Fig. 4.4). If the larvae reach the main Satilla River, they move to deeper water and are found at depth during both phases of the tide (Fig 4.4). The position within the Satilla River estuary of the *P. armatus* larvae prohibits their movement out of the estuary to the coastal ocean. Only zoea I and II are pictured in this model and neither stage shows a preference for surface or deep waters. Megalopae are not a part of this model because no *P. armatus*

megalopae were collected during this study. The megalopae may settle to the bottom where this study was unable to sample or they may not have to travel far to reach suitable adult habitats due to the retention of the zoea within the estuary.

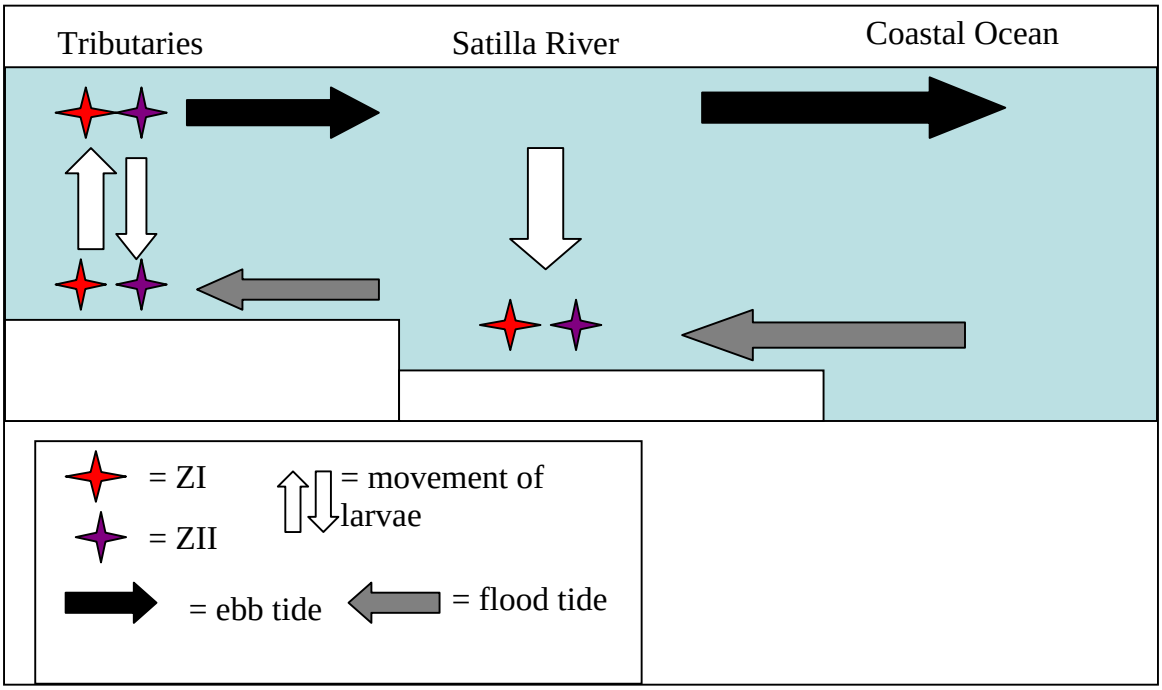

Figure 4.4: Model depicting transport of *P. armatus* larvae in the Satilla River estuary.

The large increase in *P. armatus* larval densities from 2005 to 2006 shows that the green porcelain crab has become established and has a healthy breeding population within the Satilla River estuary. The establishment of a healthy breeding population and the survival of increased amounts of larvae may have been facilitated by the higher salinities seen in August 2006.

CHAPTER 5

CONCLUSION

This examination of larval distribution and transport within the Satilla River estuary demonstrated the importance of both the physical parameters of the estuary and the biological reactions of crab larvae in determining the movement of larvae throughout the estuary and in influencing their ultimate settlement location. The two species of crab larvae investigated in this study show the large differences in biological responses of larvae to the physical parameters present within the estuary. Since *Uca* spp. larvae must travel to the higher salinities of the coastal ocean for larval development, the earlier zoeal stages were found associated with surface waters during ebb tides, which would facilitate their exit from the estuary. These findings were in agreement with Wheeler (1978), Christy (1982), Brookins and Epifanio (1985), Salmon et al. (1986), and Forward (1987), who found higher densities of *Uca* larvae at the surface during ebb tide. It is suspected that *P. armatus* larvae, with their abbreviated lifecycle and protective carapace, remain within the estuary during larval development. They were found in locations, both spatially and temporally, that would hinder their expulsion from the estuary.

The main physical parameters examined in this study include the salinity, temperature and density regimes present within the Satilla River estuary during different seasons throughout a two-year period, the flow patterns seen between the Little Satilla River and Jointer Creek tributaries, the depth-averaged velocities during different tides, and the effect of the tides on the vertical stratification. The salinity is strongly correlated with the density ($r = 0.99$) and higher salinities within the estuary resulted in higher densities throughout the study. The temperature was not correlated with density ($r =$

0.09), but temperatures increased from spring to summer and were always higher in the afternoon than in the morning. The depth-averaged velocities within the Satilla River estuary were stronger during spring tides than neap tides. As observed by Blanton et al. (2003), the stronger velocities resulted in more mixing and less vertical stratification of the water column during spring tides and less mixing and more stratification during neap tides.

Surface flow patterns between the Little Satilla River and Jointer Creek were described using the trajectories of GPS drifters deployed during the spring tides of June and July 2005. No drifters were transported from the tributaries into the main river or the coastal ocean during the full tidal cycle, indicating weak residual transport of water from the tributaries to the Satilla River even during the stronger spring currents. The movement of the drifters demonstrated that some water from the Little Satilla River flows out of that tributary during ebb tide and into Jointer Creek on the subsequent flood tide; however, little water moves from Jointer Creek to the Little Satilla or from either tributary to the main Satilla River or coastal ocean after only one tidal cycle.

The seasons and tides affected the horizontal and vertical distribution of *Uca* spp. larvae within the Satilla River estuary. More larvae were found in the late summer and early fall than during the spring months and higher densities of larvae were present in surface samples during ebb tide than during flood tide. The five stages of larvae as well as megalopae of *Uca* were collected within the estuary and the vertical distribution of the stages is consistent with movement of early stage larvae out of the estuary and transport of later stage larvae back into the estuary for settlement in suitable adult habitats. Vertical stratification of *Uca* larvae was evident in August 2006, particularly in the tributaries,

with more zoea I and II in the surface water, especially during ebb tide, and more zoea IV-V and megalopae at depth, especially during flood tide. These findings are consistent with results from a study in the Chesapeake Bay that found that the vertical distribution of *Uca* spp. was correlated with tidal phase where larvae were twice as likely to be in the surface waters during ebb tide than flood tide in order to promote quick transport downstream to the coastal ocean (Garrison, 1999). *Uca* megalopae were found in greater numbers at depth than at the surface during both phases of the tide and in both the tributaries and the main river suggesting that they move into the estuary at depth. This idea is supported by Brookins and Epifanio (1985), who also collected more megalopae at depth, but is in contrast to Little and Epifanio (1991), who collected more megalopae in the surface water during flood tide than ebb tide and stated that *Uca* megalopae use flood tides and wind events to re-enter the estuary.

The distribution of *P. armatus* larvae within the Satilla River estuary varied greatly from that of *Uca* spp. with no vertical stratification in the tributaries, aiding in retention within the system. In the main river, surface samples contained much lower densities than samples from depth during both phases of the tide, suggesting that once *P. armatus* larvae reach the main river they promptly sink out of the water column to prevent movement out of the estuary with ebbing surface water. The larval densities of *P. armatus* varied from 2005 to 2006 with much greater densities during 2006, when salinities were higher. The higher densities of *P. armatus* may also have resulted from the establishment of a healthy adult breeding population within the Satilla River estuary from 2005 to 2006. The retention of *P. armatus* larvae within the estuary and the shortened

larval cycle appear to have aided in the invasion and establishment of the large population of *P. armatus* observed by Hollebone (2006).

This study recorded any occurrence of *Callinectes sapidus* larvae found within the estuary, even though the presence of *C. sapidus* larvae was not expected due to previous research, which did not collect large numbers of *C. sapidus* larvae within the estuary (Dittel & Epifanio, 1982; Brookins & Epifanio, 1985). Only the zoea I of *C. sapidus* was collected within the estuary and only in surface samples at stations close to the mouth of the estuary during August 2006, when salinities were high, around 35 - 36 PSU. Megalopae of *C. sapidus* were found in two samples collected at depth during flood tides at the station in the Little Satilla River. The numbers of *C. sapidus* larvae present within the estuary were minimal when compared to the numbers of *Uca* spp. and *P. armatus.* The findings of this study are consistent with previous studies, which also found only *C. sapidus* zoea I in surface samples and megalopae in samples from depth and did not collect other zoeal stages near the estuary (Dittel & Epifanio, 1982; Brookins & Epifanio, 1985; Mense & Wenner, 1989; Epifanio & Garvine, 2001).

The physical parameters in the Satilla River estuary are used by three different species of crab larvae for the distribution and transport necessary for larval development and reinvasion to adult habitats. The same physical parameters result in transport in three distinct ways depending on the biology of each crab species.

Uca spp. larvae are released within the estuary, often several kilometers upriver. As a result of spawning during ebb tides, especially during the strong spring tides, the *Uca* larvae travel out to the coastal ocean for larval development. Since movement to the coastal ocean requires more than one tidal cycle, the larvae are entrained in the surface

water during ebb tide and migrate to depth during flood tide to avoid being forced back into the tributaries. Reinvasion of the estuary for settlement into adult habitats is accomplished by later stage zoea on the flood tides.

P. armatus, which have a shortened period of larval development, consisting of only two stages, are also released within the estuary. Unlike *Uca* larvae, *P. armatus* larvae are not stratified within the water column while in the tributaries. Since water is not lost from the tributaries to the main Satilla River over a tidal cycle, they are not exported quickly from the system. By sinking to deeper water once they reach the main Satilla River, the *P. armatus* larvae are able to impede their export from the estuary. No *P. armatus* megalopae were collected during this study, so their methods for settlement in adult habitats are not clear.

Larvae of *C. sapidus* are released closer to the coastal ocean than the other two species and remain in the coastal ocean until they are developed and are able to return to the estuary as megalopae. All three species are able to use the same physics present in the Satilla River estuary to be disbursed and transported to the optimal habitats for larval development for each species and then to be transported back to their distinct adult habitats.

The conclusions of this study were restricted by being constrained to specific sampling dates and by being contained within the estuary. This study may have missed periods of higher larval density or trends in larval density due to the infrequency of sampling. Future studies of decapod larval distribution along the Georgia coast should consist of sampling more often within a given month in order to compare neap and spring tides, sampling during the night to observe pulses of larval release, and sampling during

all months of the year to evaluate seasonal changes. Future studies should also travel out to the coastal ocean to observe the physical mechanisms by which larvae are able to reinvade the estuary. Additional studies should continue to examine the horizontal and vertical distribution of larvae by sampling at the surface and at depth and by comparing the densities of larvae present in the tributaries and the main Satilla River.

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APPENDIX A

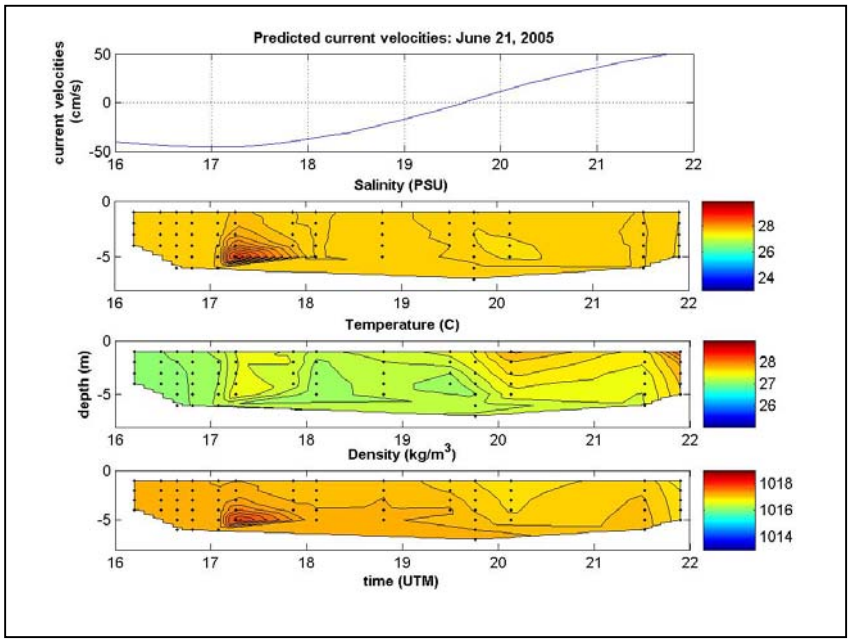

Figure A.1: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles in Jointer Creek on June 21, 2005. Black dots indicate location and depth of CTD casts.

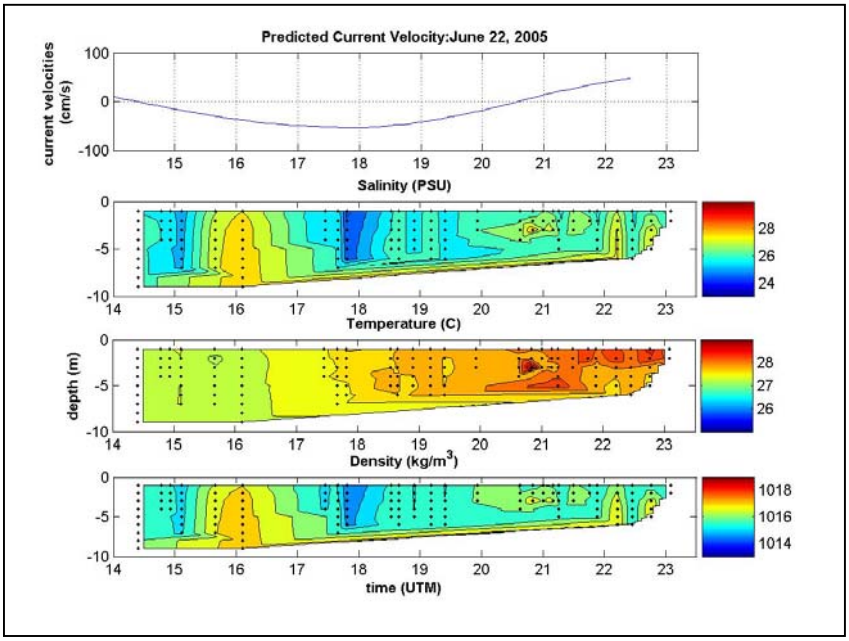

Figure A.2: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles in the Little Satilla River on June 22, 2005. Black dots indicate location and depth of CTD casts.

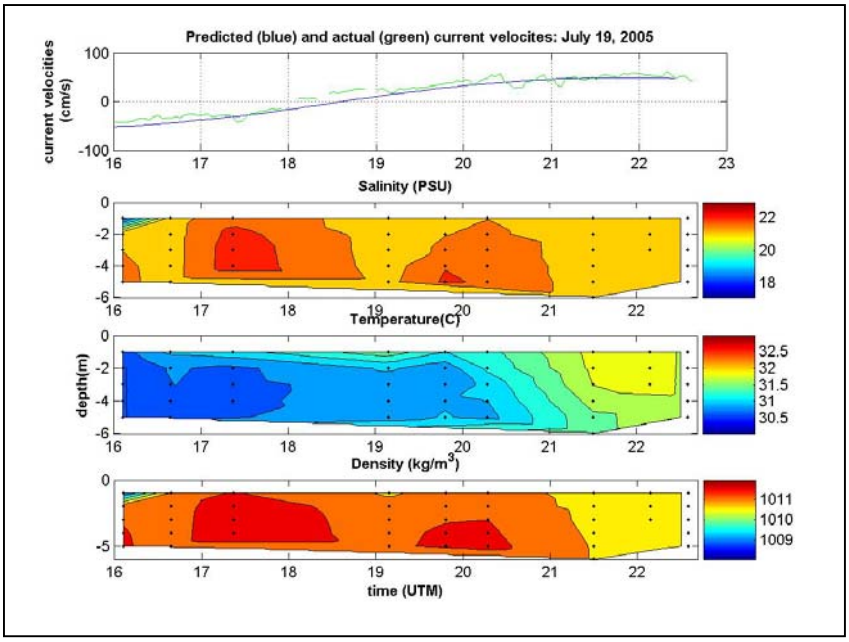

Figure A.3: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles in Jointer Creek on July 19, 2005. Black dots indicate location and depth of CTD casts.

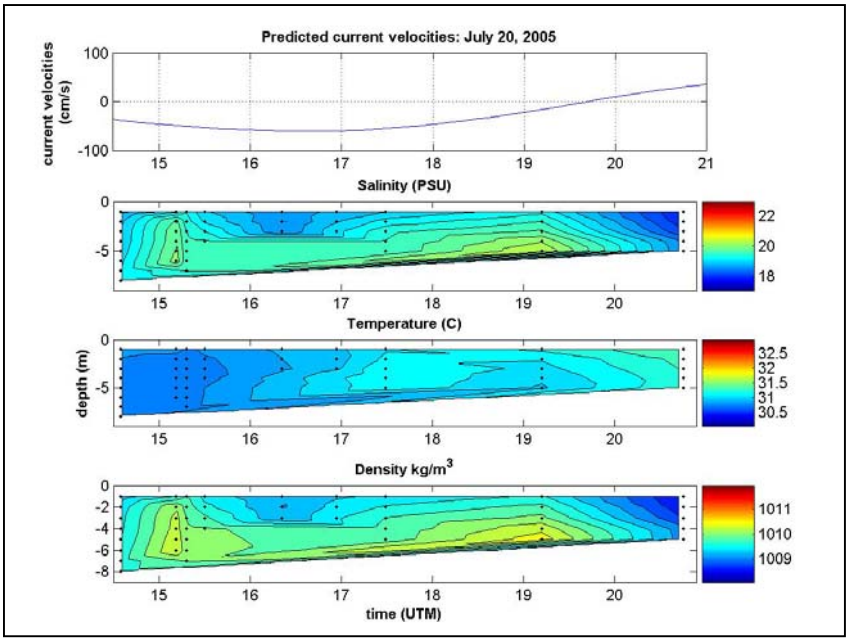

Figure A.4: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles in the Little Satilla River on July 20, 2005. Black dots indicate location and depth of CTD casts.

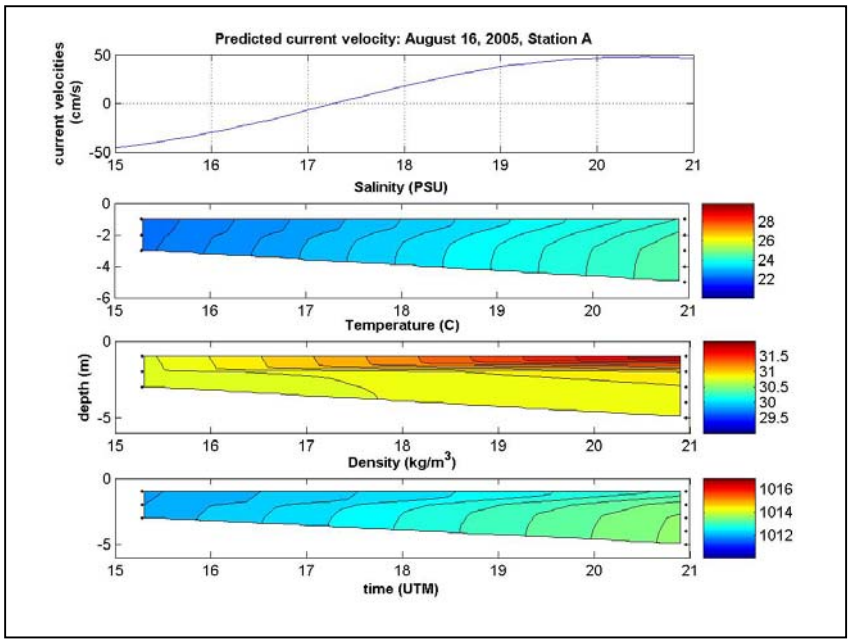

Figure A.5: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station A in the Little Satilla River on August 16, 2005. Black dots indicate location and depth of CTD casts.

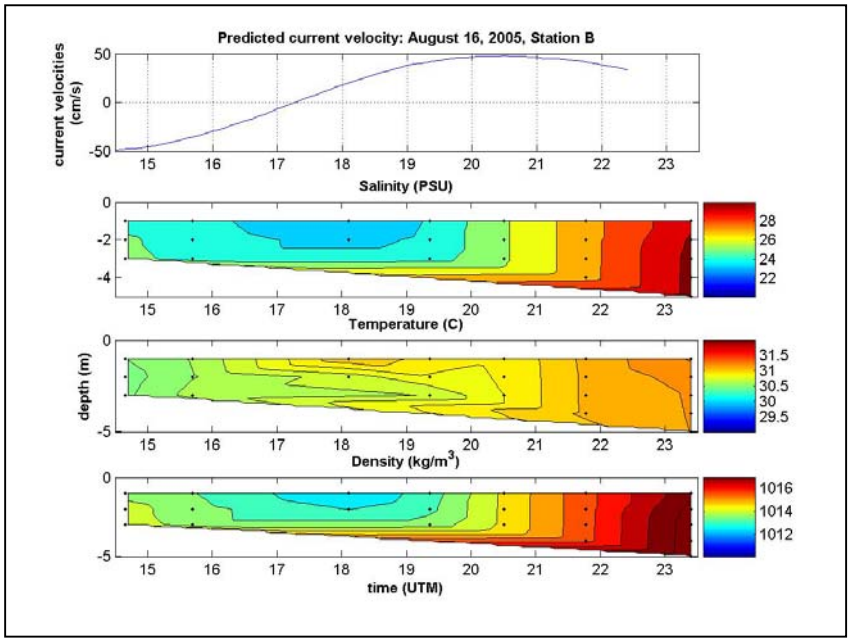

Figure A.6: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station B on August 16, 2005. Black dots indicate location and depth of CTD casts.

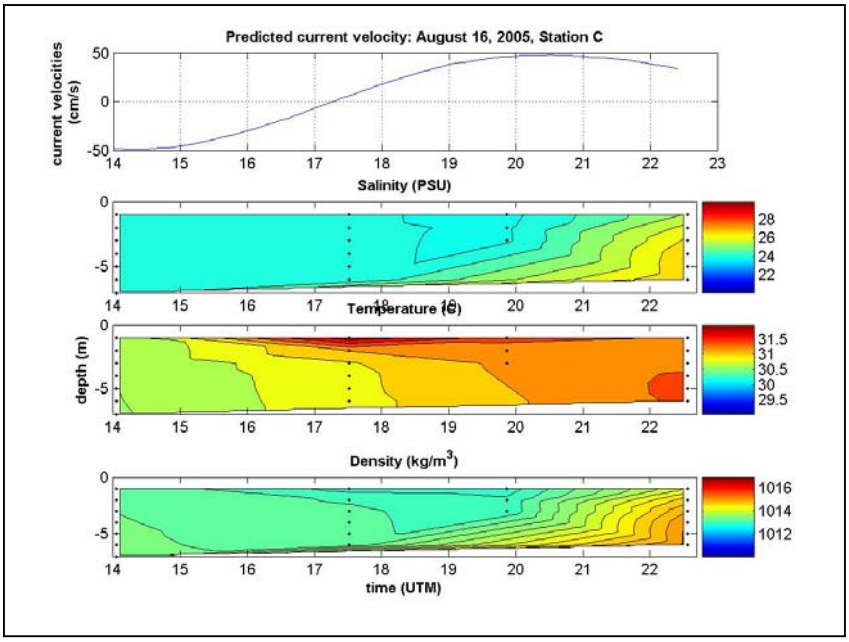

Figure A.7: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station C in Jointer Creek on August 16, 2005. Black dots indicate location and depth of CTD casts.

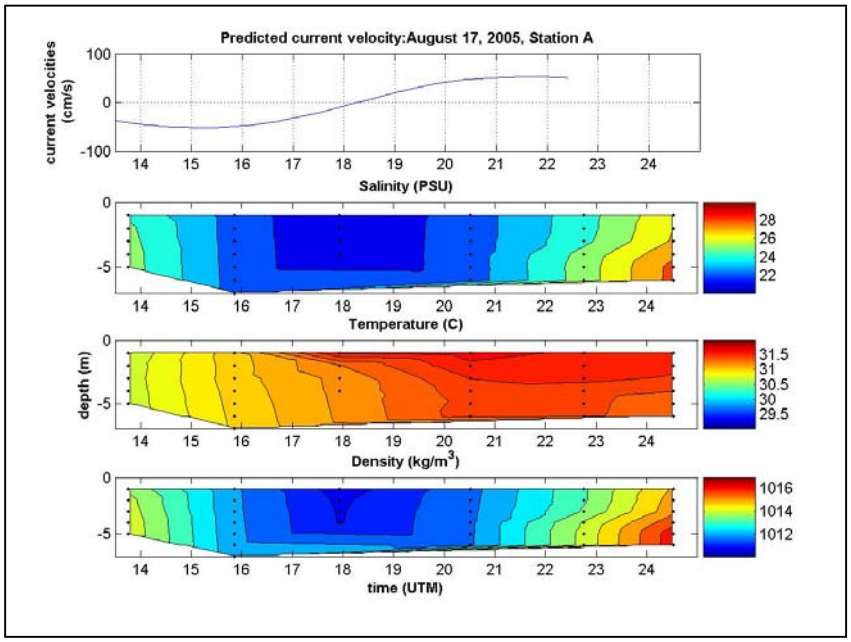

Figure A.8: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station A in the Little Satilla River on August 17, 2005. Black dots indicate location and depth of CTD casts.

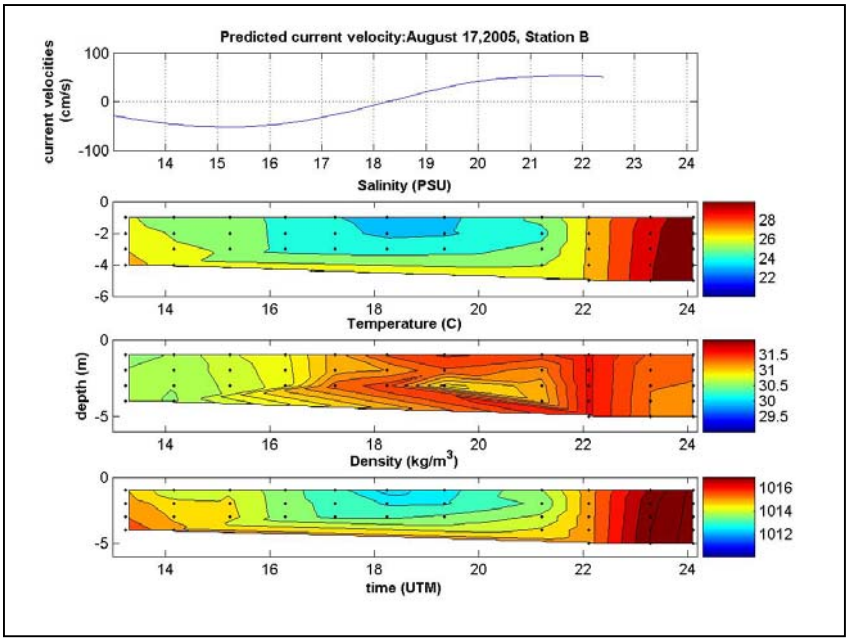

Figure A.9: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station B on August 17, 2005. Black dots indicate location and depth of CTD casts.

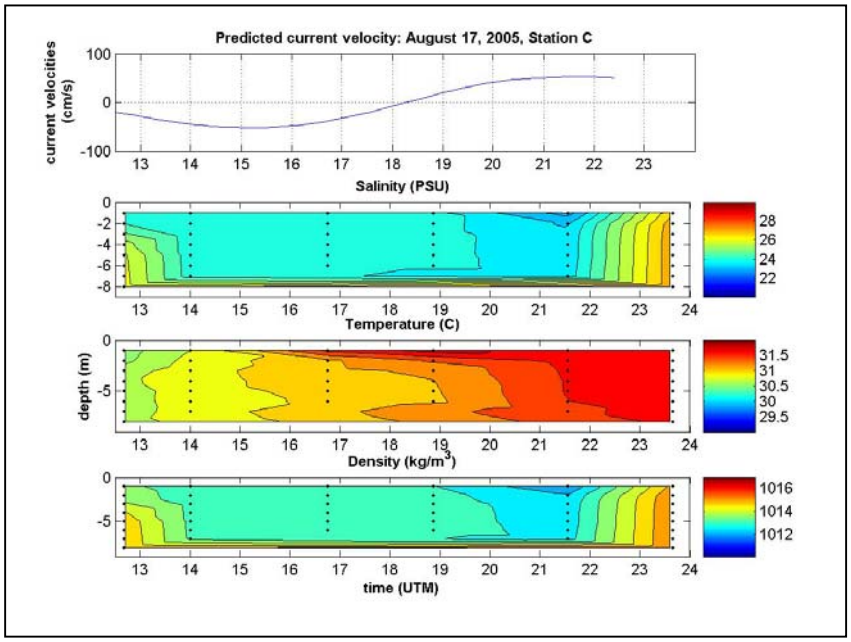

Figure A.10: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station C in Jointer Creek on August 17, 2005. Black dots indicate location and depth of CTD casts.

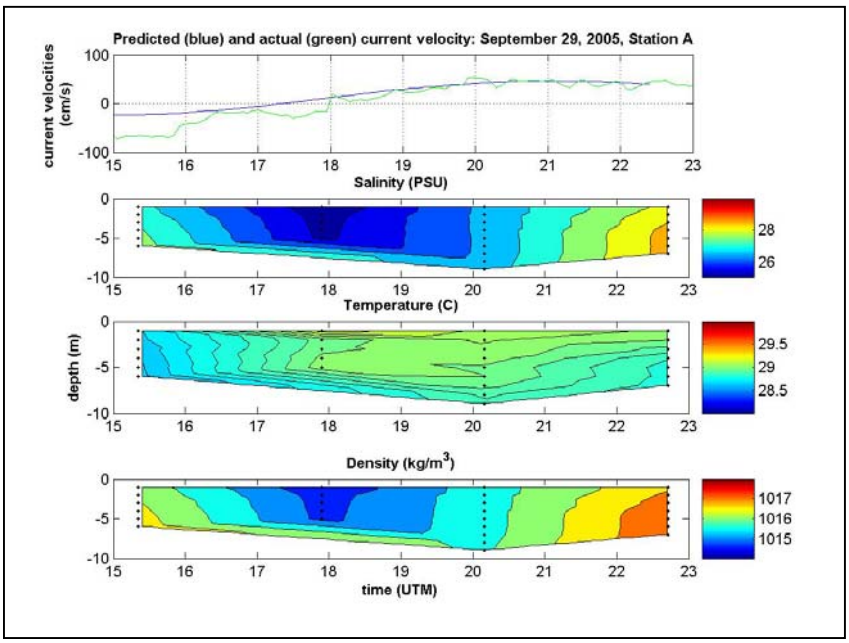

Figure A.11: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station A in the Little Satilla River on September 29, 2005. Black dots indicate location and depth of CTD casts.

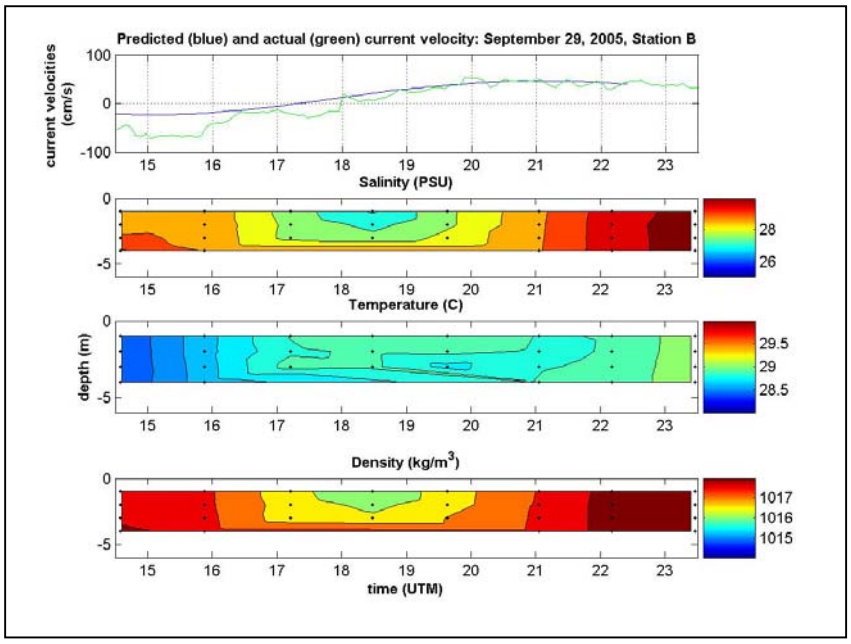

Figure A.12: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station B on September 29, 2005. Black dots indicate location and depth of CTD casts.

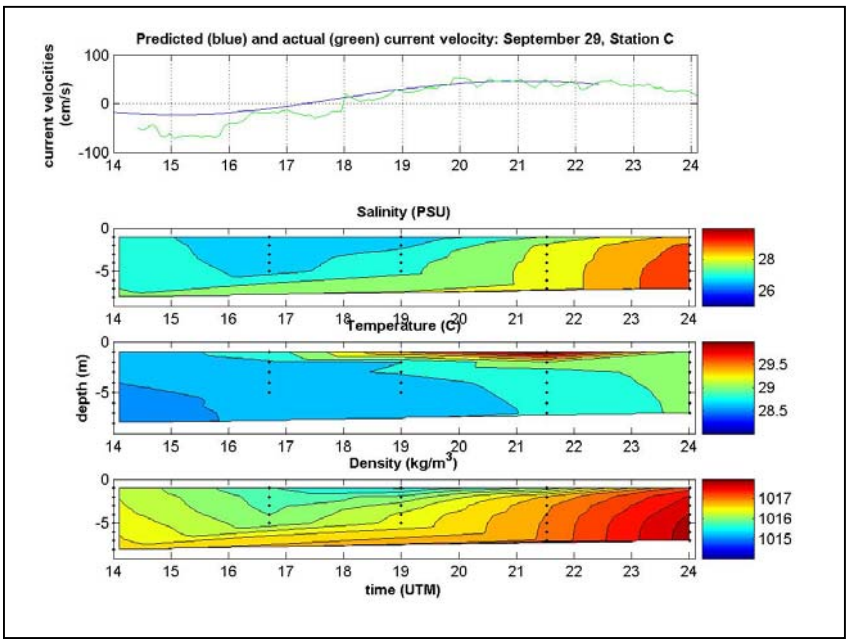

Figure A.13: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station C in Jointer Creek on September 29, 2005. Black dots indicate location and depth of CTD casts.

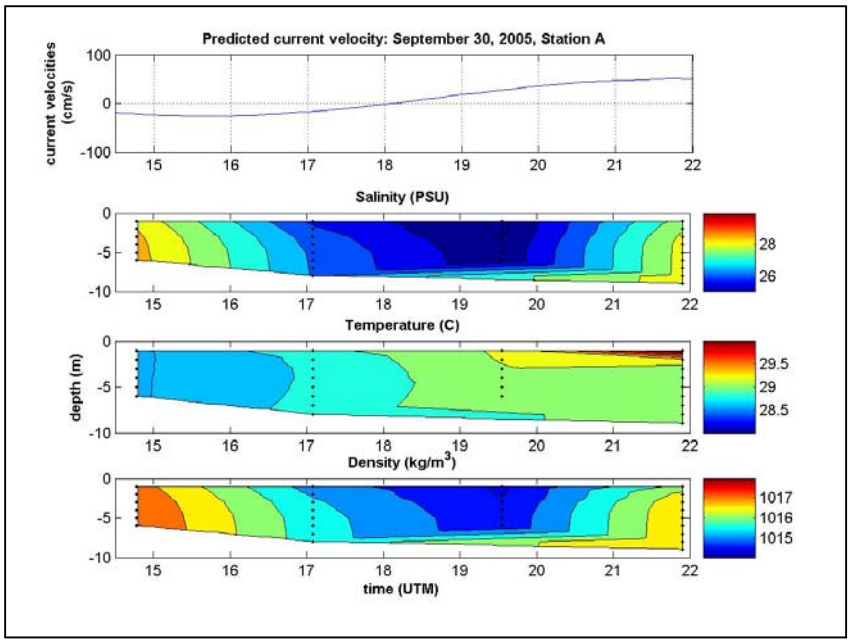

Figure A.14: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station A in the Little Satilla River on September 30, 2005. Black dots indicate location and depth of CTD casts.

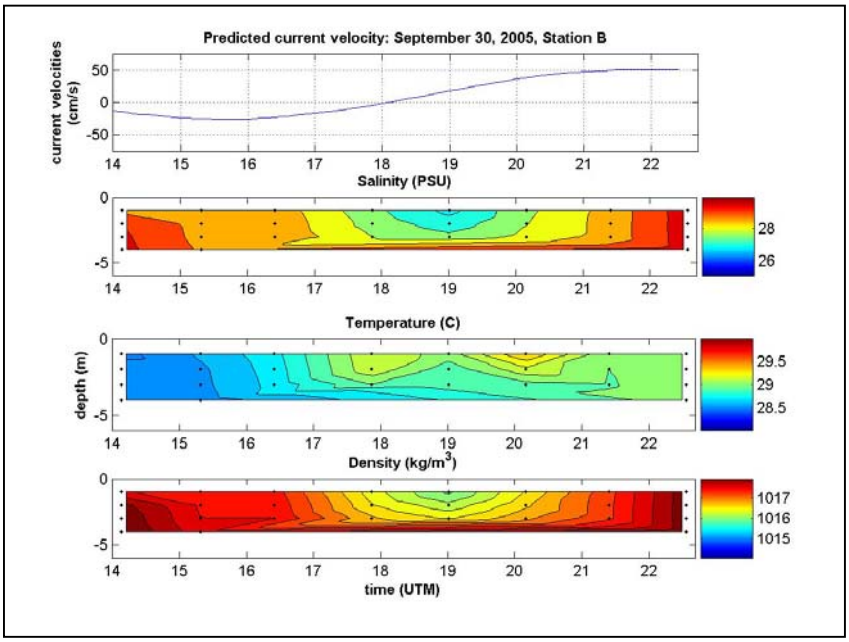

Figure A.15: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station B on September 30, 2005. Black dots indicate location and depth of CTD casts.

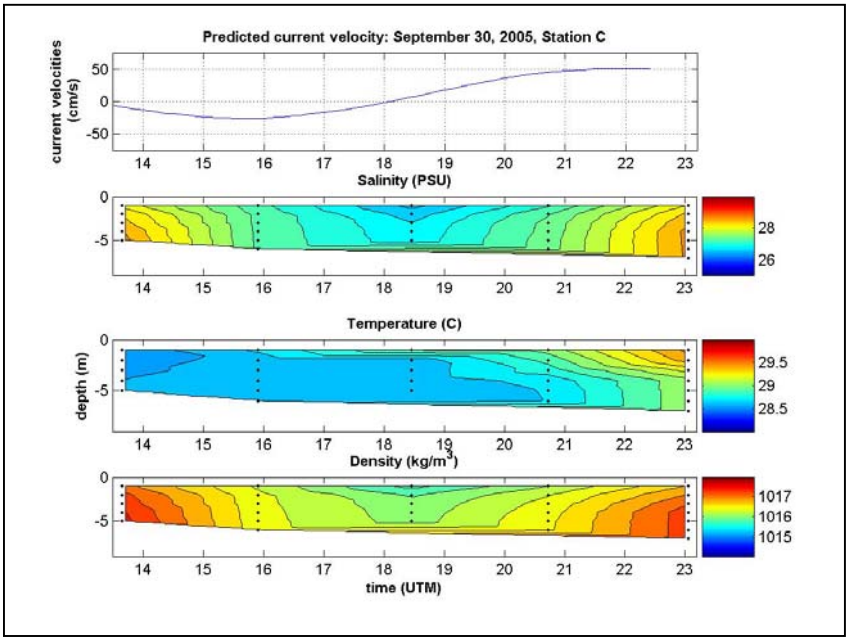

Figure A.16: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station C in Jointer Creek on September 30, 2005. Black dots indicate location and depth of CTD casts.

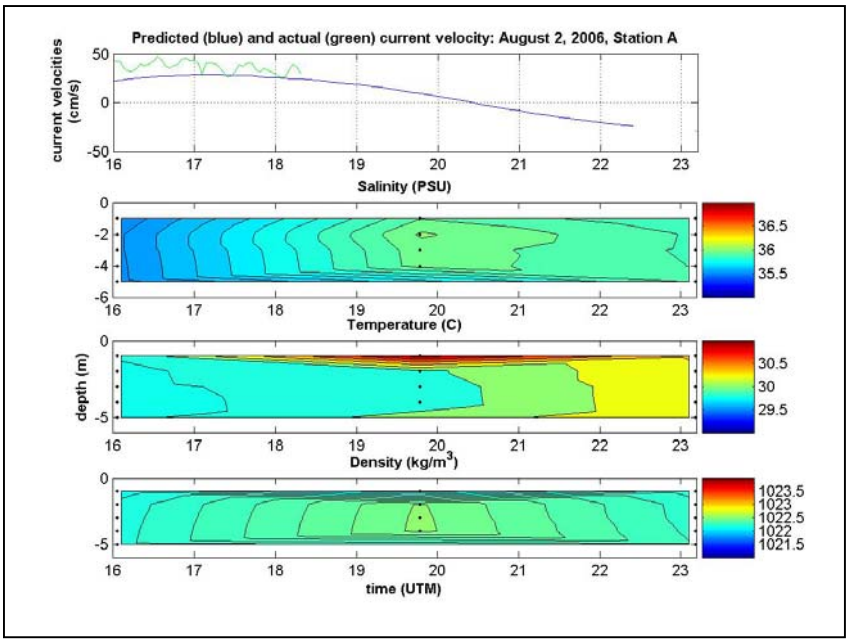

Figure A.17: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station A in the Little Satilla River on August 2, 2006. Black dots indicate location and depth of CTD casts.

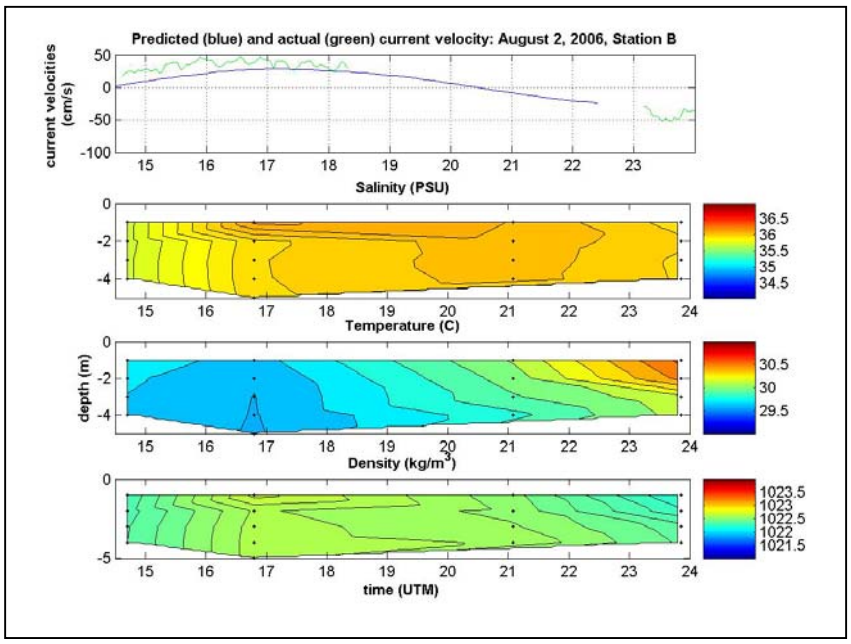

Figure A.18: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station B on August 2, 2006. Black dots indicate location and depth of CTD casts.

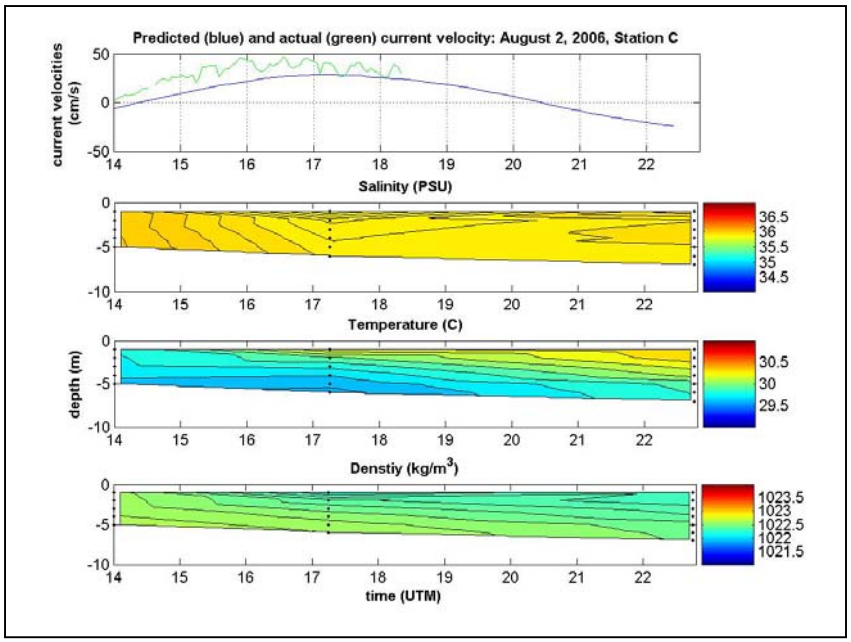

Figure A.19: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station C in the Jointer Creek on August 2, 2006. Black dots indicate location and depth of CTD casts.

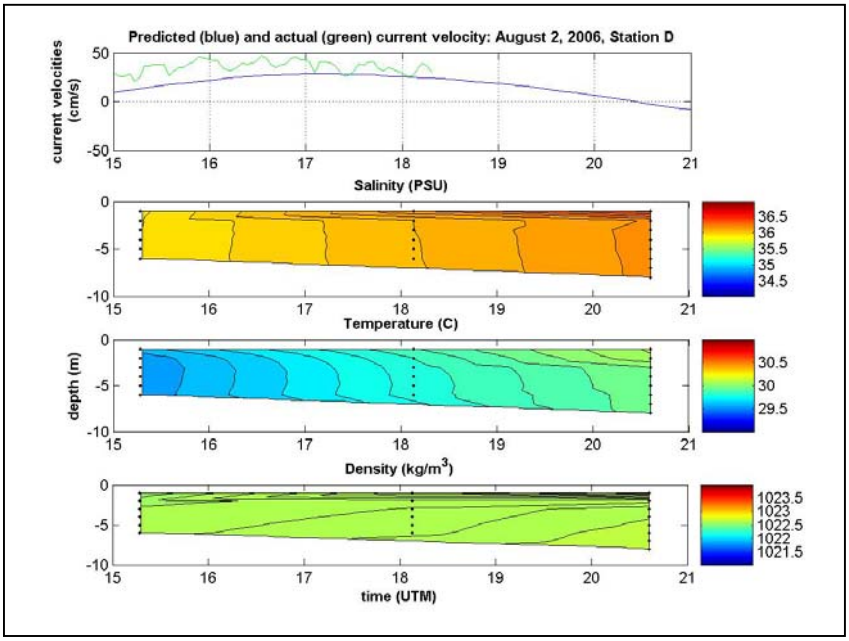

Figure A.20: Predicted depth-averaged velocities with salinity (PSU), temperature (°C), and density (kg/m³) profiles at station D on August 2, 2006. Black dots indicate location and depth of CTD casts.

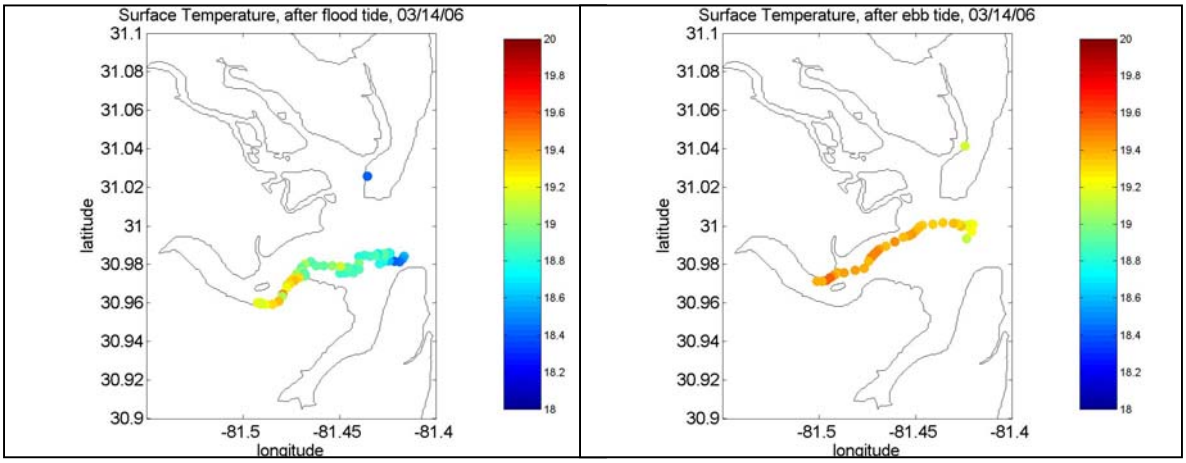

Figure A.21: Surface temperatures along the transect of the Satilla River on March 14, 2006.

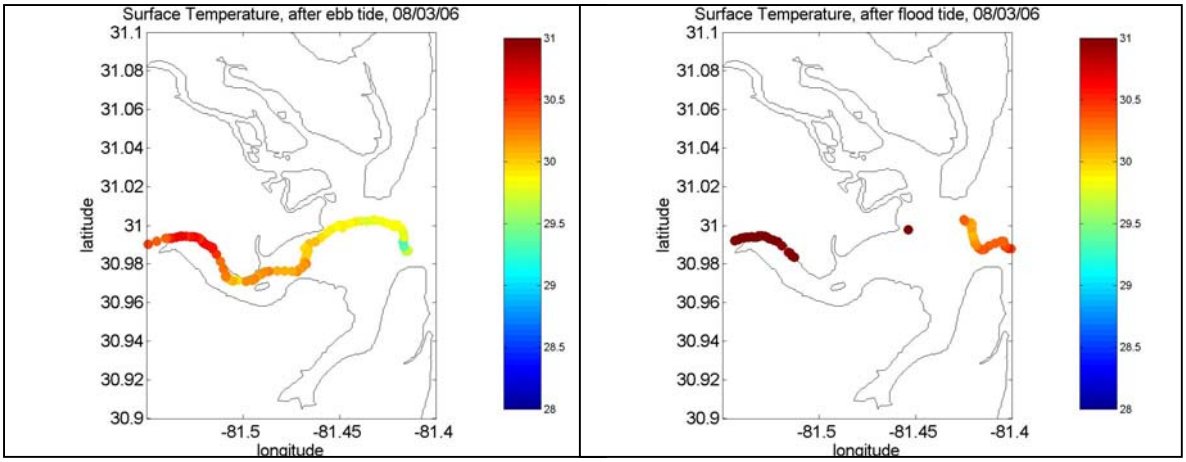

Figure A.22: Surface temperatures along the transect of the Satilla River on August 3, 2006.

APPENDIX B

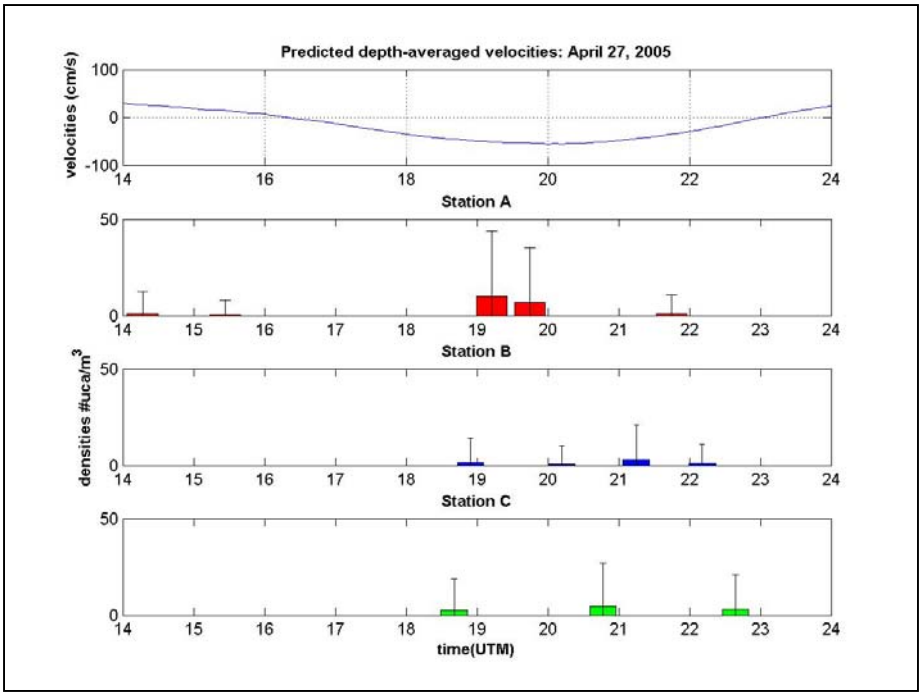

Figure B.1: Predicted depth-averaged velocities with average *Uca* larval densities at stations A, B and C as a function of time on April 27, 2005.

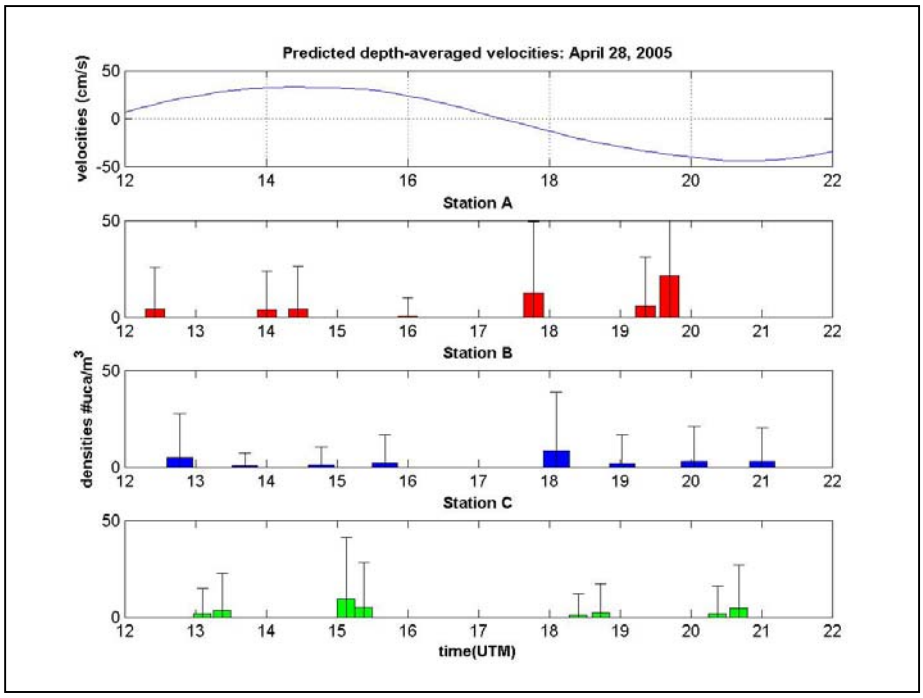

Figure B.2: Predicted depth-averaged velocities with average *Uca* larval densities at stations A, B and C as a function of time on April 28, 2005.

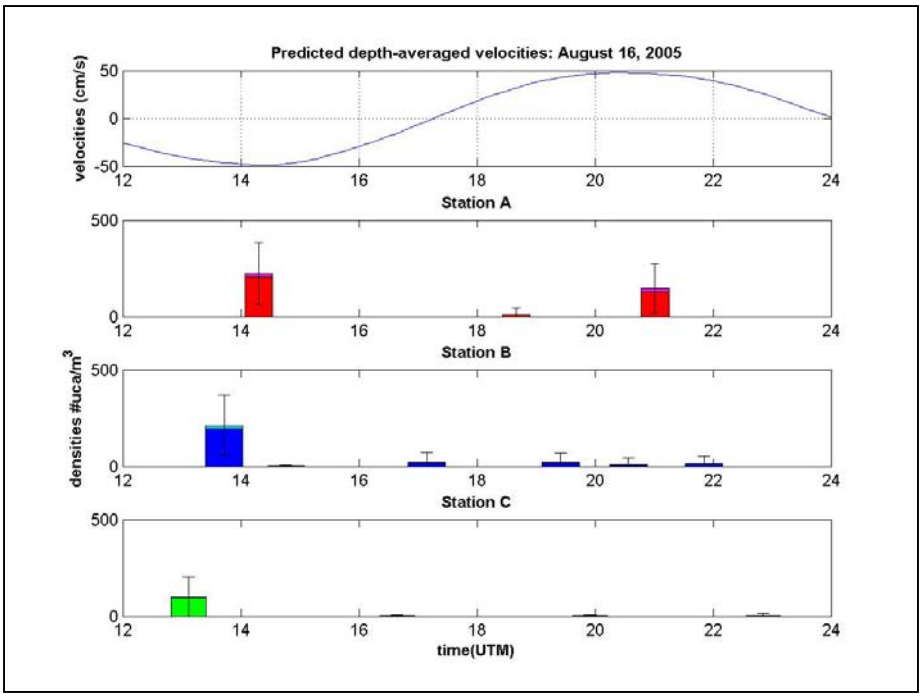

Figure B.3: Predicted depth-averaged velocities with measured *Uca* larval densities at stations A, B, and C on August 16, 2005. Multicolored bars show approximate number of Stage I (darker color) and Stage II (lighter color) larvae present.

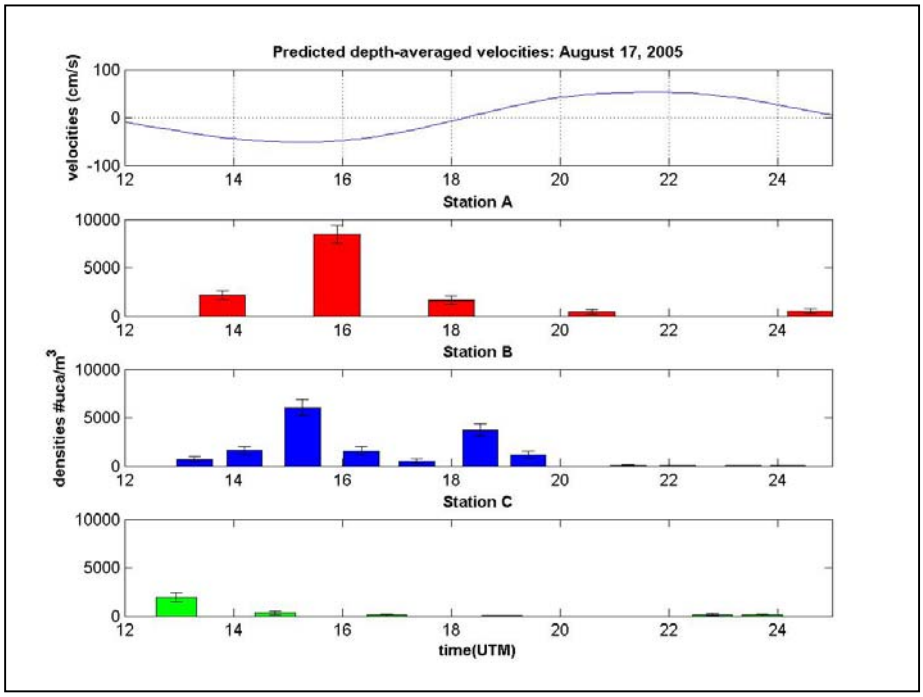

Figure B.4: Predicted depth averaged velocities with measured *Uca* larval densities at stations A, B, and C on August 17, 2005. Note the change in scale from August 16 to August 17.

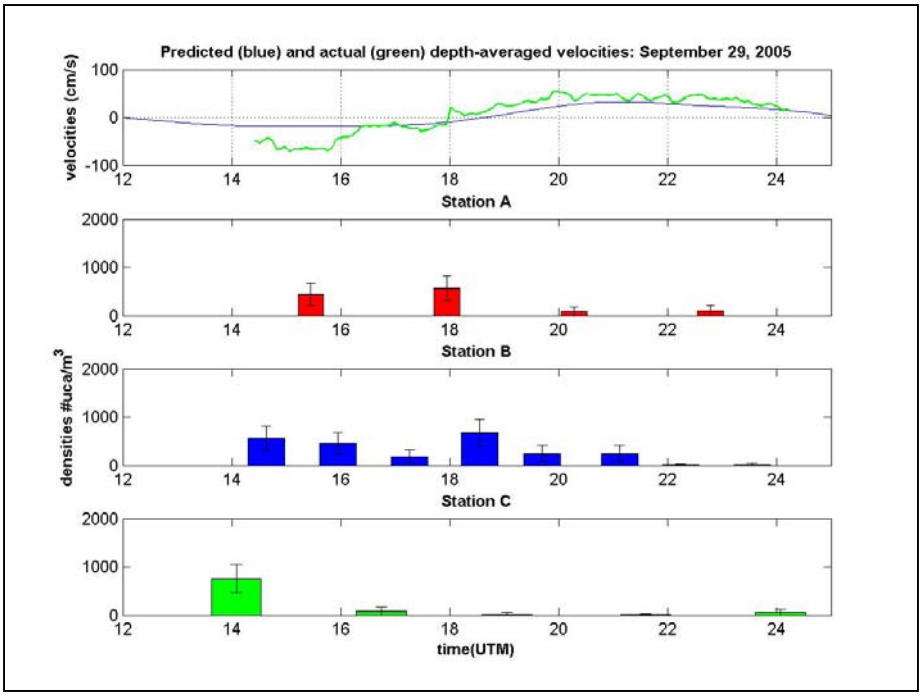

Figure B.5: Predicted and actual depth-averaged velocities with measured *Uca* larval densities at stations A (red), B (blue), and C (green) on September 29, 2005.

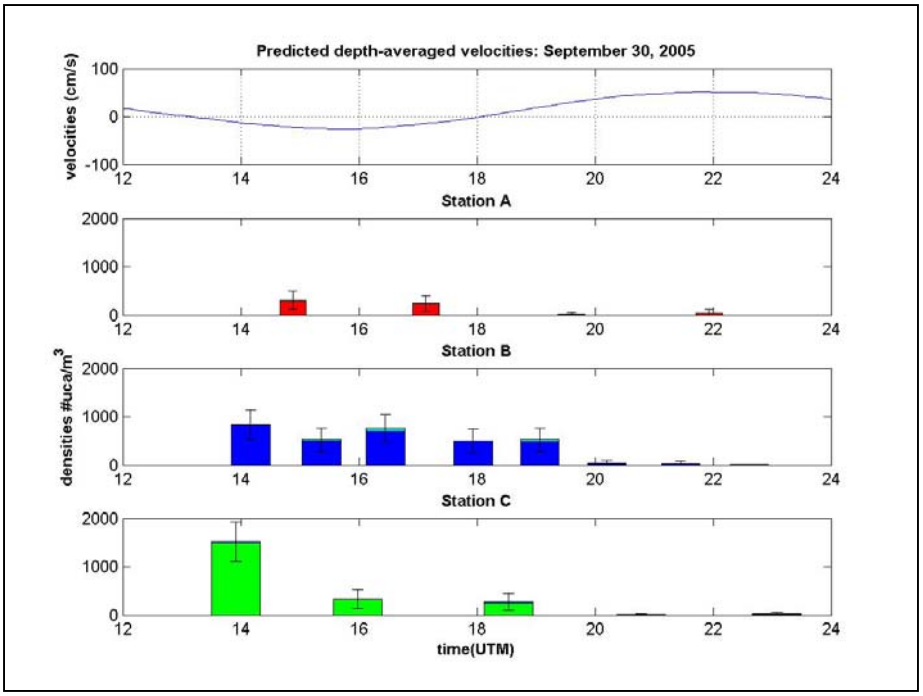

Figure B.6: Predicted depth-averaged velocities with measured *Uca* larval densities at stations A (red), B (blue), and C (green) on September 30, 2005.

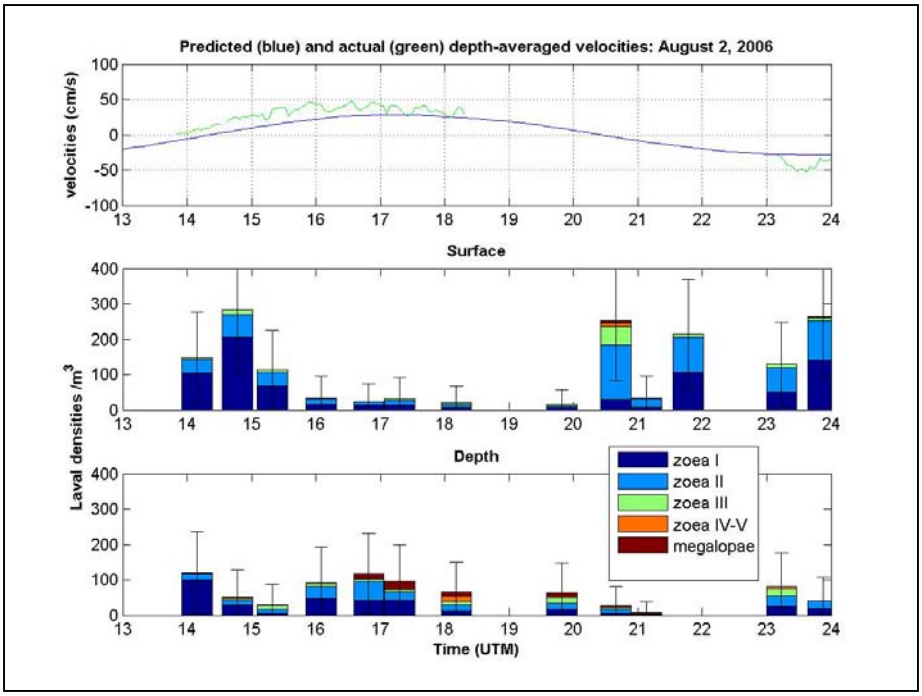

Figure B.7: Predicted and actual depth-averaged velocities with *Uca* larval densities at the surface and at depth at all stations on August 2, 2006.

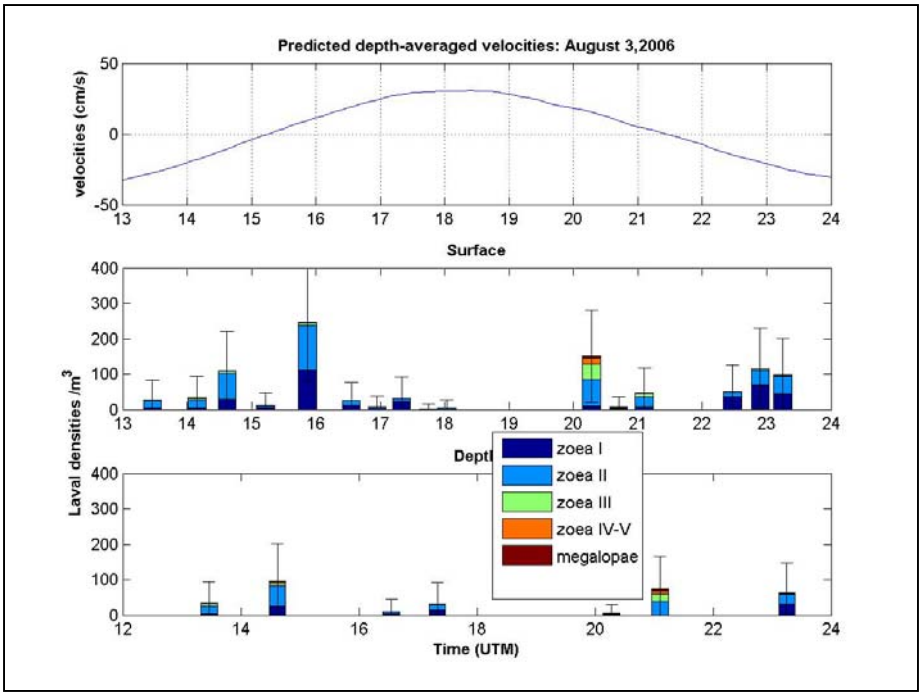

Figure B.8: Predicted depth-averaged velocities with *Uca* larval densities at the surface and at depth at all stations on August 3, 2006.

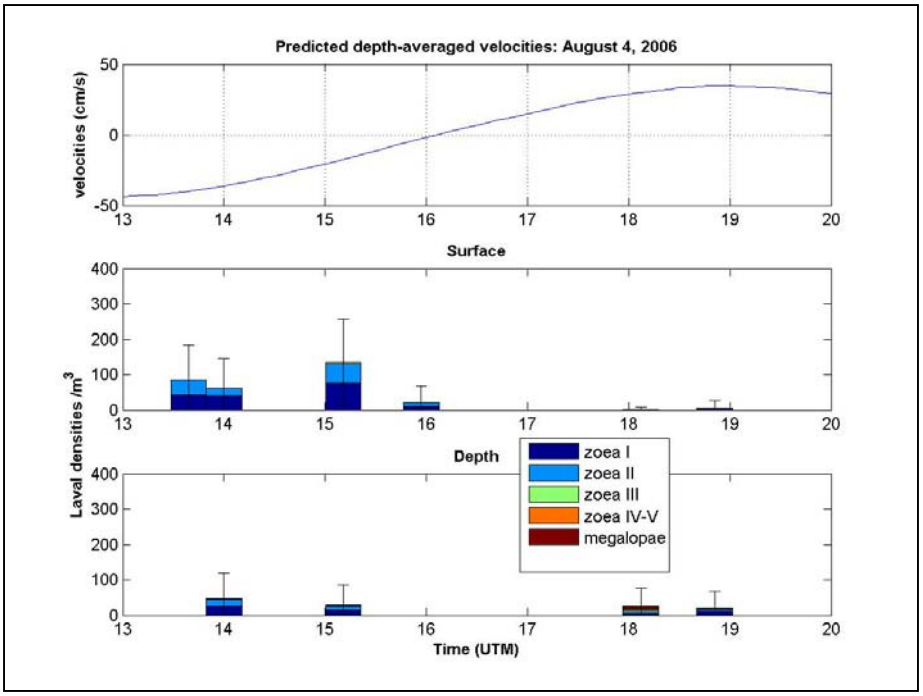

Figure B.9: Predicted depth-averaged velocities with *Uca* larval densities at the surface and at depth at all stations on August 4, 2006.

APPENDIX C

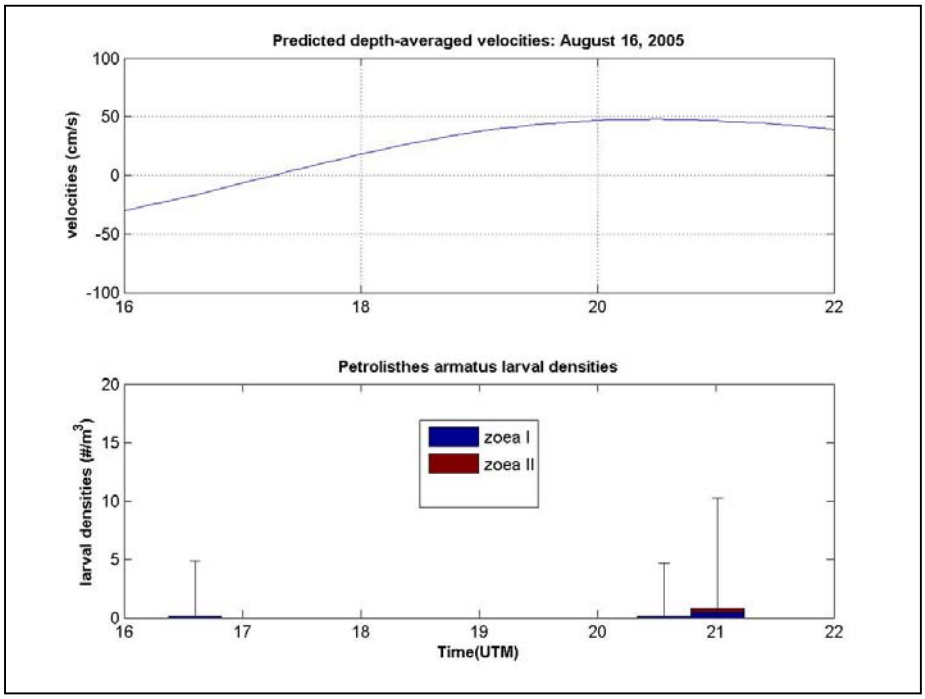

Figure C.1: Predicted depth-averaged velocities and *P. armatus* larval densities at all stations on August 16, 2005.

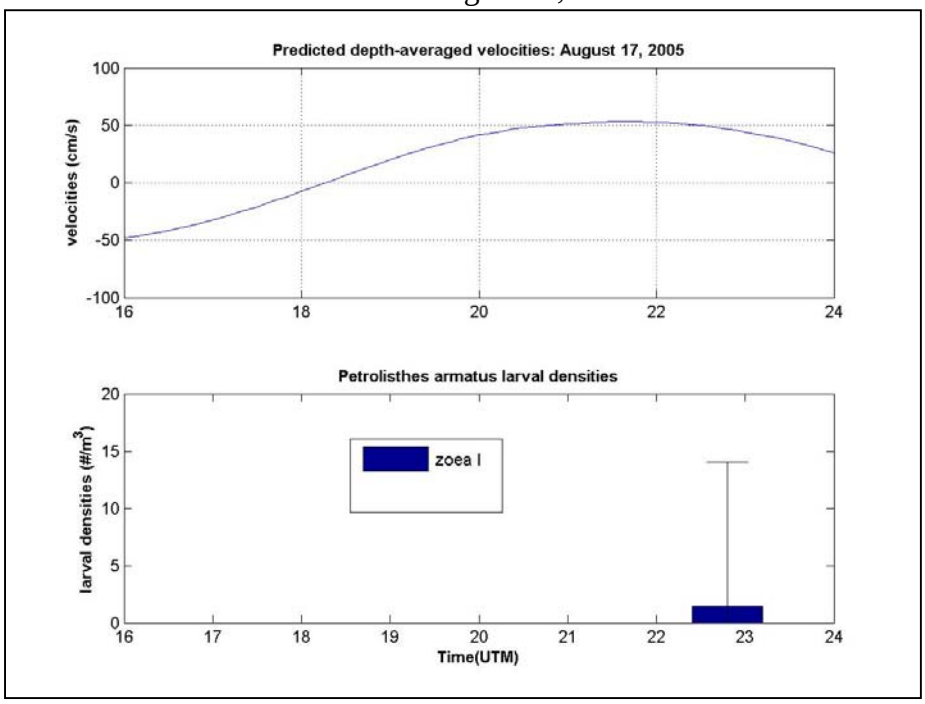

Figure C.2: Predicted depth-averaged velocities and *P. armatus* larval densities at all stations on August 17, 2005.

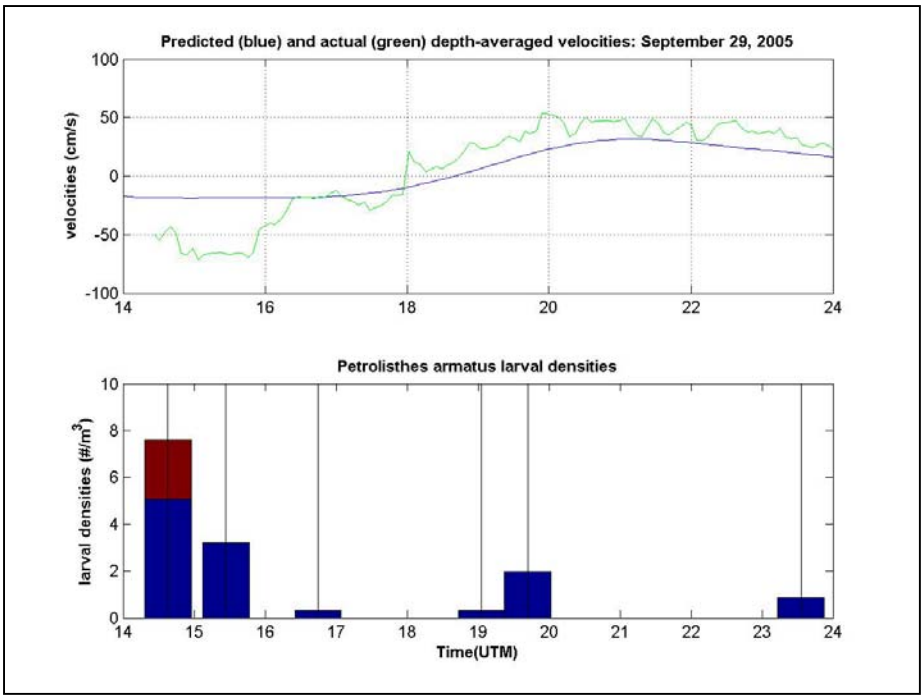

Figure C.3: Predicted and actual depth-averaged velocities with *P. armatus* larval densities at all stations on September 29, 2005.

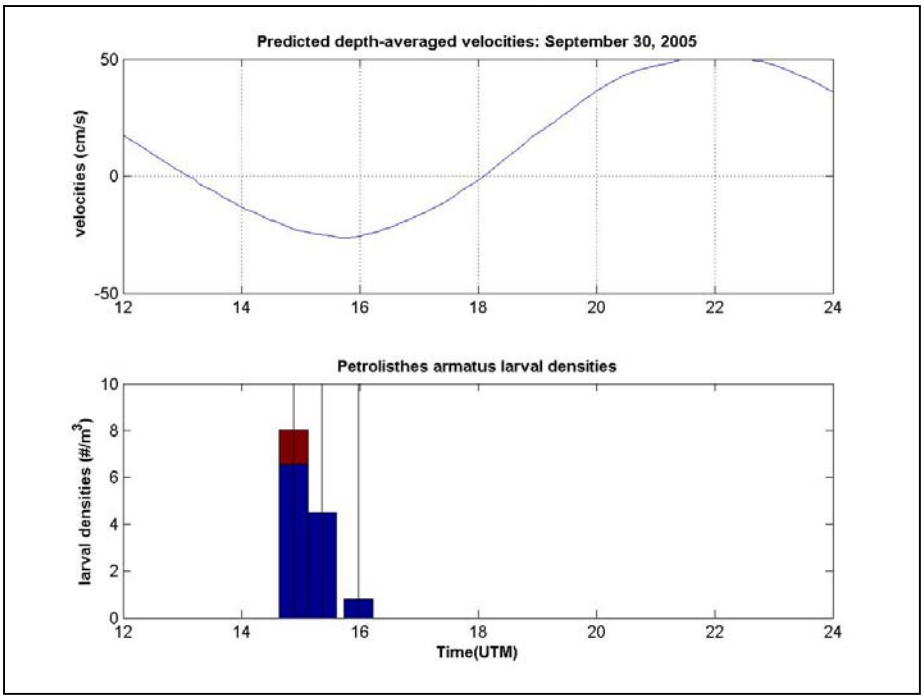

Figure C.4: Predicted depth-averaged velocities with *P. armatus* larval densities at all stations on September 30, 2005.

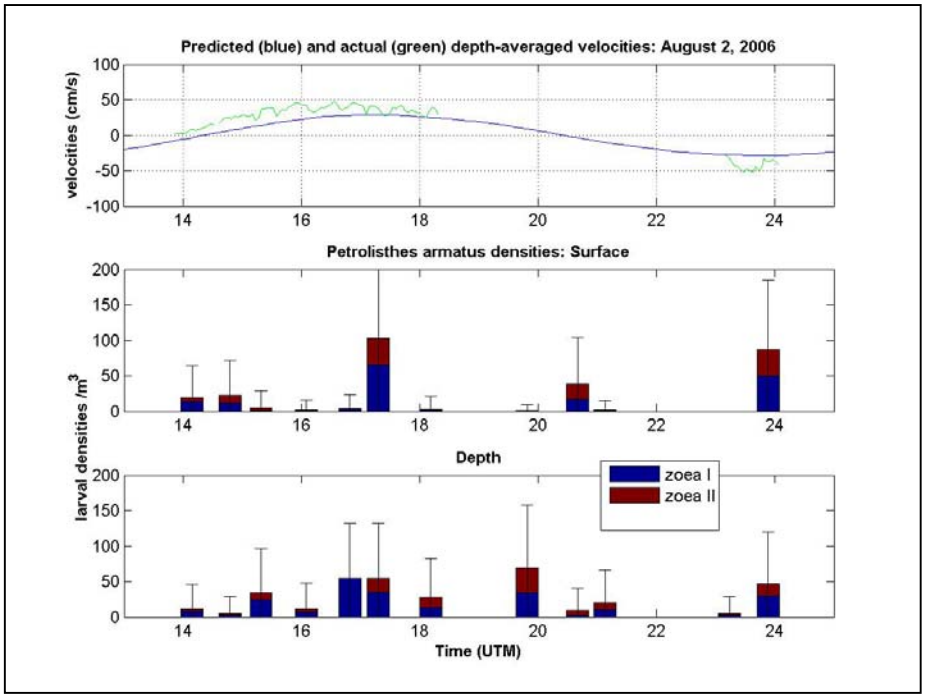

Figure C.5: Predicted and actual depth-averaged velocities with *P. armatus* zoea I (blue) and zoea II (red) larval densities at all stations on August 2, 2006.

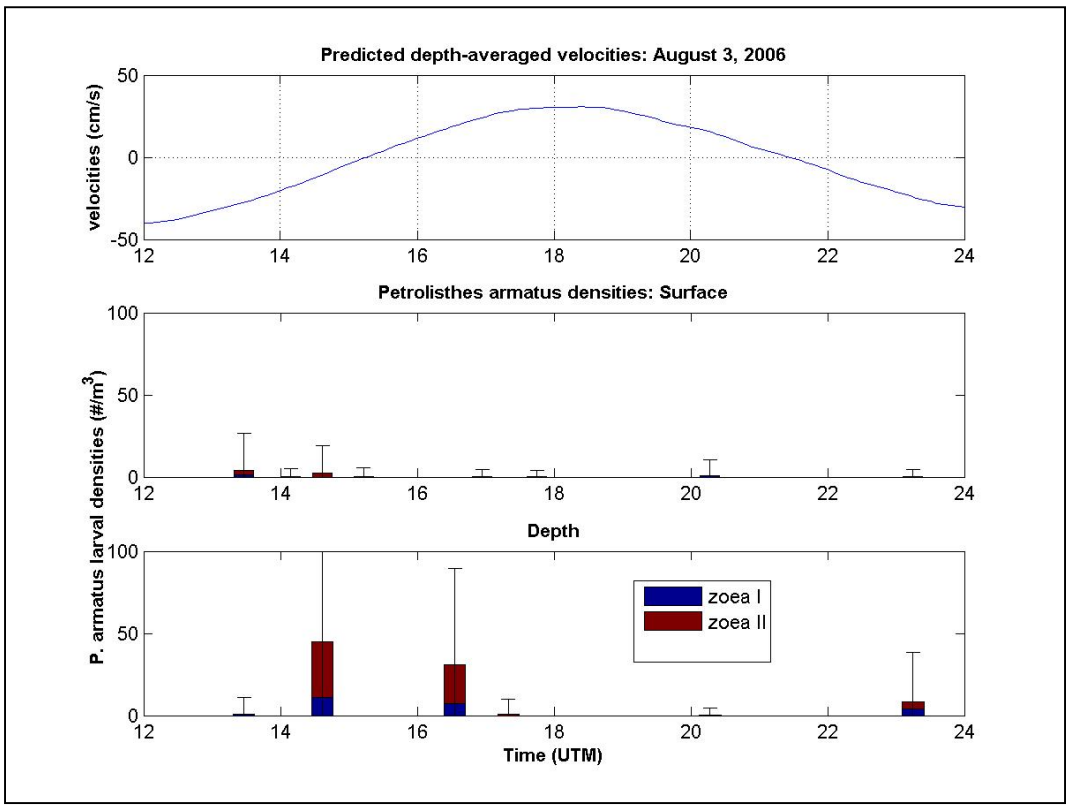

Figure C.6: Predicted depth-averaged velocities with *P. armatus* zoea I (blue) and zoea II (red) larval densities at surface and at depth at all stations on August 3, 2005.

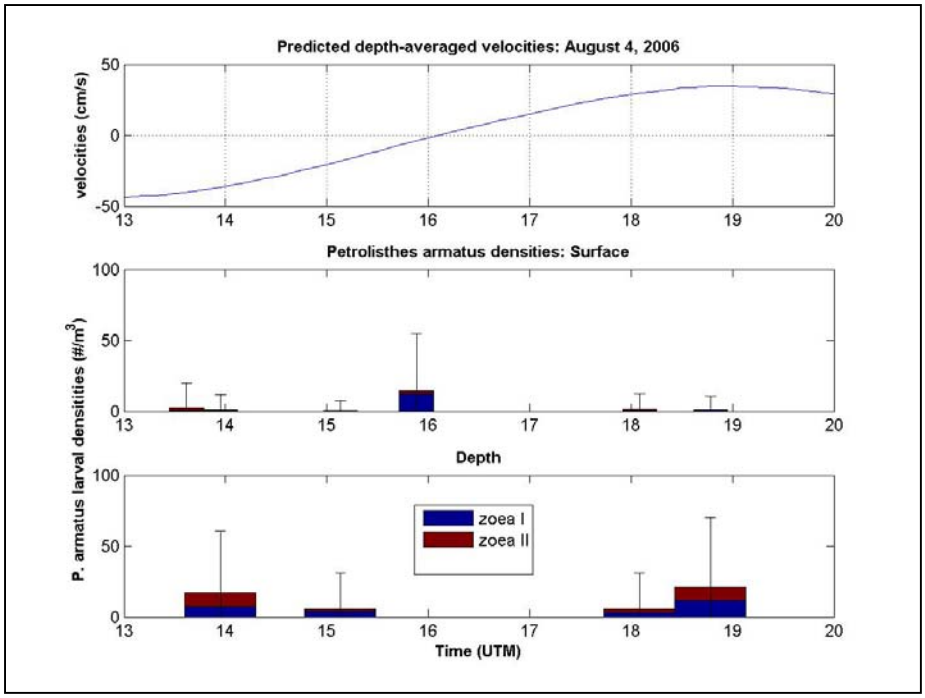

Figure C.7: Predicted depth-averaged velocities with *P. armatus* zoea I (blue) and zoea II (red) larval densities at surface and at depth at all stations on August 4, 2005.