PATTERNS OF LARVAL DISTRIBUTION AND SETTLEMENT IN A RIVER-DOMINATED ESTUARY

Russell W. Barbour

A Thesis Submitted to the
University of North Carolina at Wilmington in Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

Department of Biological Sciences

University of North Carolina at Wilmington

2003

Approved by

Advisory Committee

_____Dr. Robert D. Roer_____   _____Dr. Thomas E. Lankford____

_____Troy D. Alphin_____   _____Dr. Martin H. Posey_____
                                                           Chair

Accepted by

_____Dr. Robert D. Roer_____
Dean, Graduate School

TABLE OF CONTENTS

ABSTRACT

Several species of crabs utilize the estuary as adults, with larval development occurring in the plankton either within the estuary or offshore. Habitat selectivity necessitates postlarval movement within the estuary in order for suitable settlement sites to be reached. Postlarval dispersal and settlement are critical factors in determining adult abundances. Data on such dispersal and settlement are particularly sparse for the more poorly studied small, river-dominated systems prevalent along the southeastern coast of the United States. Night plankton tows were taken during flood tides to examine issues of postlarval distribution and transport to upper portions of the Cape Fear River Estuary (NC, USA) for several brachyuran species commonly found in the estuary. The blue crab *Callinectes sapidus* was used as a model organism to compare planktonic availability, settlement (utilizing passive larval collectors) and juvenile abundances over a broad estuarine gradient. Sampling occurred in five-day periods around both the new and full moons from July to mid-October 2001 to target peak recruitment. The four groups of megalopae present in sufficient numbers for statistical analysis: 1) *Uca* spp., 2) xanthids, 3) *Sesarma cinereum*, and 4) *Callinectes* spp. all demonstrated a high degree of spatial and within-period variability. When the abundance of *Callinectes* megalopae in plankton tows was low, settlement occurred primarily at sites closer to the mouth of the estuary, however, in mid-September when abundances in the plankton rose, the settlement pattern shifted to the upper portion of the estuary. Patterns of early juvenile abundances appeared to reflect late period settlement of *Callinectes* megalopae in the upper regions of the estuary. *Callinectes* megalopae appear to follow a mixed model settlement pattern that varies seasonally and this may have consequences for megalopal survival.

ACKNOWLEDGEMENTS

DEDICATION

I would like to dedicate this thesis to my granddad, Erwin L. Barbour and my dad, Maurice W. Barbour. They both departed this world for a better one during the course of this thesis. I miss their counsel and camaraderie each and every day. The courage, strength and wisdom they demonstrated during their lives have always served as my example. Memories of them will continue to inspire me to explore new realms, continue learning, stand up for what I believe in and to treat others with the dignity and respect they deserve.

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The abundance of food and refuge from predation offered by the varied habitats found within estuaries makes them ideal both as nurseries and adult habitats (Shenker and Dean 1979, Weinstein 1979, Boesch and Turner 1984). Although some organisms are resident in estuaries for their entire life cycle, other species utilize the estuarine environment only for a portion of their life history. For example, some crustacean species, such as penaeid shrimp, utilize estuaries mainly as juveniles (De Ben et al. 1990, Rogers et al. 1993, Cattrijsse et al. 1994), while others, such as blue crabs *Callinectes sapidus* and fiddler crabs *Uca* spp., spend most of their juvenile and adult phase within the estuary (Williams 1984, Steele and Bert 1994). Most of these crustaceans have complex life cycles where a portion of the larval stage is spent in the plankton. The populations of these organisms undergo large fluctuations with high inter-annual variability and the larval stage has been implicated as a critical phase affecting these fluctuations (Roughgarden et al. 1988). Understanding aspects of larval ecology is key to understanding population dynamics and for making accurate predictions of future population size. Larval dispersal and settlement are critical aspects of larval ecology and factor significantly in determining overall adult abundance (Eckman 1996, Palmer et al. 1996).

Different species of brachyuran crabs utilizing the estuary as adult habitat have developed different life history patterns (Strathmann 1982). While some of these crabs, such as the xanthid mud crabs *Rhithropanopeus harrisii* and *Panopeus herbstii*, have evolved life history patterns enhancing retention of larvae within the estuary (Boicourt 1982, Cronin 1982), others such as *Callinectes sapidus* and *Uca* spp., are characterized by export of larvae to offshore waters (McConaugha 1988, Johnson 1985). Reentry occurs during the megalopal and early juvenile stage (Williams 1971, Meredith 1982, De Vries et al. 1994) and the mechanisms involved are

complex and still under debate (Goodrich et al. 1989, Little and Epifanio 1991, Tankersley and Forward 1994, Tankersley et al. 1995, Garvine et al. 1997, Roman and Boicourt 1999). Ingress is episodic and highly variable over daily, monthly, and annual timescales as well as regional spatial scales (Rabalais et al. 1995, Wrona et al. 1995, Christy and Morgan 1998).

Habitat selectivity necessitates megalopal movement within the estuary for most crabs in order for their postlarval stage to reach suitable settlement sites. Upstream movement may be facilitated by selective tidal-stream transport (STST) (Forward and Tankersley 2001) and most species are found in estuarine surface waters during nocturnal flood tides (Williams 1971, Little and Epifanio 1991, Boylan and Wenner 1993, DeVries et al. 1994).

Due to its importance as a highly valued commercial fishery, the life history of the blue crab *Callinectes sapidus* has been studied extensively and represents a model species for our understanding of larval and postlarval transport dynamics. Larval ingress and settlement for *C. sapidus* has been correlated with lunar cycles with peaks occurring during both new and full moon periods (Mense et al. 1995, van Montfrans et al. 1995); however, a recent study has indicated that peaks may be more closely related to periods where the majority of the flood tide also occurs in darkness (Tankersley et al. 2002).

Blue crab megalopae can delay their metamorphosis to first crab based on conditions they encounter and have been reported to have megalopal duration periods from 19 to 68 days (Sulkin and Van Heukelem 1986, Lipcius et al. 1990). Thus, it is not surprising that they have been found in samples taken between 40 and 170 km inland from their probable point of entry from coastal waters (Cargo 1960, Tagatz 1968, Williams 1971, Sandifer 1973).

Studies in the Chesapeake Bay and the Croatan-Albemarle-Pamlico estuarine system have demonstrated the importance of submerged aquatic vegetation (SAV) to recruiting blue

crabs (Orth and van Montfrans 1987, Etherington and Eggleston 2000) and SAV provides a complex habitat that is important in reducing predation pressure on the megalopae and small juveniles of this species (Moksnes et al. 1997). Several studies in estuaries without significant SAV found juvenile blue crabs most abundantly in oligohaline and mesohaline waters when compared to the polyhaline and euhaline regions (Mense and Wenner 1989, Allen 2000, Posey and Alphin, In submission). In the absence of SAV, other habitats may serve to reduce predation pressure (Ruiz et al. 1993) and low salinity may provide one of these alternative habitats for blue crabs. Juvenile use of low salinity areas raises questions of how they reach these upper estuarine locations. There are two primary possibilities: 1) they are reaching these waters as larvae and are settling out preferentially in these areas, 2) they are settling out of the water column shortly after entering the estuary and then migrating up-estuary as early juveniles. A third possibility is some intermediate pattern such as a shift in dispersal and/or settlement up-estuary over time.

A general trend of decreasing megalopal abundance in the water column and/or decreased settlement with distance up-estuary/upriver or with decreasing salinity was found in studies that covered > 30 km upstream from the estuary mouth (Williams 1971, Johnson 1985, Mense and Wenner 1989, Morgan et al. 1996). However, relatively few studies have attempted to examine megalopal dispersal patterns for various brachyuran species over a broad estuarine gradient (Williams 1971, Sandifer 1973) or use multiple sampling methods to simultaneously compare planktonic postlarvae availability, postlarval settlement and juvenile abundances for a specific species (Mense and Wenner 1989). The current study was designed with two objectives. It examines distribution patterns of brachyuran megalopae across the estuarine gradient and then uses *C. sapidus* as a model organism to compare planktonic distribution and settlement patterns across the estuarine gradient, with relation to early juvenile abundance patterns.

METHODS

Study Site

Sampling was conducted in the lower Cape Fear River Estuary, North Carolina, USA (Fig. 1). The Cape Fear River has a total length of 684 km and a drainage basin of approximately 23,310 km^2. The estuary is approximately 45 km long with a drainage area of approximately 906 km^2. Most of the width of the estuary is characterized by broad expanses of shallows with subtidal unvegetated bottom and dredge spoil areas. The main shipping channel is approximately 12 m deep and runs from the mouth of the river to just above the city of Wilmington. Both oyster and SAV habitat are rare or absent within the estuary. Saline water moves up the estuary during flood tide as a diffuse salt wedge. Wind stirring of the waters modifies the wedge to produce a partially mixed condition within the estuary (Pietrafesa and Janowitz 1988).

Data Collection

Three collection methods were used in this study. The first involved evening/night plankton tows during flood tide to examine brachyuran megalopal distribution within the estuary. The second involved using passive larval collectors in sites adjacent to the plankton tows to observe settlement of *Callinectes* megalopae. The third method involved the use of sweep net sampling at various sites from euhaline to oligohaline reaches of the estuary to compare juvenile abundances of *Callinectes sapidus* to distribution patterns in the plankton and settlement of *Callinectes* megalopae.

Night flood tide plankton tows were conducted at five stations during summer/fall 2001 along the Cape Fear estuary in order to measure brachyuran postlarval distribution. The most

4
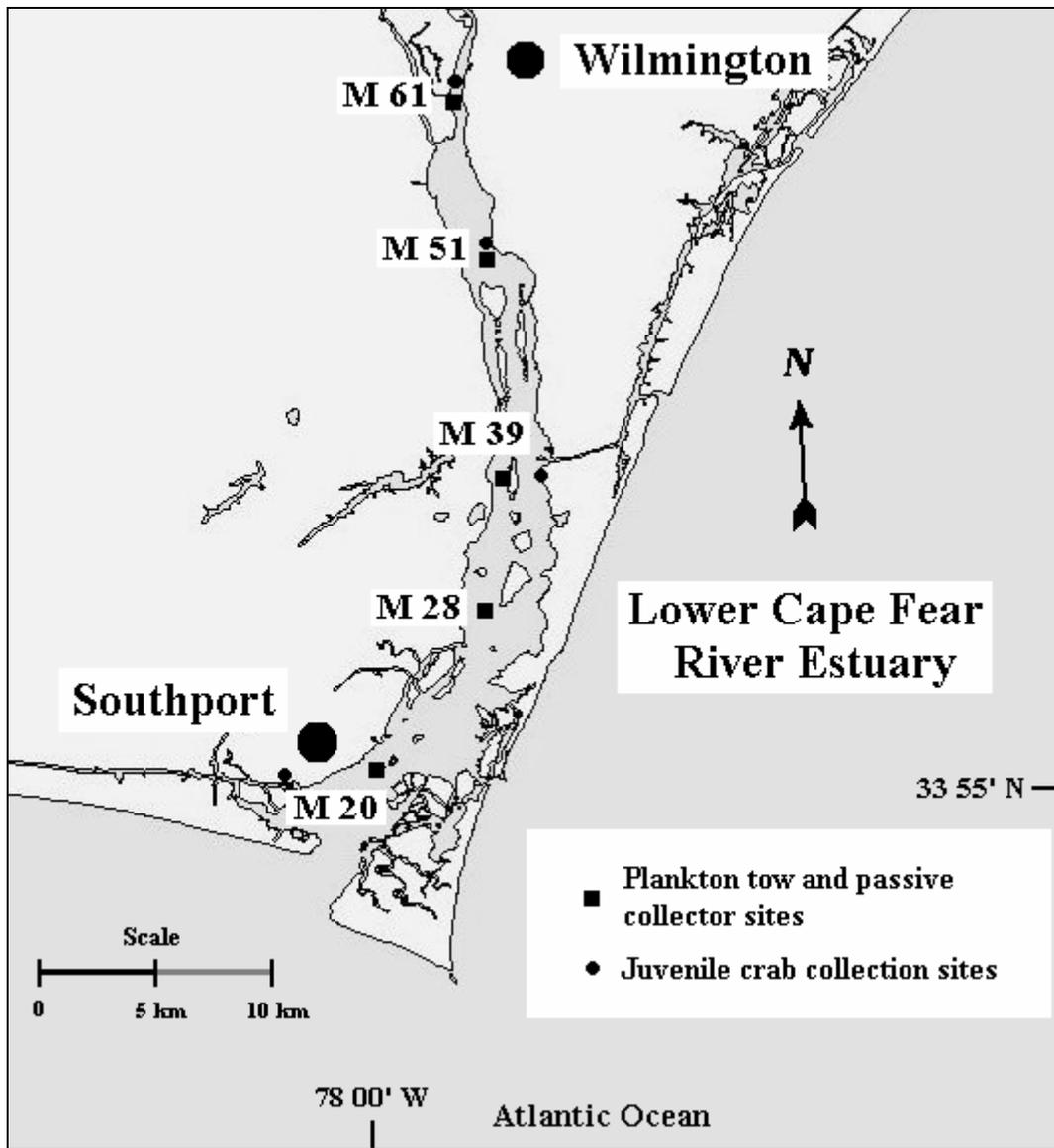
Fig. 1. Site map, Lower Cape Fear River Estuary. Plankton tow and passive collector sites indicated by small square, juvenile crab collection sites indicated by small circle.

downstream station was located at M20 (river marker 20) just upriver of the town of Southport (Fig. 1). Stations then followed upriver at M28, M39, M51, and M61 across from the Wilmington State Port facility (Fig. 1). These sites were chosen to span the estuary from euhaline (30-40 ppt) to oligohaline (0.5-5 ppt) conditions (Kennish 1986) and were approximately 8.5 km apart spanning a total distance of 42.5 km from the mouth of the river. Average salinity over the course of the year 2000 at a site near M20 was 27 ppt. Salinities averaged 15 ppt at M39, 7 ppt at M51 and 3 ppt at M61 over the same time period. There were no comparative data for site M28.

Previous studies have shown greater abundances of megalopae in surface waters during night flood tides relative to all other tide/diel combinations (Meredith 1982, Mense and Wenner 1989, Olmi 1994). Thus, sampling was conducted in the evening/night during the period of maximum velocity flood currents approximately halfway between the transition from low to high tide. This period provides the greatest potential for upstream movement of crab megalopae using tidal stream transport to reach oligohaline sites before settling out of the water column. Previous studies have also indicated a relationship between lunar period and increased numbers of megalopae in flood tides, but results vary as to whether peak ingress occurred around the new or full moon (Boylan and Wenner 1993, van Montfrans et al. 1990, Mense et al. 1995). Therefore, plankton tows in this study were conducted on lunar days 29 (one day prior to new moon), 2, 4, 14 (one day prior to full moon), 16, and 18. This sampling regime allowed a relatively broad window to be sampled around the new and full moons when pulses of megalopae were most likely to be moving into the estuary. The first day's tows during a lunar window began approximately 2 hours before sunset. As plankton tows were conducted every other day during each five-day sampling window, each successive sampling day began approximately 1 1/2 hours

after the cycle preceding it to maintain a consistent relation to the tidal cycle. Two 7 minute

tows, pulled consecutively and against the current, were conducted at each station in the main

channel. The interval was chosen to maximize the amount of time spent towing at each station

while still being able to follow the incoming flood tide up-river. Tows were pulled at a constant

speed and a flow meter was mounted in the mouth of the net in order to ensure the volume

sampled was approximately the same for every tow. Average volume per tow was 137 m^3

(range: 132-145 m^3). Tows not meeting volume criteria were rejected and immediately

reaccomplished. A straight, conical plankton net with a 60 cm diameter opening (Epifanio et al.

1989, Olmi et al. 1990) and 750 μm mesh was used for sampling. The 750 μm mesh size was

sufficiently small to capture brachyuran megalopae (Mense and Wenner 1989, Olmi et al. 1990,

Wolcott and DeVries 1994) while minimizing the amount of small zooplankton and detrital

material collected.

Passive larval collectors were used to sample *Callinectes* megalopal settlement (mostly

C. sapidus, see below) in shallow water sites (~ 2 m water depth) adjacent to the plankton tow

stations. These collectors have proven to be a reliable means for quantifying relative rates of

settlement of *Callinectes* megalopae (Metcalf et al. 1995). Each passive larval collector

consisted of a piece of PVC pipe 37.5 cm long and 16.3 cm wide covered with a sleeve of

"Hog's Hair" air-conditioning filter material. The sleeve was held in place by two rubber bands.

Each collector was anchored to the bottom of the river and floated upright in the water column

just below the surface, through use of a float and counter-weight system. Two sets of three

larval collectors each were placed at each of the five sites. The two sets of three collectors were

spaced approximately 100 m apart in order to account for potential within-site variability.

Within a set of three collectors, each collector was spaced approximately 4 meters apart. Larval

collectors were put out on lunar days 28 and 14 and were sampled daily for three days afterwards. This allowed a comparison to be made between megalopal abundance found in plankton tows in the channel vs. megalopae settling in adjacent shallows. *Callinectes* megalopae were used as a model organism in order to compare postlarval settlement to juvenile *C. sapidus* abundances recorded near collector sites (see below). Collector sleeves were soaked for 30 minutes in fresh water and the contents of bucket and sleeve subsequently were rinsed with fresh water 3 times through a 500 μm sieve (Metcalf et al. 1995).

Sweep net sampling (Posey and Hines 1991, Allen 2000) was conducted in shallow water sites adjacent to plankton and passive larval collection sites except for site M28 which was inaccessible due to security concerns surrounding the Sunny Point military complex. These samples were collected on the second or third week of every month as part of a separate study to monitor juvenile blue crab abundances (Posey et al., In review). For the purpose of relating megalopal settlement patterns to juvenile abundances, I concentrated on early juveniles (2-12 mm carapace width). The sweep net was 32 cm wide x 22 cm high, 35 cm deep, and attached to a 2 m long handle. The handle was held at ~45° with the leading edge of the sweep net in contact with the sediment. Ten 5 m long sweeps were conducted at each site by walking parallel to shore at constant speed along a depth contour between 30 and 50 cm of water.

All three sampling approaches were conducted from July through mid-October 2001. This ensured sampling covered the peak ingress period for a number of brachyuran species, especially the blue crab *C. sapidus*. Four days of plankton tows (23 July, 3,5 and 30 September) were not conducted due to severe weather and boat problems. Surface salinity and temperature were recorded during each sampling event to check for relations with both megalopal and juvenile abundance. All samples were preserved in 70% isopropyl alcohol. Brachyuran

megalopae were identified using larval keys by P. A. Sandifer (1972) and S. G. Bullard (In press) and studies by Costlow and Bookhout (1959) and Bookhout and Costlow (1977). Morphological descriptions to date are insufficient to reliably identify *Uca* megalopae beyond genus. Adult species commonly found within the estuary are *U. pugilator*, *U. minax*, and *U. pugnax*. While descriptions of xanthid megalopae were sufficient to allow some classification to species, due to the large volume and exceedingly laborious identification process, no attempt was made to identify these megalopae beyond family. Adults of this family commonly occurring in the estuary include *Panopeus herbstii*, *Eurypanopeus depressus*, and *Rhithropanopeus harrisii*. Species that were grouped into the "other" megalopae category were either present in insufficient numbers for statistical analysis such as spider crabs *Libinia* spp. and ghost crabs *Ocypode quadrata* or were not readily identifiable using the taxonomic keys available. This group constituted a low percentage of total captured. Morphological identifications of *Callinectes* spp. indicated that approximately 87% of *Callinectes* megalopae were *Callinectes sapidus*. Molecular testing of a small subset of *Callinectes* megalopae agreed with morphological identifications. *Callinectes* megalopae tested molecularly in the remaining 13% were identified as *C. similis* and *C. ornatus* (Wilbur, In prep). The expense of molecular testing precluded all *Callinectes* megalopae being tested separately for each tow.

Data Analysis

Total abundances of megalopae in plankton tows were standardized across the sampling period by dividing totals for each month by the number of sampling days conducted during that month. Statistical analysis on plankton tow data was conducted using the Mixed procedure in SAS (SAS Institute Inc., Cary, North Carolina). This is a general linear model and was used due to its ability to handle heterogeneous variances as well as a mix of fixed and random effects,

quantitative and qualitative variables and repeated measures. *Callinectes* megalopae were not found in any tows taken prior to sunset, thus time of sunset was included as a factor in the initial analysis of *Callinectes* abundances and a secondary analysis was conducted eliminating tows taken prior to sunset. The Mixed procedure doesn't require balance in order to construct estimates of effect and run corresponding tests and it allows an estimate of degrees of freedom based on observations present and where they are located.

Passive larval collector data were initially analyzed using the Mixed procedure to evaluate significant differences among sub-sites within each site. Once it was determined that there were no significant differences among sub-sites, all collectors at a site were combined for further analysis. This resulted in a more homogenous variance and allowed the use of the GENMOD procedure in SAS (SAS Institute Inc., Cary, North Carolina). This is a generalized linear model and is slightly more robust than the Mixed procedure.

A standard log transformation was performed on all abundance data used in SAS analysis. Salinity varied within a given site and increased overall in the final two months of the study, especially at the upper two sites. Moreover, in preliminary analyses, salinity provided a better fit to abundance patterns than distance from the estuary mouth (site), though the two variables did broadly covary. Thus salinity was used as a factor in statistical analysis rather than site. The effects of all statistical tests were considered significant at the 0.05 level of α.

A correlation analysis (Excel, Microsoft Corp.) was run between plankton tow data and collector data at one and two day time lags to compare distribution patterns in the plankton to settlement patterns across the estuarine gradient.

Juvenile blue crabs declined in abundance and then disappeared with decreasing water temperature in December 2001. This prevented a correlation analysis being conducted between

juvenile abundances and settling *Callinectes* megalopae (high settlement occurring in October with a likely time lag for appearance of juveniles in the size range sampled), however juvenile abundance data were compared to megalopal settlement data qualitatively in order to compare patterns based on salinity.

RESULTS

Salinity and Temperature

Salinity varied widely at each site over the course of the study (Fig. 2). Salinity was low in early July due to higher than average rainfall in the basin during June (+26% over 10 year average) and elevated in late September and early October due to below average rainfall in August and September (-16% and –45% below 10 year averages respectively) (Southeast Regional Climate Center 2003). Salinities were especially elevated above norms at stations M51 and M61 in late September and early October. At the site closest to the mouth of the estuary, M20, salinity ranged from 22 ppt to 35.5 ppt with a mean of 30.1 ppt. Site M28 experienced salinities from 16 ppt to 32 ppt with a mean of 24.6 ppt. Site M39 ranged from 9 ppt to 25.5 ppt with a mean of 17.9 ppt. Site M51 varied from 3 ppt to 22.5 ppt with a mean of 12.6 ppt and the site near the port of Wilmington, M61, experienced salinities from 0.0 ppt to 16 ppt with a mean of 7.3 ppt. Salinity varied by as much as 6 ppt between day collections and night tows at a given site on a given date. This is the result of evening/night sampling occurring on the rising tide as salt water is pushed upstream while collector retrieval occurred during slack tide after high tide the next day when fresh water from the river was pushing the salt wedge downstream. Since megalopae on collectors may be experiencing salinity fluctuations over the 24 hour period, average day/night salinities were used for analysis of collector data. Temperatures were
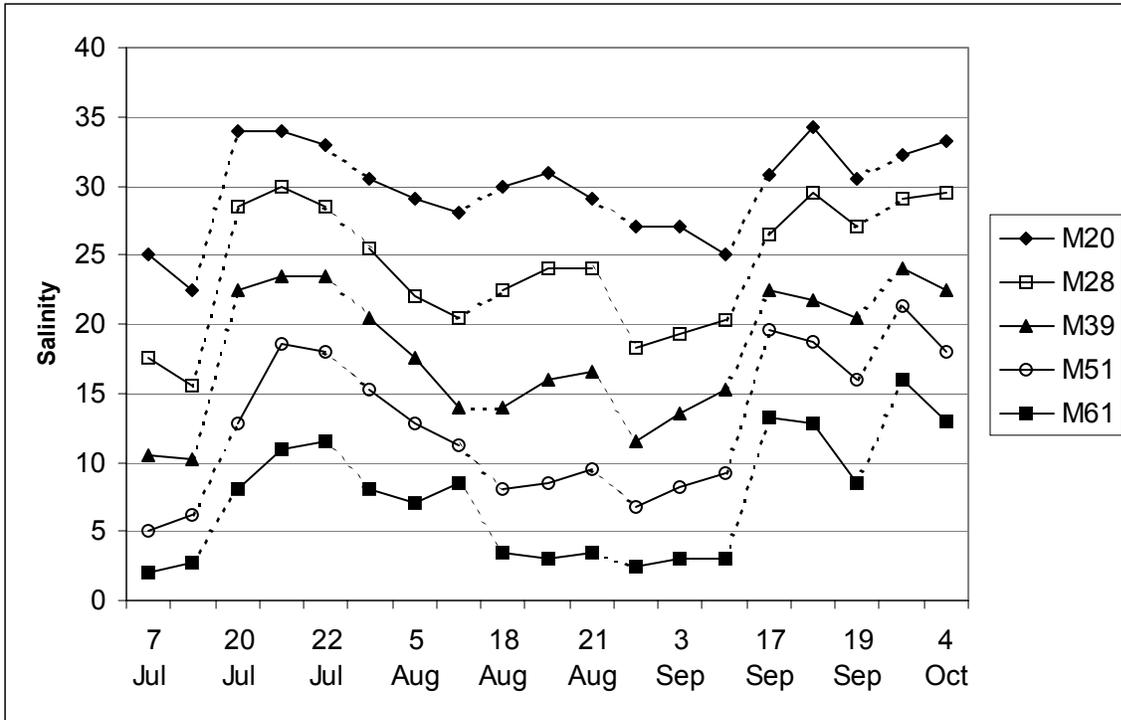
Fig. 2. Salinity in parts per thousand (ppt) across sites over the time period of collections. Dashed lines indicate periods outside of collection windows, are not to scale and do not indicate actual salinity measurements.

relatively constant over the course of the study with only 6 $^{\circ}$C difference between maximum and minimum temperature. Temperature did not vary across the estuary more than 1 $^{\circ}$C on any given sampling day.

<div align="center">Evening/Night Plankton Tows</div>

A total of 24,301 brachyuran megalopae were collected during evening/night plankton tows. With catches standardized by the number of sampling days in each month, 83.1 % fell into one of four main groups: 1) *Uca* spp., 2) Xanthidae, 3) *Sesarma cinereum*, and 4) *Callinectes* spp. *Uca* spp. comprised 60.0 % of all megalopae collected in night plankton tows. Abundances of xanthid and *Sesarma cinereum* megalopae comprised 9.8 % and 5.8 % respectively of total megalopae captured while the abundance of *Callinectes* spp. megalopae comprised 7.8 % of the total. Overall abundance was high in July with *Uca* spp. dominating catches for this month and comprising 67.7% of megalopae caught. Overall abundance decreased in August with catches for all taxa except *Callinectes* spp. declining. Again, *Uca* spp. dominated the overall numbers comprising 75.1% of the total. In September, overall catches increased with xanthid spp. showing their highest abundance. Again, overall abundance was dominated by *Uca* spp. comprising 61.1% of the total. In October, numbers of all species dropped sharply with the exception of *Callinectes* spp., which dominated the catch with 43.6% of total abundance (Table 1). While *Uca*, xanthids, and *Sesarma cinereum* abundances had a cyclical pattern over the course of the study, being high in July, lower in August, higher again in September and then lower again in October, *Callinectes* abundances showed a steady increase from July to October (Table 1).

Comparison of overall megalopal abundances by salinity from evening/night plankton tows for the four major groups analyzed (Fig. 3), shows that *Uca* spp. and *Sesarma cinereum*

Table 1. Abundance of brachyuran megalopae collected in evening/night plankton tows in the Cape Fear River Estuary, July through October 2001. Actual totals for each species for each month were divided by the number of sampling days in that month to standardize catches across months. Each individual plankton tow sampled approximately 137 m^3 of water.

Species	July	August	September	October
Uca spp.	6448	3876	5092	151
Xanthidae	618	323	1111	165
Sesarma cinereum	546	385	481	48
Callinectes spp.	29	142	464	561
Other megalopae	1885	429	1187	360
# sampling days/month	5	6	4	2
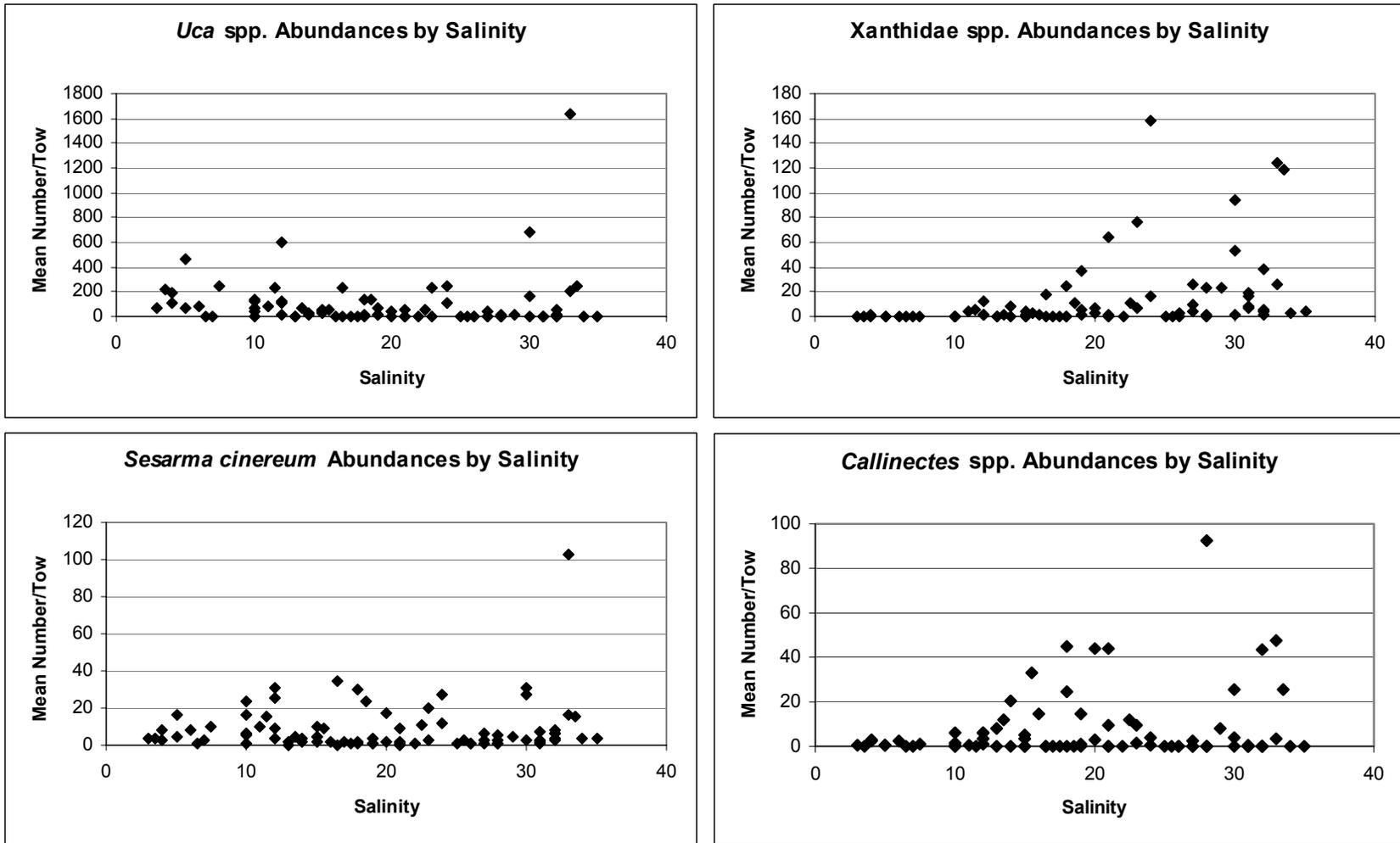
Fig. 3. Overall abundances of megalopae from evening/night plankton tows plotted by salinity for *Uca* spp., xanthids, *Sesarma cinereum*, and *Callinectes* spp. from July through October 2001. Each point represents the average number of megalopae per tow at a given site on a given day. Note charts are to different scales.

were captured in large numbers across the entire salinity gradient while xanthid and *Callinectes* spp. megalopae were found mostly in salinities above 15 ppt. However, these patterns are related to temporal variations in abundances by salinity that occurred over a monthly timescale.

Uca spp. abundance in plankton tows differed significantly by salinity and month with a strong interaction between these two factors (Table 2). Abundances for *Uca* in July were concentrated in the oligohaline/mesohaline range (Fig. 4). In August, megalopae were grouped primarily in the mesohaline range with the exception of two high abundance catches in the lower estuary (Fig. 4). The pattern shifted again in September with overall abundances decreasing and catches spread across the mesohaline/polyhaline range (Fig. 4). In October, when overall abundances were lowest, megalopae were found mostly in polyhaline salinities (Fig. 4). There was high spatial variability in abundances across the estuary over the period of the study with high abundances found in the lower, mid, and upper estuary however, peaks did not appear to occur sequentially up-estuary over time (Table 3). I expected to track pulses of *Uca* spp. megalopae up-estuary, seeing first a spike in abundance at the mouth and then movement of the peak up-estuary with decreasing abundance as it traveled upriver over the course of a five-day sampling period. Instead, I found high within-period variability where high abundances occurred in different locations within the estuary without any coherent pattern of pulse movement up-estuary (Table 3).

For xanthid megalopal abundance, the only significant difference over the course of the study was an interaction between salinity and month (Table 2). Xanthid abundances were high in salinities 10-25 ppt in July but higher abundances shifted to 25-33 ppt in August (Fig. 5). In September, with greater overall abundances, catches shifted to 15-34 ppt with a steady decrease in abundances from high to low salinity (Fig. 5). When the lowest abundances occurred in

Table 2. Analysis of *Uca* spp., xanthid, and *Sesarma cinereum* megalopal abundances in evening/night plankton tows using the Mixed procedure in SAS, Type 3 Tests of Fixed Effects.

Species			*Uca* spp.		Xanthidae		*Sesarma cinereum*	
Factor	Factor DF	Error DF	F Value	P	F Value	P	F Value	P
Salinity	1	64	6.95	0.0105	1.75	0.1911	7.13	0.0096
Month	1	14	11.60	0.0043	1.86	0.1940	14.90	0.0017
Salinity*Month	1	64	5.50	0.0221	4.53	0.0372	7.62	0.0075
Moon	1	14	0.02	0.8895	0.02	0.9029	0.01	0.9274
Salinity*Moon	1	64	0.99	0.3228	1.17	0.2839	2.50	0.1189
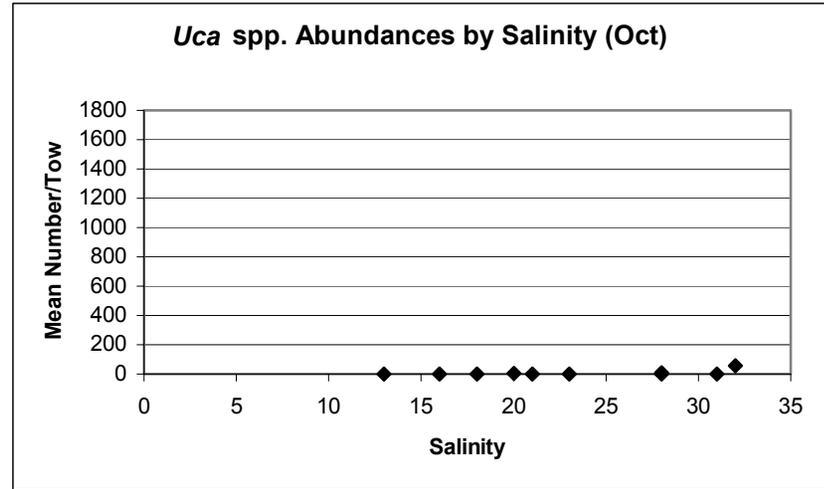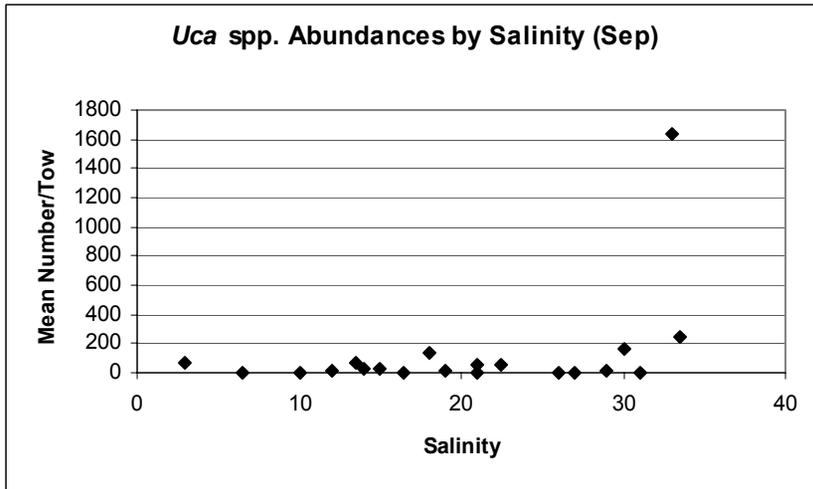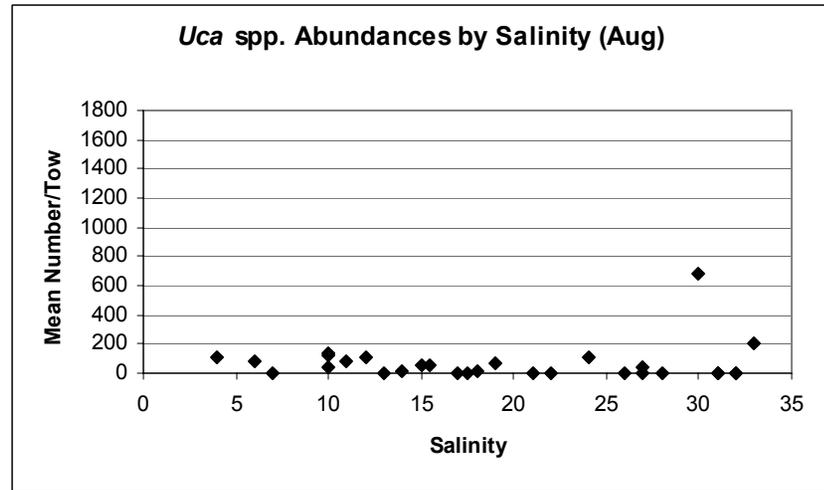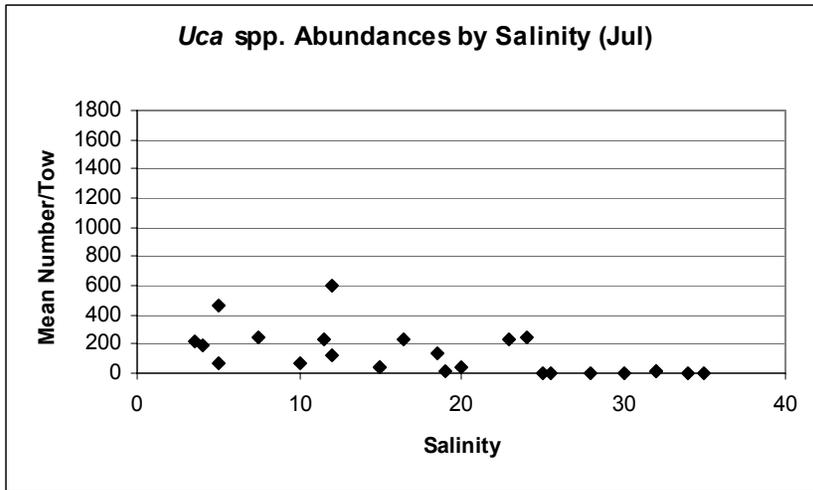
Fig. 4. Abundances of *Uca* spp. megalopae from evening/night plankton tows plotted by salinity for the months of July, August, September and October 2001. Each point represents the average number of megalopae per tow at a given site on a given day.

18

Table 3. Plankton tow data for *Uca* spp. and Xanthidae by site, tow, and date. XX indicates tows were not conducted due to overabundance of comb jellies. Tows scheduled for 23 July, 3, 5, and 30 September were not conducted due to weather or boat problems.

| Species	*Uca* spp.										Xanthidae									
Site	M20		M28		M39		M51		M61		M20		M28		M39		M51		M61	
Tow	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Date																				
7/5/01	10	14	0	0	9	63	109	32	44	82	7	4	0	1	0	0	0	0	0	0
7/7/01	0	9	5	23	722	479	579	358	214	177	0	1	0	3	16	8	0	0	1	1
7/9/01	282	175	283	168	165	294	268	214	168	266	34	119	24	11	2	10	0	0	0	0
7/19/01	3	4	7	26	0	1	106	163	116	133	3	5	2	0	0	0	9	12	4	0
7/21/01	0	1	0	2	148	345	38	52	38	53	2	4	2	2	159	158	10	3	0	1
8/3/01	0	0	0	0	0	0	0	0	71	104	15	17	3	0	0	1	0	1	3	5
8/5/01	1	4	0	0	3	24	57	49	118	117	2	15	0	0	0	0	1	5	0	0
8/7/01	147	249	8	78	78	63	73	28	46	35	27	24	1	17	5	5	1	1	1	0
8/17/01	3	0	0	0	0	0	0	0	0	9	5	2	1	6	0	0	0	0	0	0
8/19/01	2	2	1	0	XX	XX	95	127	97	58	5	3	3	3	XX	XX	2	2	0	0
8/21/01	542	829	65	166	22	15	138	141	137	74	68	38	10	24	0	0	0	1	0	0
9/1/01	0	2	0	0	0	0	0	2	71	66	1	0	0	0	0	0	0	0	0	0
9/16/01	3	5	1	1	1	0	110	158	89	43	25	13	49	2	0	0	22	26	1	2
9/18/01	2247	1034	218	112	71	46	18	20	18	24	124	123	96	91	67	60	36	38	11	6
9/20/01	212	292	21	11	39	66	49	10	15	17	84	154	23	23	7	15	6	3	1	2
10/2/01	0	0	0	0	0	2	5	3	1	0	4	9	1	0	7	7	4	2	2	1
10/4/01	64	50	13	7	2	0	3	1	0	0	31	45	31	16	2	2	1	0	0	0
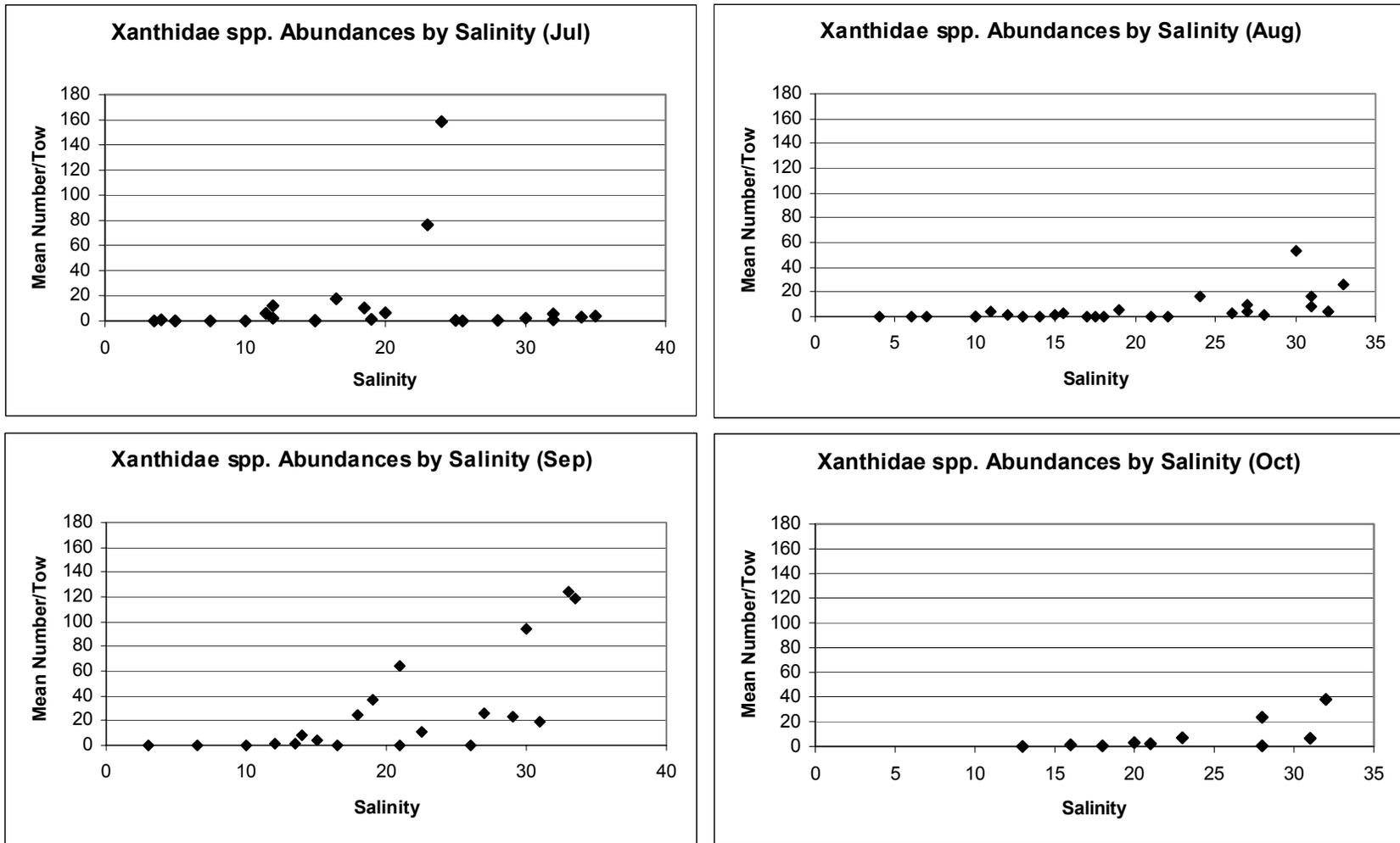
Fig. 5. Abundances of xanthid megalopae from evening/night plankton tows plotted by salinity for the months of July, August, September and October 2001. Each point represents the average number of megalopae per tow at a given site on a given day.

October, most megalopae were captured in euhaline salinities (Fig. 5). For xanthid megalopae, I expected to see movement of pulses up and down the estuary as xanthid megalopae are mostly retained within it. However, I again saw a pattern of high spatial and within period variability with no clear pattern of pulse movement (Table 3).

Sesarma cinereum abundances demonstrated significant differences by salinity and month and there was a significant interaction between salinity and month (Table 2). In July, high abundances were from oligohaline conditions to polyhaline conditions with low numbers extending into the euhaline salinities (Fig. 6). The pattern shifted in August such that abundances were low only in the extremely low salinities (< 3 ppt) and in the range of 18-23 ppt (Fig. 6). In September, abundances shifted to polyhaline and euhaline salinities and when overall abundance was lowest in October the pattern shifted such that abundances were highest at euhaline salinities with no Sesarma cinereum megalopae captured below 16 ppt (Fig. 6). Although there were peaks in abundance that demonstrated variability both spatially and within period, in general, Sesarma cinereum megalopae exhibited a much broader spread of low abundances across the length of the estuary than the previous two groups (Table 4).

As no Callinectes megalopae were captured in plankton samples taken prior to sunset, it was not surprising that the initial analysis of Callinectes spp. showed abundances in relation to sunset to be highly significant in addition to salinity. The significance of the interaction between sunset and month was expected given shifts in daylight seasonally, however there was also a significant interaction between salinity and month (Table 5). Overall abundances were very low in July and the megalopae that were present in the plankton were scattered across the estuarine gradient from 3-24 ppt (Fig. 7). In August, abundances were highest at salinities between 10 and 16 ppt with low abundances spread across 3-7 ppt and 24-34 ppt (Fig. 7). As overall abundances
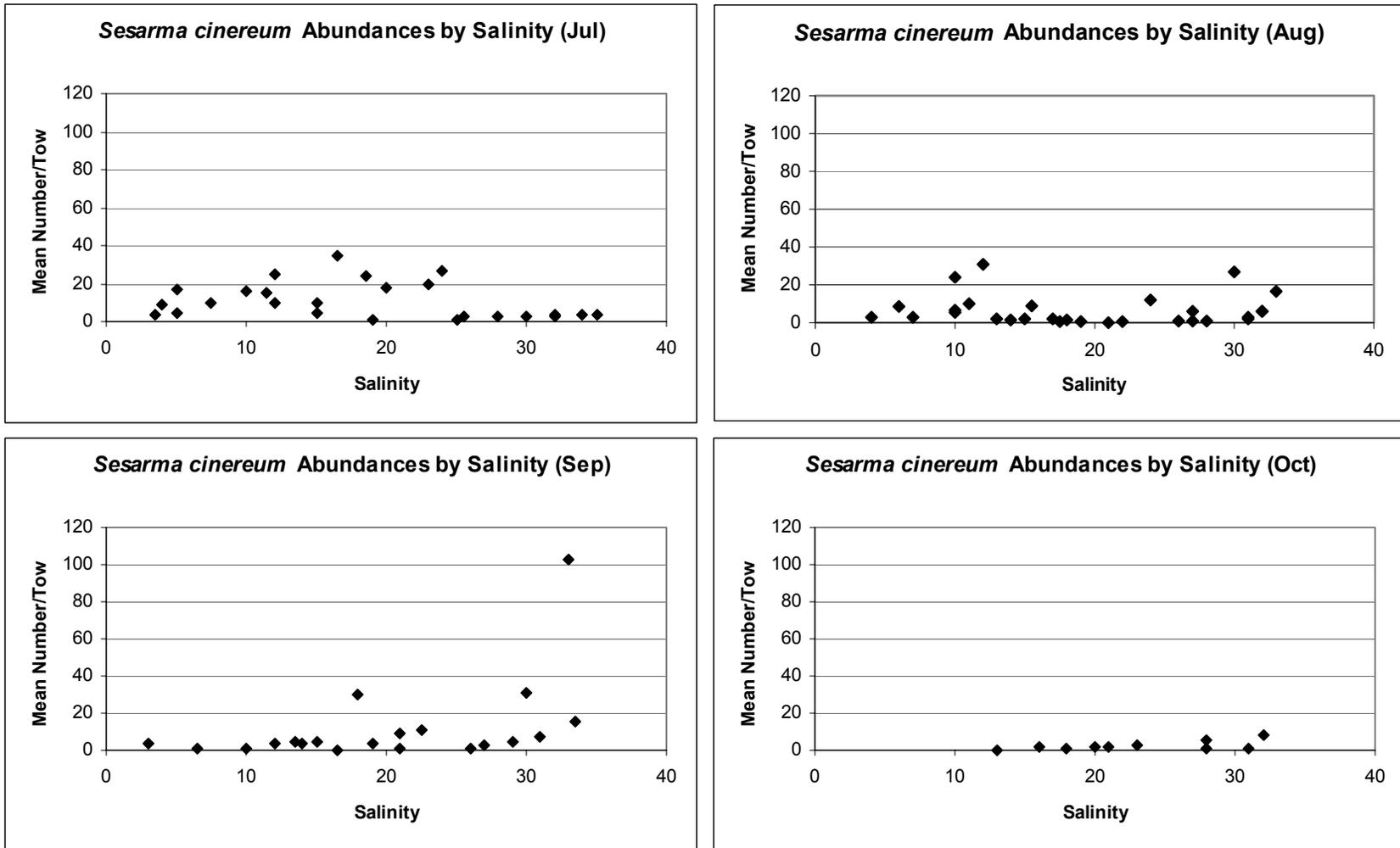
Fig. 6. Abundances of *Sesarma cinereum* megalopae from evening/night plankton tows plotted by salinity for the months of July, August, September and October 2001. Each point represents the average number of megalopae per tow at a given site on a given day.

Table 4. Plankton tow data for *Sesarma cinereum* and *Callinectes* spp. by site, tow, and date. XX indicates tows were not conducted due to overabundance of comb jellies. Tows scheduled for 23 July, 3, 5, and 30 September were not conducted due to weather or boat problems.

Species	*Sesarma cinereum*										*Callinectes* spp.									
Site	M20		M28		M39		M51		M61		M20		M28		M39		M51		M61	
Tow	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Date																				
7/5/01	4	2	1	0	4	5	26	6	4	5	0	0	0	0	0	0	1	0	0	1
7/7/01	1	5	1	1	29	21	15	18	11	6	0	0	0	0	1	6	0	1	4	1
7/9/01	20	20	52	18	20	11	9	11	3	5	0	3	0	0	0	0	1	1	0	0
7/19/01	2	6	1	7	4	2	11	37	7	12	0	0	0	0	0	0	0	0	0	2
7/21/01	4	4	2	4	28	26	11	24	7	13	0	0	0	0	0	1	3	3	0	0
8/3/01	3	1	1	1	1	0	0	1	5	15	0	0	0	0	0	0	0	0	0	1
8/5/01	2	4	0	0	2	1	6	12	7	6	0	0	0	0	0	0	52	14	1	2
8/7/01	18	15	0	2	1	0	3	1	6	5	4	3	0	5	2	0	2	5	0	0
8/17/01	9	3	8	4	0	4	1	3	1	5	0	0	0	0	0	0	0	0	0	0
8/19/01	7	5	1	1	XX	XX	21	41	7	10	0	0	0	0	XX	XX	2	10	2	3
8/21/01	25	29	8	16	2	1	16	32	3	3	6	2	4	4	0	0	5	7	2	4
9/1/01	2	0	0	0	0	1	1	0	4	4	0	0	0	0	0	0	0	0	1	0
9/16/01	6	8	2	3	0	1	29	31	6	4	1	0	0	0	0	0	27	63	22	2
9/18/01	127	78	35	26	10	9	4	3	5	3	72	23	22	29	12	7	16	13	20	21
9/20/01	11	20	9	1	13	9	8	1	5	2	19	32	8	8	15	9	5	5	8	4
10/2/01	1	1	1	0	4	1	3	1	2	1	0	0	0	0	1	18	66	22	14	15
10/4/01	7	9	5	6	3	1	2	0	0	0	6	81	121	64	54	34	19	30	10	6

Table 5. Analysis of *Callinectes* spp. abundances in evening/night plankton tows using the Mixed procedure in SAS, Type 3 Tests of Fixed Effects. All tows were included in this analysis.

Factor	Factor DF	Error DF	F Value	P
Sunset	1	60	8.33	0.0054
Salinity	1	60	5.75	0.0196
Sunset*Salinity	1	60	3.70	0.0592
Month	1	14	1.85	0.1948
Sunset*Month	1	60	9.46	0.0032
Salinity*Month	1	60	6.91	0.0109
Moon	1	14	0.02	0.8862
Sunset*Moon	1	60	0.09	0.7701
Salinity*Moon	1	60	0.01	0.9421

increased in September, peak abundances appeared in two salinity ranges, 12-23 ppt range and 29-34 ppt (Fig. 7). Virtually no planktonic megalopae were captured in salinities below 12 ppt; however, salinity was much higher in the later half of September (Fig. 2). Abundances in October showed a marked shift to polyhaline and euhaline salinities with abundances decreasing with decreasing salinity. However, it should be noted that overall salinity remained high during this month (Fig. 2) and no samples were collected at less than 12 ppt. As with *Uca* spp., I expected to see a pattern of high abundance at the mouth as postlarval pulses entered the estuary with decreasing abundance in the pulse as it traveled up-estuary. Instead, peak abundances demonstrated high spatial and within-period variation with peak abundances occurring throughout the estuary without a pattern of up-estuary movement (Table 4). The secondary analysis of *Callinectes* abundances with tows taken prior to sunset removed resulted in salinity being highly significant and the interaction between salinity and month being highly significant (Table 6) with the abundance patterns as noted above (Fig. 7).

A correlation analysis was run between evening/night plankton tows and passive larval collectors at 1 and 2 day time lags. No significant correlation was found between plankton tows and settlement collectors on either scale (r = 0.0618 for 1 day time lag, r = 0.0817 for 2 day time lag).

<div align="center">Passive Settlement Collectors</div>

An analysis was run to determine if there were significant abundance differences between the sub-sites at each of the five main sampling stations in order to ensure that within site variability was not adversely affecting the analysis of collector data. Results from this analysis demonstrated no significant differences as a result of sub-site and no interactions between sub-site and any other variable (Table 7). The analysis of collector data indicated highly significant
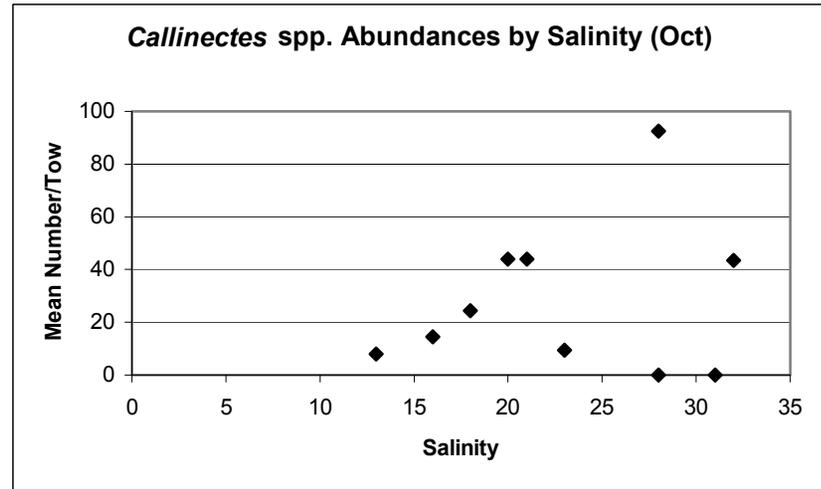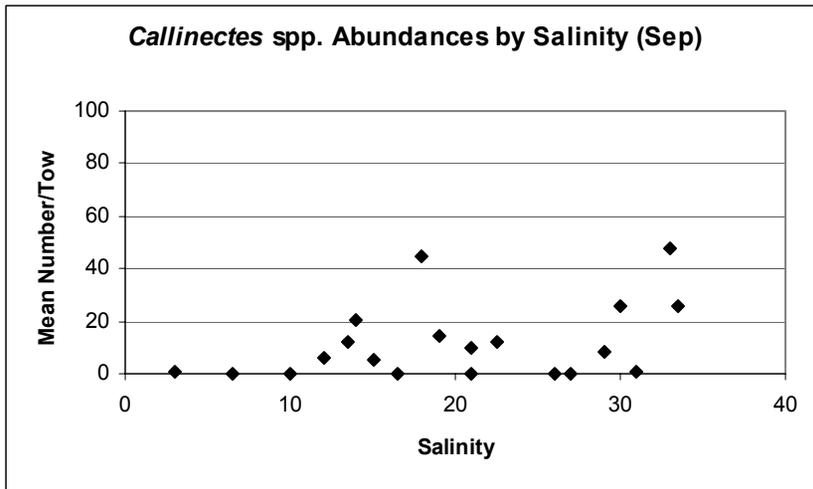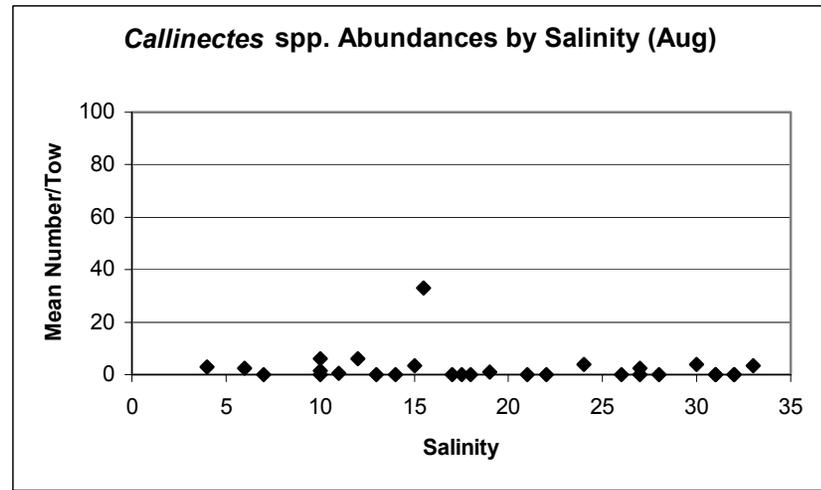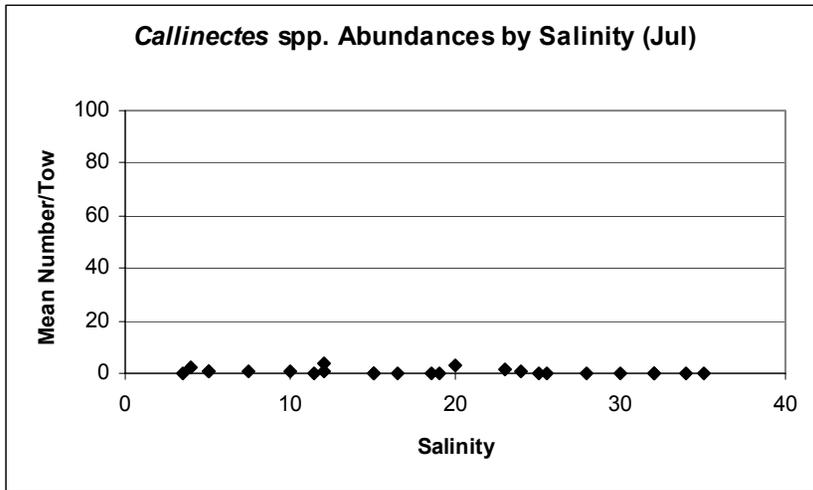
Fig. 7. Abundances of *Callinectes* spp. megalopae from evening/night plankton tows plotted by salinity for the months of July, August, September and October 2001. Each point represents the average number of megalopae per tow at a given site on a given day.

Table 6. Analysis of *Callinectes* spp. abundances in evening/night plankton tows using the Mixed procedure in SAS, Type 3 Tests of Fixed Effects. Evening plankton tows that occurred prior to sunset were eliminated from this analysis.

Factor	Factor DF	Error DF	F Value	P
Sunset	1	30	3.70	0.0640
Salinity	1	30	10.80	0.0026
Sunset*Salinity	1	30	0.93	0.3432
Month	1	13	0.05	0.8270
Sunset*Month	1	30	3.60	0.0674
Salinity*Month	1	30	12.77	0.0012
Moon	1	13	0.99	0.3388
Sunset*Moon	1	30	0.07	0.7962
Salinity*Moon	1	30	0.09	0.7651

Table 7. Analysis of sub-site comparison for *Callinectes* megalopal abundances on passive larval collectors. This analysis was run using the Mixed procedure in SAS, Type 3 Tests of Fixed Effects. Only factors involving sub-site (Group) comparisons are shown.

Factor	Factor DF	Error DF	F Value	P
Group	1	17	0.71	0.4113
Salinity*Group	1	494	0.17	0.6798
Month*Group	1	494	0.54	0.4635
Salinity*Month*Group	1	494	0.09	0.7691
Moon*Group	1	17	0.11	0.7443
Salinity*Moon*Group	1	494	0.11	0.7382
Month*Moon*Group	1	494	0.10	0.7499
Salinity*Month*Moon*Group	1	494	0.09	0.7654

results for salinity, month, and the interaction between salinity and month (Table 8). Overall settlement was scattered widely across the salinity gradient over the course of the entire study (Fig. 8). Data from both July and August showed a trend of high settlement in higher salinities near the mouth of the estuary with abundance decreasing with decreasing salinity (Fig. 9). In September, however, the pattern shifts dramatically to greater abundances in the mesohaline salinities. A closer examination of the September data reveals that a shift in settlement pattern occurs between the first and second sampling window for that month (Fig. 10). In October, the trend is the reverse of July and August with settlement increasing with decreasing salinity down to 12 ppt (Fig. 9). During October, no settlement data were collected below 12 ppt as a lack of rainfall in the river basin during August and September resulted in higher salinities at the upper estuarine sites (Fig. 2). A comparison of settlement from July to mid-September to settlement from mid-September through October demonstrated a significant change in settlement pattern between these two periods. From July through mid-September when overall abundances were low, settlement occurred as expected with highest settlement at the mouth of the estuary and then decreasing settlement with increasing distance upstream (Fig. 11). However, from mid-September through October when abundances of *Callinectes* megalopae are highest, there was a clear inverse of the expected pattern with highest settlement occurring at the upper region of the estuary and settlement decreasing towards the higher salinity waters at the mouth (Fig. 12).

Based on previous studies which found a 2 to 3 day time lag between pulses of megalopae arriving at the mouth of an estuary and when they arrived at the head of the estuary, I expected to be able to track pulses of megalopae up-estuary within the 3-day windows that collectors were deployed. While settlement patterns varied widely both spatially and within windows, there was no clear pattern of a pulse of megalopae moving up-estuary. In fact, within

Table 8. Analysis of all passive larval collector data for *Callinectes* spp. Analysis was run using the GENMOD procedure in SAS, analysis of GEE Parameter Estimates. Z value is the test statistic generated by the GENMOD procedure and can be positive or negative.

Parameter	Estimate	Standard Error	Z	P
Intercept	-28.4612	6.6563	-4.28	<0.0001
Salinity	1.0312	0.2989	3.45	0.0006
Month	3.3171	0.8186	4.05	<0.0001
Salinity*Month	-0.1254	0.0372	-3.37	0.0008
Moon	9.7889	8.6698	1.13	0.2589
Salinity*Moon	-0.2717	0.3928	-0.69	0.4891
Month*Moon	-1.3634	1.0383	-1.31	0.1891
Salinity*Month*Moon	0.0453	0.475	0.95	0.3398

Callinectes Settlement by Salinity
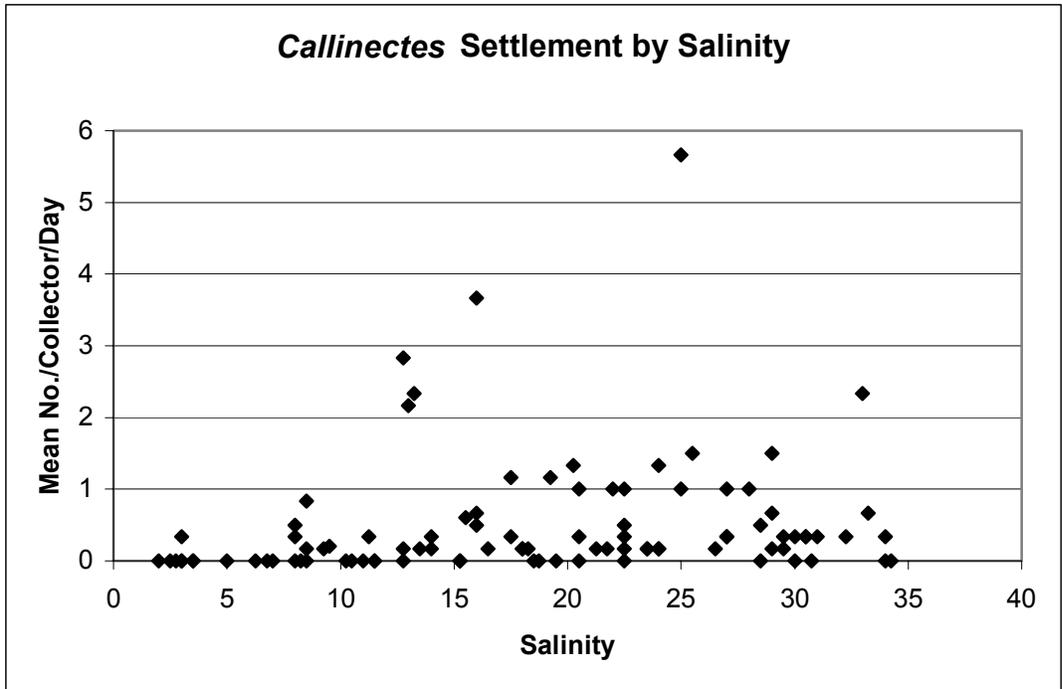
Fig. 8. *Callinectes* megalopal settlement abundances plotted by salinity from July 2001 through mid-October 2001. Each point represents the average of all collectors at a given site on a given day. Regression analysis: $r^2=0.0302$; F=2.8947; P>0.0922
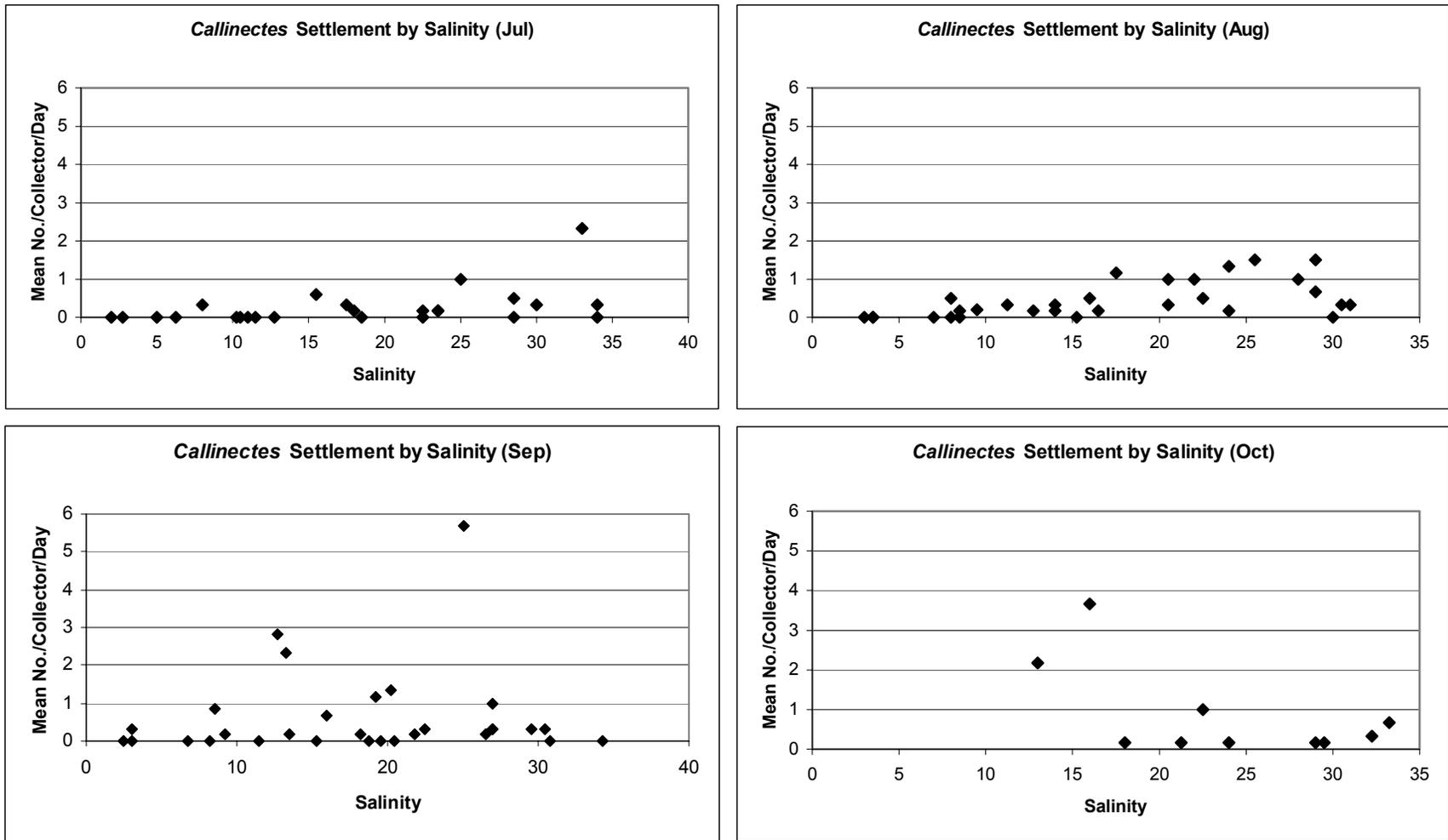
Fig. 9. *Callinectes* spp. megalopal settlement abundances plotted by salinity for July, August, September, and October 2001. Each point represents the average of all collectors at a given site on a given day.
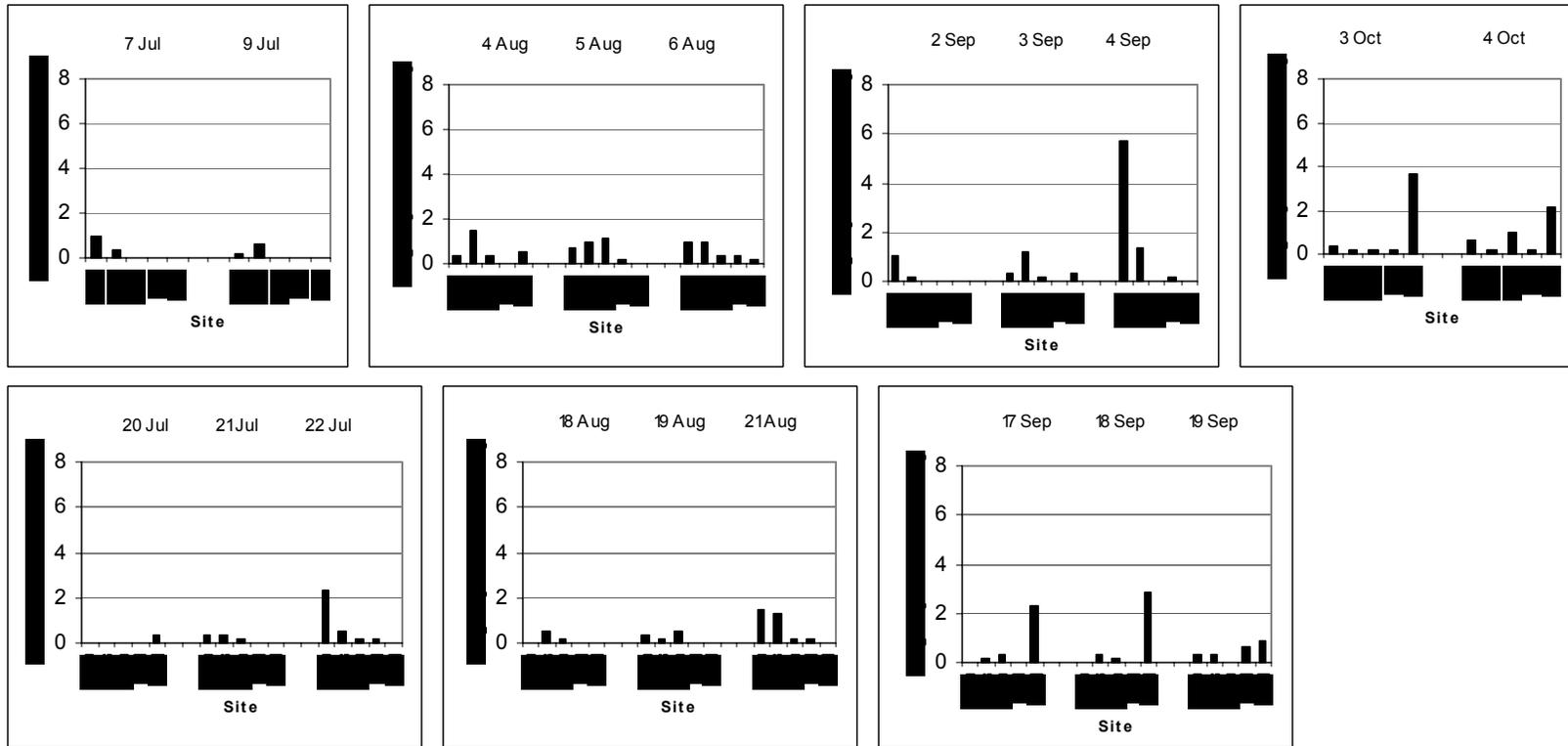
Fig. 10. *Callinectes* megalopae settlement patterns by site demonstrating within-period variation. Abundances are shown as the average of all collectors at a site per day.

33

Callinectes Settlement by Salinity Jul-Mid Sep
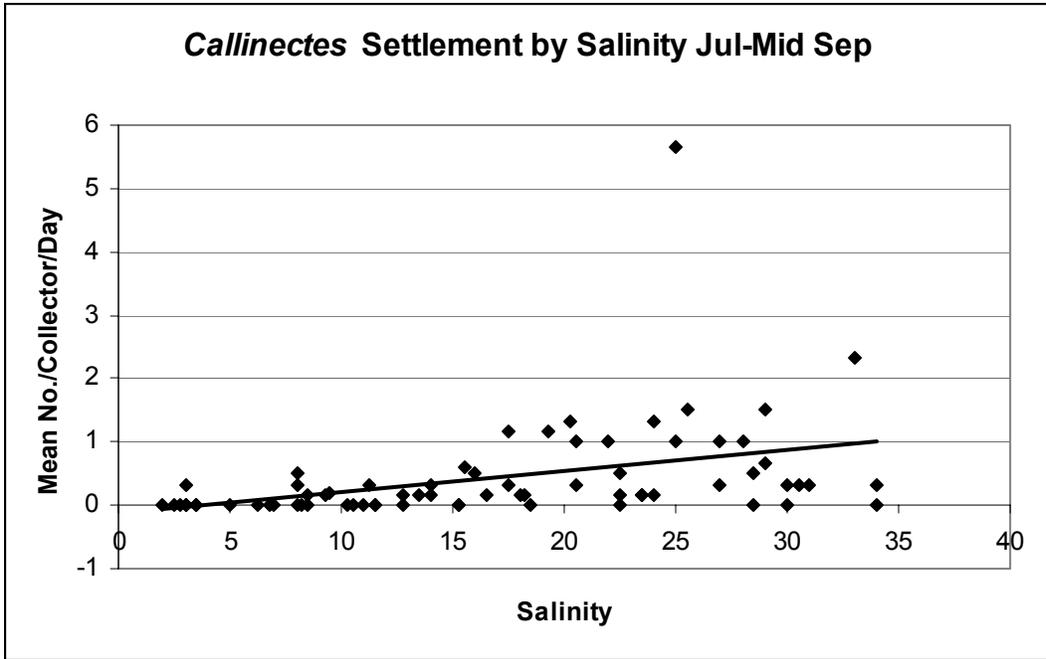
Fig. 11. *Callinectes* megalopal settlement abundances plotted by salinity from July to mid-September 2001. Each point represents the average of all collectors at a given site on a given day. Regression analysis: r^2=0.1483; F=11.8367; P<0.001
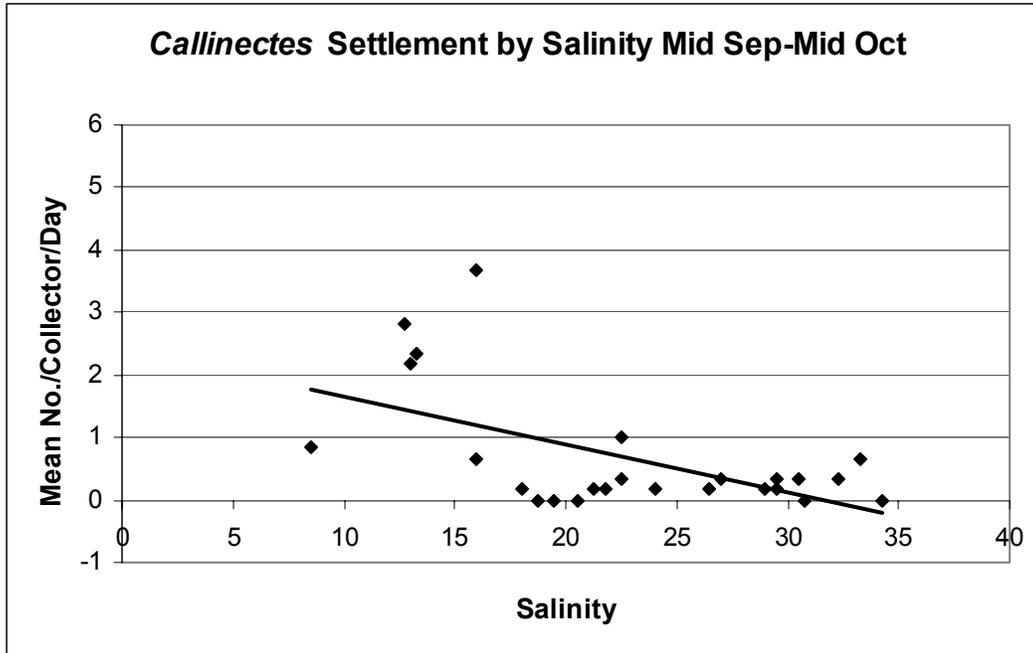
Fig. 12. *Callinectes* megalopal settlement abundances plotted by salinity from mid-September to mid-October 2001. Each point represents the average of all collectors at a given site on a given day. Regression analysis: $r^2 = 0.3149$; $F = 10.5727$; $P < 0.0035$

several sampling periods, the pattern of settlement was almost the same over the course of the three days (Fig. 10).

Juvenile Abundances for *Callinectes sapidus*

Callinectes sapidus early juvenile (carapace width 2-12 mm) abundances plotted by salinity showed a pattern of higher abundances in lower salinities (Fig. 13), with no juveniles collected at salinities greater than 20 ppt. While this trend was not significant, it did appear to correspond with the trend in settlement from mid-September to mid-October (Fig.12). If patterns of early juvenile abundances are examined by month (Fig. 14), greater abundances in October and November were found in higher salinities, however, this is somewhat misleading due to rising salinities in October and November due to the drought. These catches were primarily at the upper estuarine station.

DISCUSSION

Brachyuran postlarval abundances in the plankton in the Cape Fear River Estuary appear to be dominated by *Uca* spp. during the summer and early fall. Overall xanthid, *Sesarma cinereum* and *Callinectes* spp. megalopae abundances were an order of magnitude lower than *Uca* spp. until the sharp decline in abundances for all species except *Callinectes* in October. This is generally consistent with patterns reported for other estuaries along the North American Atlantic coast (Sandifer 1973, Brookins and Epifanio 1985, DeVries et al. 1994, Mense et al. 1995, Christy and Morgan 1998). *Uca* abundance patterns in the plankton and their shifts from month to month may be the result of the different species present in the estuary, *U. pugnax, U. pugilator,* and *U. minax* in the Cape Fear River estuary, moving/recruiting to different portions of the estuary at different times. While adult habitats do overlap to a certain degree between *Uca*
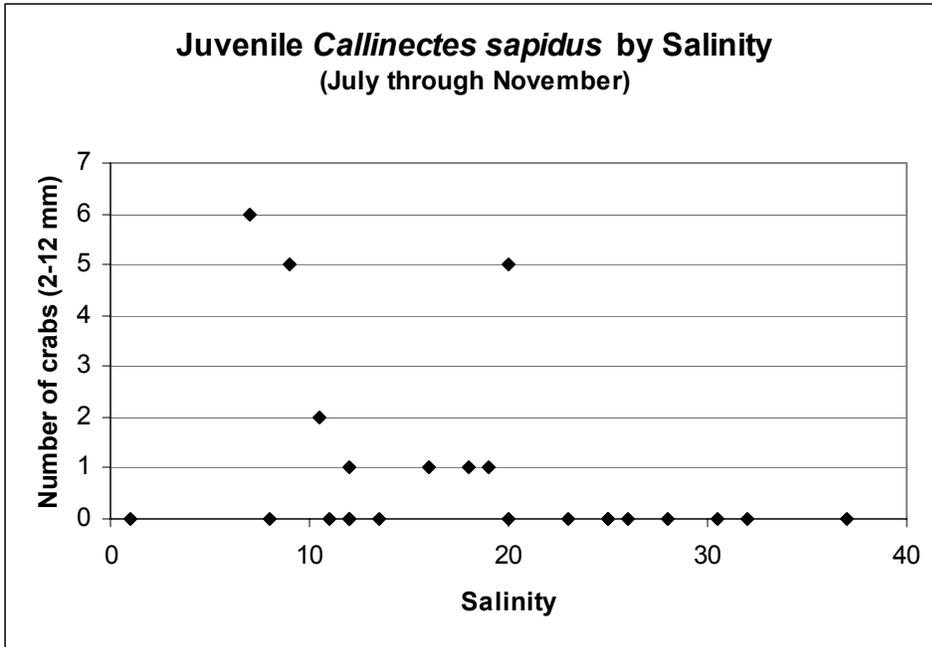
Fig. 13. *Callinectes sapidus* early juvenile (2-12 mm carapace width) abundances plotted by salinity. Regression analysis: $r^2=0.0886$; $F=2.7218$; $P>0.1$
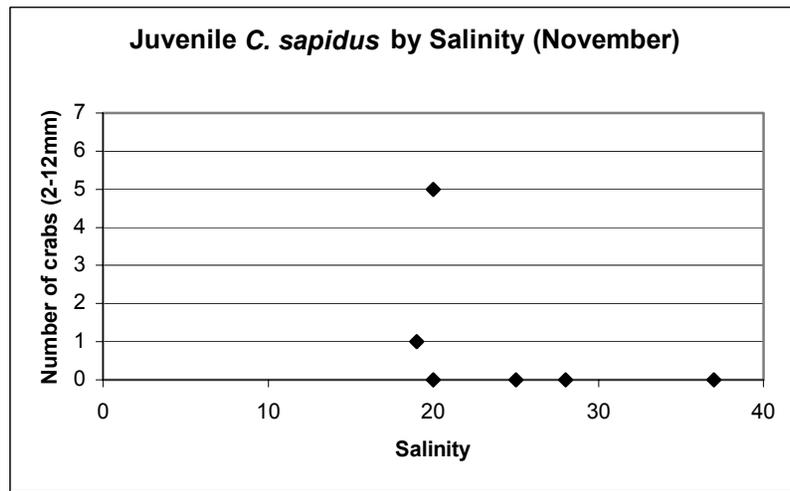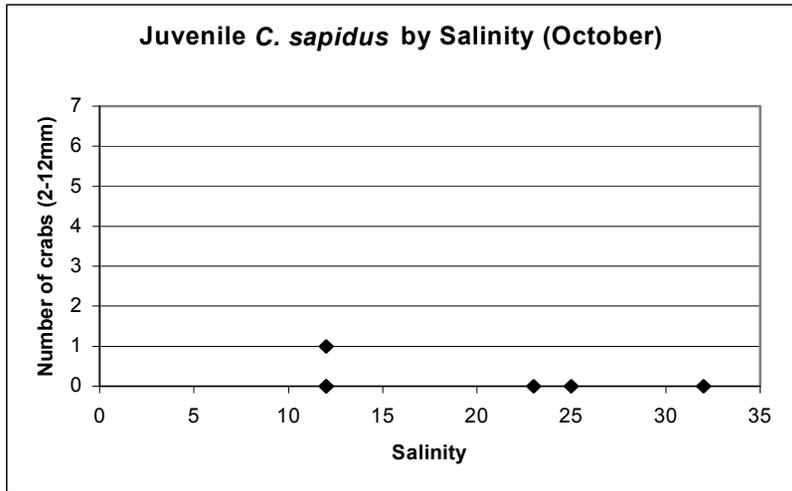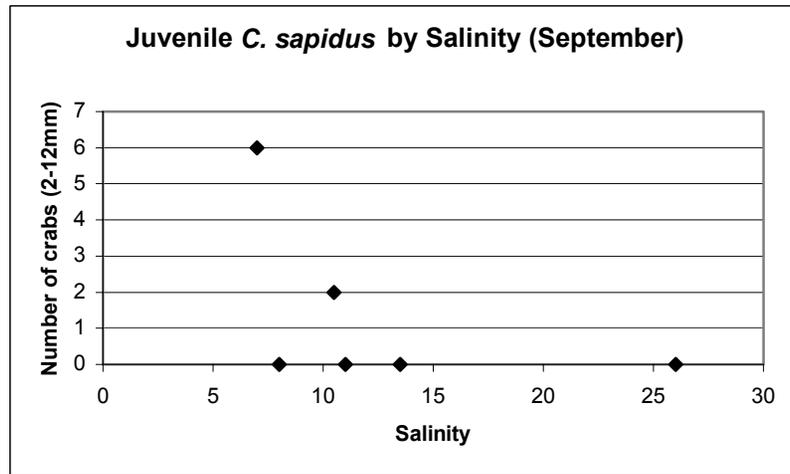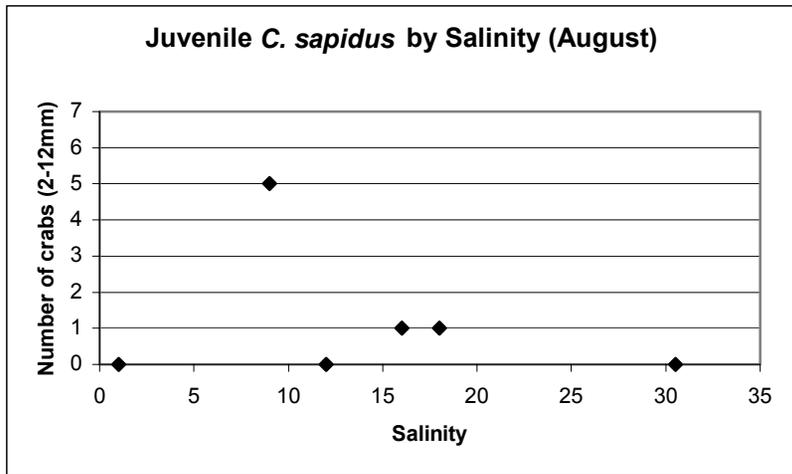
Fig. 14. *Callinectes sapidus* early juvenile (2-12 mm carapace width) abundances plotted by salinity for August, September, October, and November 2001.

species, there are varied salinity preferences among the various species (Miller and Maurer 1973). The same argument may apply for the shifting patterns noted for xanthid megalopae over the course of this study. The *Sesarma cinereum* patterns are not so easily explained. The adults are found over a broad range of the estuary (Barbour, personal observation) and this may be a result of their scattered dispersal in the plankton. The patterns of *Callinectes* abundances in the plankton are somewhat surprising. Based on the findings of previous studies (Williams 1971, Johnson 1985, Mense and Wenner 1989, Morgan et al. 1996), one would expect to see higher abundances at the high salinity sites near the mouth of the estuary with abundances decreasing with decreasing salinity due to settlement of larvae as they move up-estuary. Instead we see high spatial and within-period variability with no clear pattern of pulses moving upstream. One possibility for the lack of a consistent pattern is that current speeds in the Cape Fear are greater than in other estuaries where upstream movement was tracked. This could have resulted in up-estuary movement faster than the 2 to 3 day time lag noted in other studies (Morgan et al. 1996). There is also the possibility that the faster current speeds resulted in greater mixing of the water column thus obscuring pulse patterns. This may hold true for all brachyurans captured in plankton tows.

The lack of any correlation between plankton abundances and settlement data for *Callinectes* is also surprising. Settlement patterns for July and August followed the expected pattern of high settlement in high salinities with decreasing settlement with decreasing salinity, in spite of the presence of *Callinectes* megalopae in the plankton across the estuarine gradient, albeit in low abundance. The dramatic shift in settlement patterns in the middle of September is difficult to explain. It is possible that the lack of rainfall in August and September slowed outflow rates of the Cape Fear to the extent that the megalopae were able to penetrate farther into

the estuary but this does not appear to be supported by the plankton tow data for that time period. Another possibility is that as overall salinities rose, marine predators were able to penetrate to the lower sites to a greater extent and reduced the numbers of megalopae on settlement collectors at the higher salinity sites (Weinstein et al. 1980).

A more interesting possibility is that *Callinectes* megalopae were actively avoiding settlement at the lower stations in late September and early October in order to preferentially settle in lower salinity juvenile habitat. There are a number of possible reasons for this behavior. There could be a selective advantage for juvenile blue crabs in lower salinity water such as avoidance of parasites and predators or increased growth rates as a result of more rapidly increasing temperatures in estuarine shallows compared to waters more heavily influenced by marine waters (Weinstein 1979). Another possibility is avoidance of conspecifics (Welch et al. 1997). Early settlers in higher salinities may have already molted to first crab and be preying on new megalopal arrivals. Without a structurally complex habitat such as SAV to provide a refuge from cannibalistic encounters (Mosknes et al. 1997), later arrivals may continue up-estuary seeking more favorable conditions.

None of the groups analyzed demonstrated any difference in abundance in plankton tows or passive larval collectors for the new or full moon periods. This finding differs from other studies (Olmi et al. 1990, van Montfrans et al. 1995). While this study covered ten days of every month, it was not designed to cover an entire lunar cycle as peak megalopal abundances were found to correlate with new and full moons in a nearby study of ingress of *Callinectes* megalopae during 1990-1992 (Mense et al. 1995). Lunar patterns could have been masked by the broad area coverage of the current study. Another explanation may lie in the relationship between the lunar cycle and flood tides. Morgan et al. (1996) found that recruitment for *Callinectes* megalopae

was more closely associated with the tidal amplitude cycle than the lunar cycle. Tankersley et al. (2002), found that the greatest number of *Callinectes* megalopae undergo flood tide transport when both the flood tide and the slack before ebb occur during the night. They suggested that the lunar patterns noted in various studies for *Callinectes* megalopae settlement, which vary from location to location, possibly result from the phase relationship between flood tide and the light/dark cycle.

This study highlights an interesting and complex pattern of temporal and spatial variability in planktonic distribution of brachyuran megalopae. There was no clear pattern of up-estuary movement of megalopal pulses and no temporally consistent correlation between planktonic availability of *Callinectes* megalopae and postlarval settlement. There does however, appear to be evidence of a shift in *Callinectes* settlement patterns in mid-September to mid-October and this appears to be related to early juvenile *C. sapidus* abundances in the upper estuary. This provides evidence for a mixed-model explanation of juvenile blue crab distribution with megalopae settling in the lower estuary prior to mid-September (with possible subsequent juvenile movement) and megalopae settling at upper estuarine sites after mid-September (where juveniles are most abundant).

Examining the relationship between flow dynamics in the Cape Fear River Estuary and the spatial location of megalopae in the water column across a section of the estuary might prove valuable in explaining patterns of brachyuran planktonic distribution and perhaps shed some light on the lack of correlation between planktonic availability and settlement data. The shift in settlement patterns to the upper estuary as *Callinectes* megalopal abundances increased is interesting and warrants further study to determine if this pattern is consistent on an inter-annual basis and across regional weather conditions (i.e. flood vs. drought). Further research on

whether low salinity regions offer competitive advantages for either megalopae or juveniles of

Callinectes sapidus would also be useful in unraveling this puzzle.

Literature Cited

Allen ND (2000) Distribution and abundance of the juvenile blue crab (*Callinectes sapidus*) in the Cape Fear Estuary. M.Sc. Thesis, University of North Carolina at Wilmington, Wilmington N.C., 43 p.

Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460-468

Boicourt WC (1982) Estuarine larval retention mechanisms on two scales. In: Estuarine comparisons. V.S. Kennedy (ed.). New York: Academic Press, pp. 445-457

Bookhout CG, Costlow JD Jr (1977) Larval development of *Callinectes similis* reared in the laboratory. Bulletin of Marine Science 27: 704-728

Boylan JM, Wenner EL (1993) Settlement of brachyuran megalopae in a South Carolina, USA, estuary. Marine Ecology Progress Series 97: 237-246

Brookins KG, Epifanio CE (1985) Abundance of brachyuran larvae in a small coastal inlet over six consecutive tidal cycles. Estuaries 8: 60-67

Cargo DG (1960) A megalops of the blue crab, *Callinectes sapidus* in the Patuxent River, Maryland. Chesapeake Science 1:110

Cattrijsse A, Makwaia ES, Dankwa HR, Hamerlynck O, Hemminga MA (1994) Nekton communities of an intertidal creek of a European estuarine brackish marsh. Marine Ecology Progress Series 109: 195-208

Christy JH, Morgan SG (1998) Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. Marine Ecology Progress Series 174: 51-65

Costlow JD Jr, Bookhout CG (1959) The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biological Bulletin (Woods Hole) 116: 373-396

Cronin TW (1982) Estuarine retention of larvae of the crab *Rhithropanopeus harrisii*. Estuarine, Coastal and Shelf Science 15: 207-220

De Ben WA, Clothier WD, Ditsworth GR, Baumgartner DJ (1990) Spatio-temporal fluctuations in the distribution and abundance of demersal fish and epibenthic crustaceans in Yaquina Bay, Oregon. Estuaries 13: 469-478

De Vries MC, Tankersley RA, Forward RB Jr, Kirby-Smith WW, Luettich RA Jr (1994) Abundance of estuarine crab larvae is associated with tidal hydrologic variables. Marine Biology 118: 403-413

Eckman JE (1996) Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. Journal of Experimental Marine Biology and Ecology 200: 207-237

Epifanio CE, Masse AK, Garvine RW (1989) Transportation of blue crab larvae by surface currents off Delaware Bay, U.S.A. Marine Ecology Progress Series 54: 35-41

Etherington LL, Eggleston DB (2000) Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. Marine Ecology Progress Series 204: 179-198

Forward RB Jr, Tankersley RA (2001) Selective tidal-stream transport of marine animals. Oceanography and Marine Biology: an Annual Review 39: 305-353

Garvine RW, Epifanio CE, Epifanio CC, Wong K-C (1997) Transport and recruitment of blue crab larvae: a model with advection and mortality. Estuarine, Coastal and Shelf Science 45: 99-111

Goodrich DM, van Montfrans J, Orth RJ (1989) Blue crab megalopal influx to Chesapeake Bay: evidence for a wind-driven mechanism. Estuarine, Coastal and Shelf Science 29: 247-260

Johnson DF (1985) The distribution of Brachyuran crustacean megalopae in the waters of the York River, Lower Chesapeake Bay and adjacent shelf: implications for recruitment. Estuarine, Coastal and Shelf Science 20: 693-705

Kennish MJ (1986) Ecology of Estuaries, V. 1, Physical and Chemical Aspects. CRC Press, Boca Raton Florida, 250 p.

Little KT, Epifanio CE (1991) Mechanism for the re-invasion of an estuary by two species of brachyuran megalopae. Marine Ecology Progress Series 68: 235-242

Lipcius RN, Olmi EJ III, van Montfrans J (1990) Planktonic availability, molt stage and settlement of blue crab postlarvae. Marine Ecology Progress Series 58: 235-242

McConaugha JR (1988) Export and reinvasion of larvae as regulators of estuarine decapod populations. American Fisheries Society Symposium 3: 90-103

Mense DJ, Wenner EL (1989) Distribution and abundance of early life history stages of the blue crab, *Callinectes sapidus*, in tidal marsh creeks near Charleston, South Carolina. Estuaries 12: 157-168

Mense DJ, Posey MH, West T, Kincheloe K (1995) Settlement of brachyuran postlarvae along the North Carolina coast. Bulletin of Marine Science 57: 793-806

Meredith WH (1982) The dynamics of zooplankton and micronekton community structure across a salt marsh-estuarine waters interface of lower Delaware Bay. Ph. D. Dissertation, Univ. of Delaware, Newark, DE., 381 p.

Metcalf KS, van Montfrans J, Lipcius RN, Orth RJ (1995) Settlement indices for blue crab megalopae in the York River, Virginia: temporal relationships and statistical efficiency. Bulletin of Marine Science 57(3): 781-792

Miller KG, Maurer D (1973) Distribution of the fiddler crabs, *Uca pugnax* and *Uca minax*, in relation to salinity in Delaware Rivers. Chesapeake Science 14: 219-221

Moksnes P-O, Lipcius RN, Pihl L, van Montfrans J (1997) Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. Journal of Experimental Marine Biology and Ecology 215: 157-187

Morgan SG, Zimmer-Faust RK, Heck KL Jr, Coen LD (1996) Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply. Marine Ecology Progress Series 133: 73-88

Olmi EJ III, van Montfrans J, Lipcius RN, Orth RJ, Sadler PW (1990) Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. Bulletin of Marine Science 46: 230-243

Olmi EJ III (1994) Vertical migration of blue crab *Callinectes sapidus* megalopae: implications for transport in estuaries. Marine Ecology Progress Series 113: 39-54

Orth RJ, van Montfrans J (1987) Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. Marine Ecology Progress Series 41: 283-294

Palmer MA, Allan JD, Butman CA (1996) Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. Trends in Ecology and Evolution 11: 322-326

Pietrafesa LJ, Janowitz GS (1988) Physical oceanographic processes affecting larval transport around and through North Carolina inlets. American Fisheries Society Symposium 3: 34-50

Posey MH, Hines AH (1991) Complex predator-prey interactions within an estuarine benthic community. Ecology 72(6): 2155-2169

Posey MH, Alphin TD, Harwell H, Allen B (2003) Importance of low salinity areas for juvenile blue crabs, *Callinectes sapidus* Rathbun, in river-dominated estuaries of Southeastern United States. Journal of Experimental Marine Biology and Ecology. In Review

Rabalais NN, Burditt FR Jr, Coen LD, Cole BE, Eleuterius C, Heck KL Jr, McTigue TA, Morgan SG, Perry HM, Truesdale FM, Zimmer-Faust RK, Zimmerman RJ (1995) Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. Bulletin of Marine Science 57(3): 855-876

Rogers BD, Shaw RF, Herke WH, Blanchet RH (1993) Recruitment of postlarval and juvenile brown shrimp (*Penaeus aztecus* Ives) from offshore to estuarine waters of the northwestern Gulf of Mexico. Estuarine, Coastal and Shelf Science 36: 377-394

Roman MR, Boicourt WC (1999) Dispersion and recruitment of crab larvae in the Chesapeake Bay plume: physical and biological controls. Estuaries 22: 563-574

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. Science 241: 1460-1466

Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Marine Ecology Progress Series 99: 1-16

Sandifer PA (1972) Morphology and ecology of Chesapeake Bay decapod crustacean larvae. Ph.D. Dissertation Univ. of Virginia, Charlottesville, VA., 532 p.

Sandifer PA (1973) Distribution and abundance of decapod crustacean larvae in the York River Estuary and adjacent Lower Chesapeake Bay, Viginia, 1968-1969. Chesapeake Science 14: 235-257

Shenker JM, Dean JM (1979) The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2: 154-163

Steele P, Bert TM (1994) Population ecology of the blue crab, *Callinectes sapidus* Rathbun, in a subtropical estuary: population structure, aspects of reproduction, and habitat partitioning. Florida Marine Research Publications 51: 1-24

Strathmann RR (1982) Selection for retention or export of larvae in estuaries. In: Kennedy VS (ed) Estuarine comparisons. Academic Press, New York, p 521-536

Sulkin SD, Van Heukelem WF (1986) Variability in the length of the megalopal stage and its consequence to dispersal and recruitment in the portunid crab *Callinectes sapidus* Rathbun. Bulletin of Marine Science 39: 269-278

Tagatz ME (1968) Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. Fishery Bulletin 67(1): 17-33

Tankersley RA, Forward RB Jr (1994) Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. Marine Biology 118: 415-423

Tankersley RA, McKelvey LM, Forward RB Jr (1995) Response of estuarine crab megalopae to pressure, salinity, and light: implications for flood-tide transport. Marine Biology 122: 391-400

Tankersley RA, Welch JM, Forward RB Jr. (2002) Settlement times of blue crab (*Callinectes sapidus*) megalopae during flood-tide transport. Marine Biology 141: 863-875

van Montfrans J, Peery CA, Orth RJ (1990) Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in the York River, Virginia: 1985-1988. Bulletin of Marine Science 46(1): 95-104

van Montfrans J, Epifanio CE, Knott DM, Lipcius RN, Mense DJ, Metcalf KS, Olmi EJ III, Orth RJ, Posey MH, Wenner EL, West TL (1995) Settlement of blue crab postlarvae in western north Atlantic estuaries. Bulletin of Marine Science 57: 834-854

Weinstein MP (1979) Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fishery Bulletin 77: 339-357

Weinstein MP, Weiss SL, Walters MF (1980) Multiple determinants of community structure in shallow marsh habitats, Cape Fear River Estuary, North Carolina, USA. Marine Biology 58: 227-243

Welch JM, Rittschoff D, Bullock TM, Forward RB Jr. (1997) Effects of chemical cues on settlement behavior of blue crab *Callinectes sapidus* postlarvae. Marine Ecology Progress Series 154: 143-153

Williams AB (1971) A ten-year study of meroplankton in North Carolina estuaries: annual occurrence of some brachyuran developmental stages. Chesapeake Science 12: 53-61

Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institutional Press, Washington, D.C. 550 p.

Wolcott DL, De Vries MC (1994) Offshore megalopae of *Callinectes sapidus*: depth of collection, molt stage and response to estuarine cues. Marine Ecology Progress Series 109: 157-163

Wrona AB, Wiegert RG, Bishop TD (1995) Initial report of settlement patterns of brachyuran megalopae at Sapelo Island, Georgia, U.S.A. Bulletin of Marine Science 57: 807-820