Abstract—We measured growth and movements of individually marked free-ranging juvenile white shrimp (*Litopenaeus setiferus*) in tidal creek subsystems of the Duplin River, Sapelo Island, Georgia. Over a period of two years, 15,974 juvenile shrimp (40–80 mm TL) were marked internally with uniquely coded microwire tags and released in the shallow upper reaches of four salt marsh tidal creeks. Subsequent samples were taken every 3–6 days from channel segments arranged at 200-m intervals along transects extending from the upper to lower reach of each tidal creek. These collections included 201,384 juvenile shrimp, of which 184 were marked recaptures. Recaptured shrimp were at large an average of 3–4 weeks (range: 2–99 days) and were recovered a mean distance of <0.4 km from where they were initially marked. Mean residence times in the creek subsystems ranged from 15.2 to 25.5 days and were estimated from exponential decay functions describing the proportions of marked individuals recaptured with increasing days at large. Residence time was not significantly correlated with creek length (Pearson=–0.316, P=0.684), but there was suggestive evidence of positive associations with either intertidal (Pearson r=0.867, P=0.133) or subtidal (Pearson r=0.946, P=0.054) drainage area. Daily mean specific growth rates averaged 0.009 to 0.013 among creeks; mean absolute growth rates ranged from 0.56–0.84 mm/d, and were lower than those previously reported for juvenile penaeids in estuaries of the southeastern United States. Mean individual growth rates were not significantly different between years (t-test, P>0.30) but varied significantly during the season, tending to be greater in July than November. Growth rates were size-dependent, and temporal changes in size distributions rather than temporal variation in physical environmental factors may have accounted for seasonal differences in growth. Growth rates differed between creeks in 1999 (t-test, P<0.015), but not in 1998 (t-test, P>0.5). We suggest that spatial variation in landscape structure associated with access to intertidal resources may have accounted for this apparent interannual difference in growth response.

Individual growth rates and movement of juvenile white shrimp (*Litopenaeus setiferus*) in a tidal marsh nursery*

Stacey Webb

Florida Department of Environmental Protection
Water Quality Standards and Special Projects Program
2600 Blair Stone Road, M.S. 3560
Tallahassee, Floida 32399
E-mail address: stacey.feken@dep.state.fl.us

Ronald T. Kneib

UGA Marine Institute
Sapelo Island, Georgia 31327

In 2001, shrimp became the most popular seafood in the United States when per capita consumption (1.54 kg) surpassed that of canned tuna (1.32 kg) for the first time in recorded history (NOAA[1]). Although 77% of the catch is from the Gulf of Mexico, commercial fisheries in Atlantic coastal states of the southeastern United States also depend heavily on penaeid shrimp populations. Of the three most common estuarine-dependent penaeid species (*Litopenaeus setiferus, Farfantepenaeus aztecus,* and *F. duorarum*)[2] harvested in the South Atlantic Bight, white shrimp *Litopenaeus setiferus* dominate, comprising >70% of the catch in the region (North Carolina to the east coast of Florida) and 75–87% in South Carolina and Georgia (NMFS[3]).

Concerns over the possibility of depleting the resource as early as the 1930s led to intensive studies of the life cycle (Lindner and Anderson, 1956; Williams, 1984). The white shrimp has an annual life cycle that can be divided into offshore (oceanic) and inshore (estuarine) phases. Adults spawn in Atlantic waters in spring and the postlarvae migrate into estuaries, aided by flood tides and wind-generated currents (Lindner and Anderson, 1956; Wenner et al., 1998). Postlarvae penetrate into the shallow upper reaches of the nursery habitat where juveniles achieve a substantial portion of their adult body mass before moving into deeper creeks, rivers, and sounds where they approach maturity and emigrate seaward to spawning areas (Muncy, 1984; Williams, 1984).

Given the commercial importance and early interest in this species, surprisingly little research has focused on the juvenile stages within tidal marsh nursery habitats (Minello and Zimmerman, 1985; Zein-Eldin and Renaud, 1986; Knudsen et al., 1996; McTigue and Zimmerman, 1998). Seasonal migrations and ontogenetic movements of white shrimp between coastal ocean spawning grounds and estuarine nurseries are well known (Dall et al., 1990), as are the sometimes extensive migrations of adult shrimp along the Atlantic coast, primarily to the south during fall and early winter, and northward in late winter and early spring (Lindner and Anderson, 1956; Shipman, 1983). Within the estuary, juvenile white

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shrimp, in contrast to other penaeid species, are found across a wider range of environmental conditions and habitats (Kutkuhn, 1966) and often make tidal excursions between subtidal and vegetated intertidal habitats to forage (Mayer, 1985; Kneib, 1995; 2000). However, relatively little is known about movements within subtidal creeks of the primary nursery areas, and the degree to which individuals exhibit fidelity to a particular tidal creek drainage system is unknown.

Direct measurement of juvenile shrimp growth rates within the nursery have also been rare. Most growth estimates for free-ranging juvenile shrimp are based on analyses of size-frequency data, which can be misleading (Loesch, 1965). Shrimp grow rapidly while in the estuarine nursery throughout the summer and early fall, and juveniles approach adult, or commercially harvestable size within 2–4 months after immigration to the estuary (Kutkuhn, 1966; Williams, 1984). Mean absolute growth rates of 0.7–1.1 mm/d are commonly reported for many penaeids (Dall et al., 1990). However, growth studies are difficult to compare because the rate of growth may vary between years and among seasons, as well as with size, age, and sex of individuals (Perez-Farfante, 1969). Growth estimates for *Litopenaeus setiferus* range widely, from 10 to 65 mm/month (Williams, 1984). Previous estimates were based on a variety of approaches including experimental studies in aquaria and ponds (Pearson, 1939; Johnson and Fielding, 1956), size distributions from tagging studies of adults (Lindner and Anderson, 1956), length-frequency distributions of juveniles in field samples (Gunter, 1950; Williams, 1955; Loesch, 1965; Harris, 1974; Mayer, 1985), mark-recapture of uniform size ranges of subadults and adults (Klima, 1974), and mark-recapture of shrimp in marsh ponds (Knudsen et al., 1996). Many estimates of growth for small (<80 mm TL) juvenile *L. setiferus* have been extrapolated from mark-recapture studies of larger (>100 mm TL) individuals (Lindner and Anderson, 1956; Harris, 1974; Klima, 1974). However, there is a paucity of empirical data on growth rates of small, free-ranging juvenile white shrimp within natural estuarine nursery habitats. The purpose of the present study was to provide reliable data on growth and movements of individual juvenile white shrimp within a natural estuarine nursery environment and to initiate an assessment of spatial variation in habitat quality in relation to tidal marsh landscape structure.

Recent innovations in tagging techniques have produced an effective way to obtain information on individual organisms through the use of sequentially numbered binary-coded microwire tags (Northwest Marine Technology, Inc. Shaw Island, WA). Microwire tags were first used in tagging experiments by Jefferts et al. (1963) and have since been used successfully to tag a variety of crustaceans including prawns (Prentice and Rensel, 1977), crayfish (Isely and Eversole, 1998), blue crabs (van Montfrans et al., 1986; Fitz and Weigert, 1991), and lobsters (Krouse and Nutting, 1990; Uglem and Grimsen, 1995). Results of these studies and others generally show that tag retention rates are high and tagging has little effect on the growth or survival of the fishes and crustaceans in which

microwire tags have been used. In a laboratory study involving 240 juvenile white shrimp, Kneib and Huggler (2001) confirmed that tag retention was high (~98%), growth rates between tagged and control individuals were not significantly different, and the best location (based on tag retention and survival) for tag injection was in the muscle tissue of the abdomen. This type of tag allows for identification of individuals because each tag is etched with a unique number encoded in binary form. In addition, the tag is completely internal and inconspicuous, thus eliminating problems associated with external tags (e.g., streamer-type tags) that might interfere with molting or increase predation risk (Garcia and LeReste, 1981; van Montfrans et al., 1986; Isely and Eversole, 1998).

Materials and methods

Study area

All samples were collected from four tidal creek subsystems associated with the Duplin River on the west side of Sapelo Island, Georgia. The Duplin River tidal drainage (~11 km^2) includes almost 10 km^2 of tidal salt marsh that is inundated twice daily by unequal tides with a mean range of 2.1 m (Wadsworth, 1980). Smooth cordgrass (*Spartina alterniflora*) is the dominant vegetation in the intertidal marshes of this area. Seasonal water temperatures average between 10°C and 30°C, and salinity is characteristically polyhaline, ranging from 15 to 30 ppt (Kneib, 1995). Freshwater flow into the system is intermittent and originates largely from local upland runoff and indirect flows by several interconnected tidal channels from the Altamaha River about 8 km to the southwest (Ragotzkie and Bryson, 1955).

Tidal creeks included in this study were Post Office Creek (PO) and Stacey Creek (SC) in 1998, and the East and West forks (EF, WF, respectively) of the upper Duplin River in 1999 (Fig. 1). Logistical constraints precluded sampling shrimp populations from more than two creek systems within the same year, and different pairs of creeks were chosen in each of the two years to broaden the spatial coverage of the study. High-resolution black and white photographs (1:16000 scale) from an aerial survey of the region in December 1989 were used to measure broadscale structural characteristics of the creek systems, including areal extent of the intertidal and subtidal portions of each drainage. The metrics and methods of extracting the information from the photographs are fully described elsewhere (see Webb and Kneib, 2002).

Field sampling

Shrimp were collected by cast net along the shallow (<1 m depth) edges of the subtidal portion of each creek system during low tide. Preliminary studies showed that 1.52-m diameter nets with ca. 1-cm mesh size collected the range of juvenile shrimp sizes (40–80 mm) targeted for marking in this study. All samples were collected within 2–3 hours of low tide to ensure that the shrimp popula-

Figure 1

Map of the salt marsh estuary in the vicinity of Sapelo Island, Georgia, showing locations of the tidal creek subsystems within the tidal drainage of the Duplin River.

tion was restricted to the tidal creek channels and had no refuge in the intertidal vegetation. A series of stations, at intervals of approximately 200 m, was established along the length of the subtidal portion of each creek from the upper reaches to the mouth, so that the number of stations within a creek depended on the navigable length of the subtidal channel. There were 13 stations in PO, 11 in SC, 9 in EF, and 7 in WF. Salinity, water temperature, and dissolved oxygen were measured near the surface (<1 m depth) at the mouth of the tidal creek on each day of sampling by using a YSI model 85 meter (YSI, Inc. Yellow Springs, OH). Juvenile shrimp were marked with uniquely coded microwire tags (1.1 mm long×0.25-mm diameter, Northwest Marine Technology [NMT], Inc. Shaw Island, WA), which were injected into the muscle tissue of the first abdominal segment. We used a hand-held multishot injector (NMT) that was designed to cut, magnetize, and inject sequentially coded tags from a continuous stainless-steel wire spool. Each tag was etched with six lines of binary code that could be read under a microscope (25×) and translated into a set of numbered coordinates. Only three of the coded lines were required to identify a unique individual. A master line contained a distinguishing sequence code that was necessary to properly interpret codes on data lines designated D3 and D4. The numeri-

cal values associated with these coded lines were entered into a sequential tag conversion computer program (GR [Growth Rate], version 1.3, Northwest Marine Technology, Inc. Shaw Island, WA) that output the unique tag number corresponding to those coordinates.
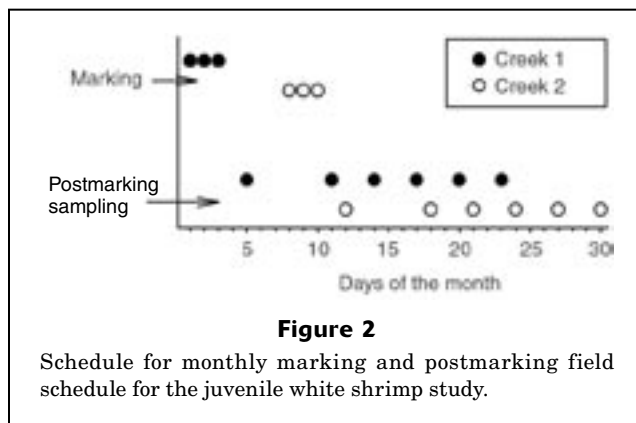
A reference tag was archived for every shrimp marked in order that the code on either side of the tag injected into a shrimp was known with certainty. This was necessary to ensure positive identification of recaptured individuals because the injector was designed only to cut tags to a known length (1.1 mm) and did not distinguish between the beginning and end of sequential codes and often cut tags that included a portion of two adjacent codes. Prior to their release, marked shrimp were passed across a magnetometer (NMT) which signaled the presence of the ferromagnetic tag with an audible tone and flashing light. All shrimp collected after these marking sessions were scanned in the same manner and when a tag was detected, it was removed from the recaptured shrimp, cleaned and read under the microscope. The two reference tags bracketing the recovered tag were then located in the archive set to determine the date, location, and initial length at release of the marked shrimp. Thus the growth rate, time at large, and distance between points of release and recapture could be determined with certainty for individual shrimp.

Shrimp were marked and released only in the upper reaches of each tidal creek. During the marking process, small batches of shrimp (<50 individuals) were collected and held in insulated plastic coolers. Water in the coolers was exchanged each time a new batch of shrimp was collected. Only active individuals, 40–80 mm total length (TL, tip of the rostrum to end of the telson) and in apparently good condition, were candidates for marking. The marking process required a minimum field crew of two researchers. One measured shrimp and recorded data, while the other injected tags and released marked shrimp at the edge of the tidal creek.

We attempted to mark 1000 shrimp during a 3-day period in each tidal creek near the beginning of every month from July to November in both years. It was not possible to tag shrimp in both creeks simultaneously; therefore shrimp were marked and released in week 1 during the first week of the month, then in creek 2 during the second week of the month. The remainder of the month was spent collecting marked shrimp (Fig. 2). Inclement weather and mechanical problems with the tagging equipment sometimes prevented us from achieving the goal of tagging 1000 shrimp per creek within the first week of each month. In August 1998, the tag injector malfunctioned on the first day of tagging in SC and was unavailable for several weeks while it was being refurbished. Consequently, sampling was suspended in SC during that time. Although the same problem occurred while we attempted to mark shrimp from the EF in September 1999, we continued sampling in an attempt to recapture shrimp tagged in previous months.

A total of 6 sampling events after marking were planned in each creek per month (Fig. 2). A sample consisted of the combined contents of 10 haphazard casts of the net along the edge of the tidal creek within each station per sampling date. Shrimp populations were usually sampled at 3-day intervals for 21 days beginning from the midpoint of the marking period. A consistent exception was the second sample in the series, which occurred at a 6-day interval to accommodate the marking effort in the second creek and to keep the sampling effort consistent in all creeks. Inclement weather interrupted the sampling schedule on occasion and when unfavorable conditions persisted for more than 3 days, some of the planned sampling events after marking were cancelled; some months were represented by fewer than 6 sampling events. Sampling was terminated when, as a result of normal seasonal emigration from the nursery areas, shrimp densities declined to the point that they could no longer be consistently collected from the tidal creeks by cast net (19 November 1998 and 21 November 1999).

Catches of marked shrimp from each station were retained in separate plastic bags, placed on ice, and transported to the laboratory. A subsample of shrimp from each station (every tenth individual) was measured (TL, mm) to construct size distributions. If a sample included fewer than 100 shrimp, all were measured. Sex was not determined. All individuals were scanned for the presence of tags and when a marked shrimp was detected, it was measured (TL, mm) before the tag was removed and stored in a plastic vial for reading at a later date. For each recapture,

Figure 2
Schedule for monthly marking and postmarking field schedule for the juvenile white shrimp study.

we recorded date, creek, station of recapture (i.e., distance from original release site) and size of fish.

Daily instantaneous (specific) growth rates (mm/[mm/d]) were calculated as

$$[(\ln L_2 - \ln L_1)/t],$$

where L_2 = total length (mm) of an individual on the date of recapture;
L_1 = initial total length (mm) on the date of tagging; and
t = number of days at large.

Daily absolute growth rates (mm/d) also were calculated ($L_2–L_1/t$) to facilitate comparison with estimates from previous studies. Displacement (distance moved) was determined by comparing the location of recapture with the original location at marking. Residence time within a tidal creek was determined from a plot of the proportion of recaptured individuals against time-at-large for each creek system. First, using the Regression Wizard in the computer program SigmaPlot® (version 8.0, SPSS, Inc. Chicago, IL), we fitted the data to an exponential decay function:

$$(y = a \times e^{-bt}),$$

where y = the proportion of total recaptures;
t = time at large; and
a and b = the estimated parameters.

Constraints imposed on the fit were a=1 (because the proportion of total recaptures could not exceed 1) and b>0 (because this was an exponential decay function). Mean residence time for shrimp in each creek was then estimated from the area below the fitted curves describing the proportion of recaptures with time at large. This was calculated with the macro function "area below curves" included in the "Toolbox" menu selection of SigmaPlot® (vers. 8.0, SPSS, Inc. Chicago, IL) which uses the trapezoidal rule to estimate the area under curves.

Statistical analyses

Most of the data analyses used statistical procedures in version 8.0 of the computer software package Systat®

(SPSS, Inc. Chicago, IL). When parametric tests were performed, residuals were analyzed to determine whether the data met the required assumptions (Sokal and Rohlf, 1995). Levene's test was used to evaluate conformity to the assumption of variance homogeneity among groups. When this assumption was violated, the data were transformed and retested. If the assumptions were still not met, then an appropriate nonparametric test was applied (e.g., Kruskal-Wallis one-way analysis of variance). Two sample *t*-tests were used to compare spatial and temporal variation in water temperature, salinity, and dissolved oxygen between creeks within a year and between years. August was omitted in comparisons of data between creeks in 1998, and between years because sampling in SC was suspended during August 1998. Regression analyses were performed to determine whether there were significant linear relationships between initial shrimp length and growth rates within each tidal creek. One-way ANOVA (controlling for the covariate initial length) was used to test for differences in growth rates between creeks within each year. A similar approach (controlling for initial size) was used to test for monthly (seasonal) differences in growth rate within years. If growth rates did not differ significantly between creeks, the data were pooled within year, otherwise creeks were treated separately. Only individuals at large for a month or less (to ensure that growth was representative of individual months) were included in the analyses.

Shrimp at large for fewer than 3 days were excluded from the statistical analyses to reduce certain anticipated biases associated with estimating growth rates. These included 1) measurement error (assumed to be at least 1 mm), which would likely represent a substantial proportion of the growth rate estimate when absolute change in size was small; 2) increments of growth associated with molting (Dall et al., 1990), which could either underestimate growth for shrimp that had been at large for a short time or had not molted since they were tagged or overestimate growth if shrimp were recaptured shortly after the first molt following marking; and 3) size-specific growth, where shrimp marked at a relatively small size and smaller shrimp exhibit a higher relative growth, so that early recaptures could represent larger than average growth rates.

Results

Physical parameters

Average water temperature, salinity, and dissolved oxygen (measured at the mouth of each tidal creek) were similar between creeks within years (see Table 1 in Webb and Kneib, 2002). In 1998, temperature ranged from 18.9 to 33.4°C, salinity from 18.2 to 28.0 ppt, and dissolved oxygen from 1.4 to 11.3 mg/L. In 1999, temperature ranged from 15.0 to 33.4°C, salinity from 23.9 to 32.5 ppt, and dissolved oxygen from 0.8 to 7.1 mg/L. Temperature followed expected seasonal patterns each year; mean values were highest in summer and declined toward autumn. Results

of *t*-tests with separate variance estimates showed no significant differences between years in either mean temperature (=0.14, df=134.0, P=0.80) or dissolved oxygen (t=1.82, df=115.9, P=0.07) but mean salinity was significantly (t=11.63, df=122.7, P<0.01) higher in 1999 (28.1 ppt) than in 1998 (24.8 ppt). Cumulative rainfall was 83.9 cm/yr in 1998 and 82.9 cm/yr in 1999 (Garbisch[4]). These values were indicative of drought conditions because they were well below the long-term mean annual precipitation value of ca. 132 cm/yr reported for Sapelo Island between May 1957 and March 2003 (Southeast Regional Climate Center[5]).

Growth

Shrimp collections during recapture efforts ranged from 20,077 to 78,724 individuals, but the proportion of marked individuals recaptured was low in both years, averaging just over 1% (Table 1). However, the recaptures included 184 individuals for which growth rates and net movements within the nursery were known precisely.

Daily absolute growth rates of individuals, which ranged from 0.25 to 2.5 mm, averaged 0.86, 0.78, 0.84, and 0.61 mm at PO, SC, WF and EF, respectively. The mean values are on the low end of the range reported in previous studies of juvenile *Litopenaeus setiferus* with other methods and conducted in different locations (Table 2). Daily specific growth rates were size-dependent in both years. Negative linear relationships between growth rate and initial size (i.e., smaller shrimp grew relatively faster) was the prevalent trend in all creeks (Fig. 3). No significant difference (t=1.19, df=74, P=0.237) in growth was detected between PO and SC, where mean (±SD) specific (instantaneous) daily growth rates were 0.014 ±0.006 and 0.012 ±0.007, respectively. In 1999, shrimp exhibited significantly (t=2.12, df=56, P=0.038) higher mean specific growth rates in the WF (0.014 ±0.008) compared to the EF (0.010 ±0.006) of the Duplin River. The physical environment was similar at these sites (Webb and Kneib, 2002), and there was no significant difference (t=1.43, df=81, P=0.156) in the mean final sizes of shrimp recaptured from these sites. However, the mean (±SD) initial size of marked shrimp at EF (61.3 ±8.3) was significantly (t=2.20, df=81, P=0.031) larger than at WF (56.0 ±10.9); therefore a lower specific growth rate was to be expected at EF.

On a finer temporal scale, seasonal variation in growth rates occurred in both years, more rapid growth early in the season, and a general increase in the mean size of individuals as the season progressed were evident (Fig. 4). The earlier observation that specific growth rate declined with size (Fig. 3) opens the possibility that seasonal variation in growth rates could be explained simply by

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[4] Garbisch, J. Unpubl. data. Univ. Georgia Marine Institute Flume Dock Monitoring Station, NOAA, Sapelo Island National Estuarine Research Reserve. Univ. Georgia Marine Institute, Sapelo Island, GA 31327.

[5] Southeast Regional Climate Center. Unpubl. data. Website: http://water.dnr.state.sc.us/water/climate/sercc/climateinfo/historical/historical_ga.html. [Accessed 21 November 2003].
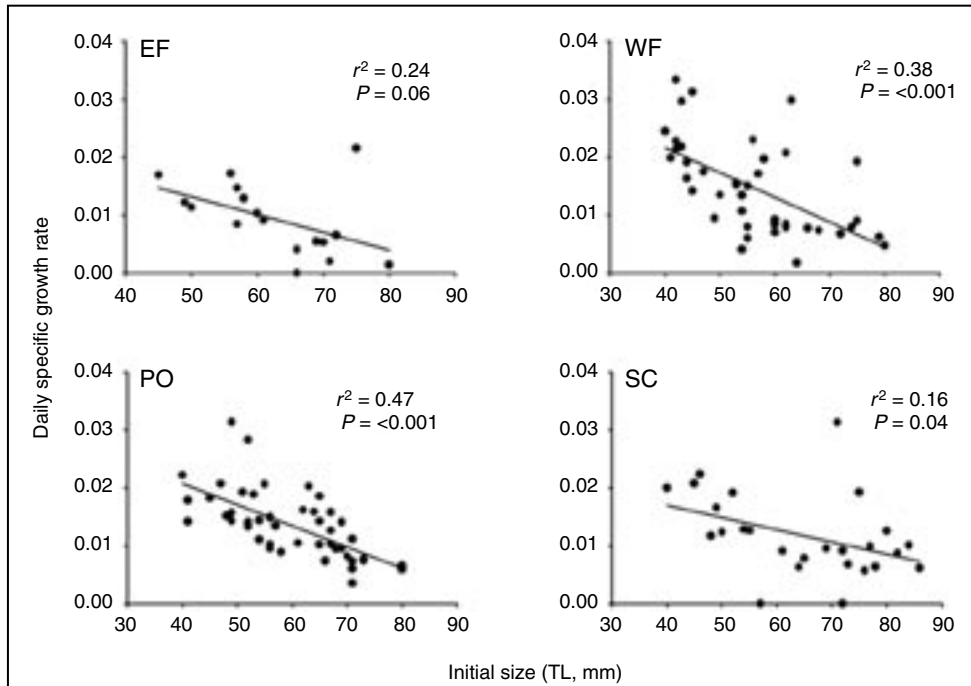
Figure 3

Scatter plots and linear regression results for the relationships between individual specific growth rates and initial sizes of recaptured juvenile shrimp in each tidal creek subsystem: EF = East Fork of Duplin River, WF = West Fork of Duplin River, PO = Post Office Creek, SC = Stacey Creek.

Table 1

Monthly summary of the number of shrimp tagged, number collected in subsequent sampling, and the number of tagged shrimp recaptured in each tidal creek.

Collection site and sampling process	July	August	September	October	November	Total
Post Office Creek						
Number tagged and released	1004	1077	1025	1000	779	4885
Number collected after tagging	7477	13,851	4730	8384	1298	35,740
Number of tags recaptured	13	16	16	22	1	68
Stacey Creek						
Number tagged and released	719	91	804	862	623	3099
Number collected after tagging	5877	0	5466	6376	2358	20,077
Number of tags recaptured	2	0	12	16	3	33
East Fork of Duplin River						
Number tagged and released	812	1000	0	1024	1003	3839
Number collected after tagging	23,080	14,490	11,020	14,804	3449	66,843
Number of tags recaptured	7	11	0	4	4	26
West Fork of Duplin River						
Number tagged and released	1008	1000	447	696	1000	4151
Number collected after tagging	32,130	17,926	10,954	10,600	7114	78,724
Number of tags recaptured	27	16	3	4	7	57

Table 2

Summary of estimated mean daily absolute growth rates for juvenile *Litopenaeus setiferus*. Growth rates were converted to mm/d if reported in other units.

Reference	Location	Growth rate (mm/d)	Method and notes
Gunter, 1950	Gulf of Mexico, Texas	0.8–1.3	Size frequency in field samples, juveniles 28–100 mm
Williams, 1955	coastal North Carolina	1.2	Size frequency in field samples, progression of maximum sizes of juveniles, 32–117 mm
Johnson and Fielding, 1956	Florida	1.3	Pond culture, juveniles
Lindner and Anderson, 1956	South Atlantic Bight and Gulf of Mexico	1.0–1.3	Extrapolated for juveniles 40–80 mm from Walford plot results using field mark-recapture (disc tags) data for individuals 70–205 mm
Loesch, 1965	Mobile Bay, Alabama	0.6–1.0	Size frequency from spring and summer field samples; progression of maximum sizes of juveniles 50–135 mm
		2.2	juveniles 15–70 mm
Klima, 1974	Galveston Bay, Texas	1.4–1.8	Extrapolated for juveniles 40–80 mm from Walford plot results determined from field mark-recaptured (stain-injected) subadults (117 mm)
	coastal Louisiana	1.0–1.3	Extrapolated for juveniles 40–80 mm from Walford plot results determined from field mark-recaptured (stain-injected) subadults (120 mm)
Mayer, 1985[1]	Sapelo Island, Georgia	0.9–1.5	Estimated from modal size-frequency data for juveniles 20–120 mm
Knudson et al., 1996	coastal Louisiana	0.3–0.7	Mark-recapture (injected pigments) of juveniles 45–58 mm (initial size) from coastal marsh ponds
This study	Sapelo Island, Georgia	0.6–0.9	Monthly mark-recapture (coded ferromagnetic tags) of juveniles 40–80 mm (initial size) from subtidal creeks

[1] Mean growth rates reported in Table 3 of Mayer (1985) were inconsistent with cohort data in Figure 8 of that thesis; rates reported here were derived directly from the data points shown in Figure 8 of Mayer's thesis.

changes in the average size of shrimp within the nursery over time.

We tested this hypothesis by comparing mean growth rates among months after controlling for initial length as a covariate. For these analyses, the 1998 data from PO and SC were pooled because there was no evidence of a difference in growth rates between these two creeks; the 1999 data from EF and WF were analyzed separately because mean growth rates differed between these two systems. After removing the effect of initial size, there was no significant difference among months in 1998, nor in 1999 at EF, but significant differences in mean growth remained detectable among months at WF (Table 3). The findings from WF also were unusual in that the covariate (initial length) was not a significant factor in the analysis. *Post hoc* multiple comparisons (Bonferroni, experiment-wise $\alpha=0.05$) of mean growth rates among months (without accounting for the covariate) indicated that the specific growth rate in July (0.021) was significantly greater than that in the other months (0.007 to 0.011). This was the
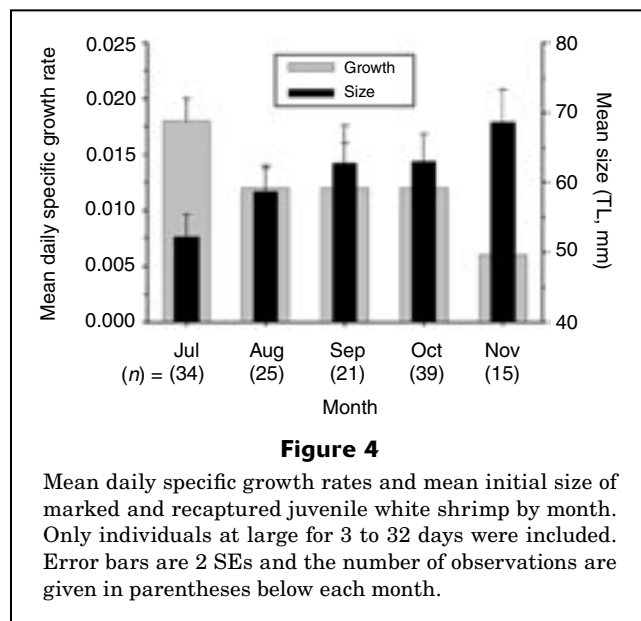
only statistically significant evidence of seasonal variation in growth apparently not associated with shrimp size distributions.

With respect to spatial variation in growth rates of juvenile shrimp, the most notable observation in this study was the relatively low mean growth rate observed at EF compared to the other sites. This difference could have resulted from the larger mean initial size of individuals tagged at EF (61.3 mm) compared with those at WF (56.0) in 1999. However, a similar difference in mean initial sizes of marked shrimp between tidal creek subsystems (SC, 64.2 mm; PO, 59.6 mm) in the previous year did not result in a significant difference in growth rates. When we considered the structural characteristics of each tidal creek at a landscape level, the EF subsystem had the largest tidal drainage area (119.5 ha.) compared to the other sites (58.6 to 104.9 ha.), but proportionally less of that area was intertidal drainage. There was a stronger correlation between mean growth rate (pooled across all individuals within a creek) and the proportion of the drainage area that was

Table 3

Summary of ANOVA results for the effects of month on specific growth rate of *Litopenaeus setiferus* after controlling for the covariate initial length. Only individuals at large between 3 and 32 days were included in the analyses. PO = Post Office Creek; SC = Stacey Creek; EF = East Fork of Duplin River; and WF = West Fork of Duplin River. Prob. = probability.
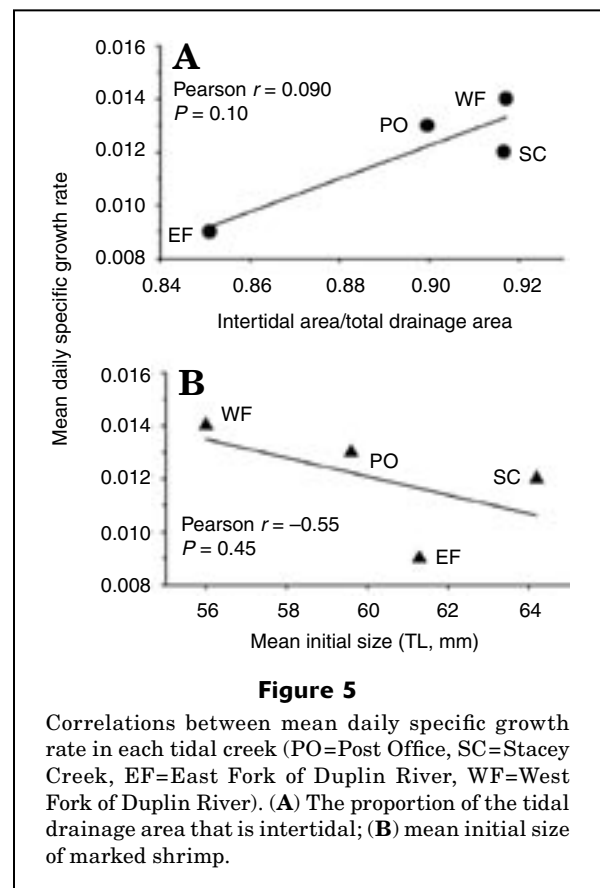
Source	1998 (PO and SC)			EF			WF		
	df	*F*-value	Prob.	df	*F*-value	Prob.	df	*F*-value	Prob.
Covariate (initial size)	1	30.77	<0.01	1	1.42	0.26	1	1.42	0.24
Month	4	1.25	0.30	3	0.74	0.55	4	4.32	<0.01
Error	70			11			36		

Figure 4

Mean daily specific growth rates and mean initial size of marked and recaptured juvenile white shrimp by month. Only individuals at large for 3 to 32 days were included. Error bars are 2 SEs and the number of observations are given in parentheses below each month.

Figure 5

Correlations between mean daily specific growth rate in each tidal creek (PO=Post Office, SC=Stacey Creek, EF=East Fork of Duplin River, WF=West Fork of Duplin River). (**A**) The proportion of the tidal drainage area that is intertidal; (**B**) mean initial size of marked shrimp.

intertidal (Fig. 5A) than there was between growth and mean initial size (Fig. 5B) at the landscape level. There was almost no correlation between proportion of drainage area that was intertidal and initial mean size of marked shrimp (Pearson *r*=−0.18, *P*=1.0).
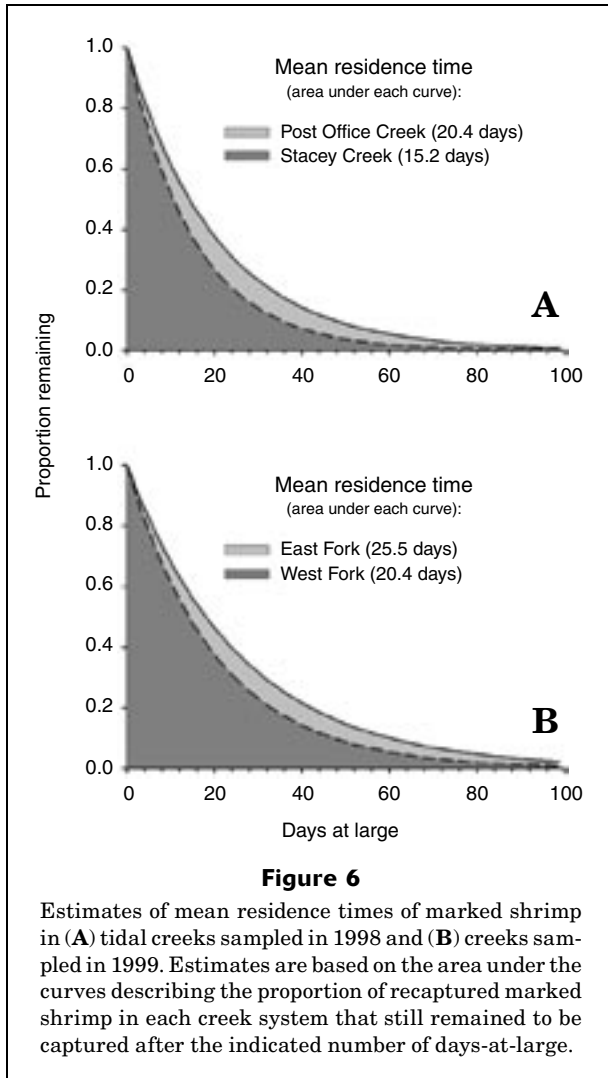
Residence time and movement of marked shrimp

Recaptured shrimp were at large for up to 99 days, but mean residence time for individuals marked in all four tidal creeks was between 15 and 26 days (Fig. 6). Mean residence time was greatest at EF and least at SC. During their time-at-large, net displacement (distance between mark and recapture sites) of the marked individuals ranged from 0 to 3000 m , but averaged 258–373 m in all creeks. There was no evidence of a significant relationship between time-at-large and mean net displacement (linear regression *F*=1.48; df=1,45; *P*=0.23), but movement was slightly related to shrimp size, and larger individuals showed greater displacement (Fig. 7). Variation in residence time among creek 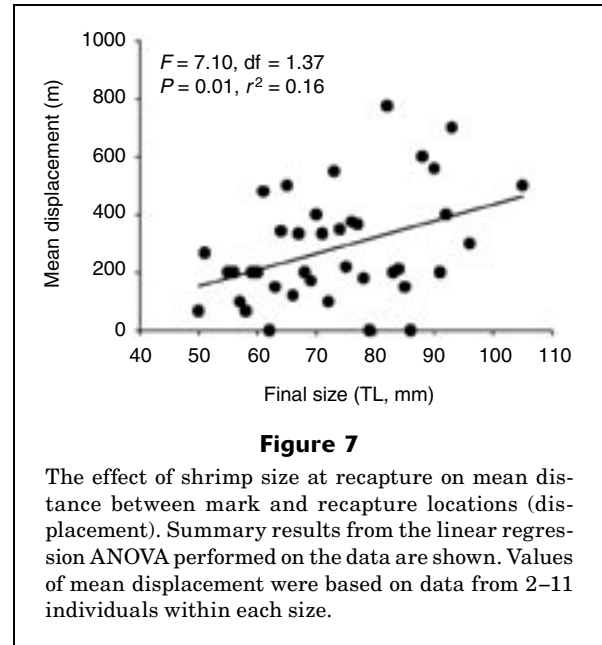subsystems was not significantly correlated with length of the creek mainstem (Pearson *r*=−0.32, *P*=0.684), but there was evidence of positive associations with the amount of intertidal (Pearson *r*=0.87, *P*=0.133) and subtidal (Pearson *r*=0.95, *P*=0.054) drainage areas within each subsystem.

Most shrimp (93%) were recaptured in the same tidal creek subsystem in which they were originally marked, but there was some evidence of movement among creeks and between the subtidal and intertidal components of the shrimp nursery within creeks. The marked individual at large for the longest time (99 days) was recaptured at the same station where it was originally marked (net

Figure 6

Estimates of mean residence times of marked shrimp in (**A**) tidal creeks sampled in 1998 and (**B**) creeks sampled in 1999. Estimates are based on the area under the curves describing the proportion of recaptured marked shrimp in each creek system that still remained to be captured after the indicated number of days-at-large.

Figure 7

The effect of shrimp size at recapture on mean distance between mark and recapture locations (displacement). Summary results from the linear regression ANOVA performed on the data are shown. Values of mean displacement were based on data from 2–11 individuals within each size.

the interior of the intertidal marsh drained by that tidal creek subsystem. The flume weir samples were part of an ongoing study (Kneib, unpubl. data) to determine nekton use of the intertidal marsh surface (see Kneib, 1991, 1997; Kneib and Wagner, 1994).

Discussion

Growth

Mean growth rates of juvenile white shrimp measured in this study (0.6–0.9 mm/d) were near the lower end of the range of estimates previously reported for juvenile white shrimp along the U.S. Atlantic and Gulf coasts (Table 2). The principal difference between the present and previous studies is that the values presented in this study were based on direct measurements of free-ranging individual juvenile shrimp rather than on extrapolations from batch mark-recaptures of larger individuals or changes in modal size frequencies. The open nature of estuarine ecosystems, prolonged seasonal recruitment to the nursery, and ontogenetic differences in mortality and movement all may confound the interpretation of size-frequency data (Haywood and Staples, 1993). Given that our growth values were based on actual changes in the size of individuals rather than estimated from the apparent growth trajectories of cohorts, we are confident that the mean growth rates reported here accurately reflect those of free-ranging juvenile white shrimp (40–80 mm TL) in the polyhaline portion of the tidal marsh nursery habitat of coastal Georgia.

Temporal differences in observed growth rates in this study may have resulted from either variation in environmental conditions or spatial variation in habitat quality.

displacement=0 m). In contrast, one shrimp marked at PO demonstrated a net displacement of 3 km when it was recaptured at SC after 61 days at large. Nine shrimp (at large from 18 to 49 days) marked at WF were recaptured at EF, and two (at large 19 and 45 days) tagged at EF were recaptured at WF. It was not possible to determine precisely when these shrimp moved out of the creek in which they were tagged or how long they were present in the creek subsystem where they were ultimately recaptured. For the growth rate analyses, it was assumed that most growth occurred while the shrimp were in the creek and where individuals were marked. The mean (±SD) final size (mm, TL) of individuals that moved between creek subsystems was significantly (separate variance estimate t=2.62, df=16.9, P=0.018) larger (78.9 ±7.4) than that of the group tagged and recaptured in the same subsystem (71.3 ±13.1); the initial mean size of the two groups was nearly identical (57.5 ±10.8 and 57.7 ±10.4, respectively). Two shrimp (at large 7 and 17 days) tagged at EF were recaptured at high tide in flume weirs located 25 m into

Penaeids are most abundant in tidal marsh nurseries when physical conditions (eg., temperature and salinity) appear optimal for their growth and survival (Zein-Eldin and Renaud, 1986), but environmental variability is characteristic of most estuaries and therefore is an obvious starting point for explaining observed differences in shrimp growth among sites or times. Salinity was the only environmental factor we measured that showed a significant difference between years but could not be associated with any interannual difference in mean growth rates.

Temperature may affect the growth and estuarine distribution of juvenile penaeids more than salinity (Vetter, 1983), and interactions between salinity and temperature may have even greater effects than variation in either factor alone (Zein-Eldin and Renaud, 1986). Mean temperatures throughout our study period (with the exception of November) in both years were largely within the optimum range for growth of white shrimp which, in the laboratory, was reported to be between 25° and 32.5°C (Zein-Eldin and Griffith, 1969). Higher temperatures generally contribute to faster growth in young penaeids (Perez-Farfante, 1969; Muncy, 1984), and therefore it seems reasonable to expect seasonal variation in temperature to be reflected in growth rates. However, this interpretation is confounded by the fact that growth rates also are size dependent (Fig. 3, Table 3) and that increases in mean size of juvenile white shrimp (Fig. 4) occurred while temperature in the nursery habitat was decreasing from the July maxima. It seems likely that growth rates of juvenile white shrimp were robust over the relatively narrow range of seasonal variation in temperature and salinity observed in the present study.

Alternatively, differences in growth between certain sites could be the result of spatial variation in habitat quality. This variation need not be a function of water quality, but rather a function of some structural aspect of the nursery habitat. There was a strong correlation between mean growth rates and the proportion of tidal creek drainage area that was intertidal. Only four creek subsystems were examined in ours study, and we recognize that this is an insufficient sample size to justify anything more than a suggestive hypothesis. However, evidence of relationships between the amount of intertidal habitat and penaeid shrimp production (Turner, 1977, 1992), as well as the amount of intertidal creek edge and juvenile shrimp abundance in adjacent subtidal creeks (Webb and Kneib, 2002), supports the contention that intertidal accessibility is an important component of nursery habitat quality for juvenile white shrimp. We propose that the ratio between intertidal and shallow subtidal habitat may be a key feature of white shrimp nursery habitat quality. When tidally inundated, the intertidal portion of marsh creek drainage systems is used extensively by juvenile white shrimp (Kneib, 1995, 2000), most likely as a rich foraging area (Kneib, 1997), and the shallow subtidal portion functions as a low tide refuge and corridor for the seasonal migration of postlarvae and subadults between the open estuary and coastal ocean spawning grounds and the juvenile nursery (Kneib, 1997, 2000).

Movement and residence time

Understanding the causes of broad-scale migration of penaeids has obvious implications for predicting commercial catches and therefore these causes have been the focus of research on shrimp movements for decades (Perez-Farfante, 1969; Muncy, 1984). However, finer-scale movements, which may affect growth and survival of juvenile shrimp within the estuary, are not as well known. Emigration of white shrimp from estuaries is determined by size, maturity, and environmental conditions (Muncy, 1984), and size plays a principal role (Dall et al., 1990). In the South Atlantic Bight, larger white shrimp (>100 mm TL) begin emigrating from the nursery to commercial fishing areas in the nearshore coastal ocean in August (Lindner and Anderson 1956, Shipman, 1983). We collected few shrimp >100 mm in the tidal marsh creeks, which is consistent with previous observations of ontogenetic migration to deeper waters. According to growth rates measured in this study, a shrimp of 40 mm TL would become large enough to emigrate from the estuary to the coastal ocean in 2–3 months (i.e., a shrimp tagged at 40 mm TL could reach 85–108 mm TL in 2.5 months).

The presence of high densities of small juvenile white shrimp in the upper reaches of Georgia's tidal marsh creeks (Harris, 1974; Hackney and Burbanck, 1976; Webb and Kneib, 2002) has supported the contention advanced by Weinstein (1979) that these areas are primary nurseries for juvenile fish and shellfish. However, it has been unclear whether these aggregations represent stable resident populations or are composed of tidal transients that constantly migrate among creek subsystems within the broader estuarine nursery. Young shrimp are known to move short distances to avoid unfavorable physiochemical conditions (Hackney and Burbanck, 1976; Dall et al., 1990) and routinely make tidally mediated excursions between subtidal and intertidal portions of the nursery to forage or escape predators (Kneib, 1995, 1997). Our findings showed that juvenile white shrimp also tended to remain resident in the upper reaches of tidal creeks where they were originally tagged until attaining a size (80–100 mm) at which they normally begin to emigrate from the nursery (Perez-Farfante, 1969).

Although there was some movement between tidal creek subsystems, the high level of site fidelity demonstrated by juvenile white shrimp was remarkable given the openness and degree of tidal flux in the Duplin River system (mean tide range=2.1 m). Data from the chemical analysis of shrimp tissue composition also suggest limited movements of juvenile penaeids within estuarine nurseries. Using the stable isotopes of carbon and nitrogen from muscle tissues of pink shrimp (*Farfantepenaeus duorarum*), Fry et al. (1999) traced shrimp movements within and between seagrass and mangrove habitats of southwestern Florida. They found distinct differences among individuals sampled from similar inshore habitat types separated by small (3–5 km) open water distances, indicating that individuals remained "resident" in specific portions of the estuary at least for several weeks. Noting a similar study in coastal Louisiana, Fry et al. (2003) suggested that

small juvenile brown shrimp (*Farfantepenaeus aztecus*) are more transient in suboptimal habitat (open bays and deeper channels) and exhibit less movement upon reaching optimal habitat (ponds and shallow channels).

The only study with which we can directly compare our findings on residence time and movements was conducted by Knudsen et al. (1996) near Calcasieu Lake, Louisiana, where tidal flux was considerably lower (mean tide range <0.6 m) and the system (marsh impoundments) was less open than that in the present study. Knudsen et al. (1996) marked batches of juvenile white shrimp (45–69 mm TL) by injection of colored pigments and released them into a pair of 35-ha. impoundments, each connected to the open estuary through a narrow channel that was fitted with screen deflectors and traps designed to collect all emigrating nekton. The mean time from release to emigration of juvenile white shrimp ranged from 30.2 to 59.9 days. Our estimates of tidal creek residence time for juvenile shrimp in Georgia tidal creeks was about half that reported for impoundments in Louisiana and may be explained by the differences in tidal flux and openness between the two systems. However, the values we observed were likely underestimates of the actual residence period of survivors within the creeks because they included losses due to mortality as well as emigration.

It seems clear from the studies conducted thus far that juvenile penaeids, once having entered the estuarine nursery, tend to remain within a limited spatial range where they are exposed to local conditions for several weeks. Our findings also provide evidence of spatial variation for both residence time and growth rate of juvenile white shrimp that is possibly attributable to structural differences in tidal creek subsystems. We suggest there may be an optimal value for the ratio of subtidal to intertidal drainage area within marsh creek systems that can achieve a favorable balance between suitable habitat (space) at low tide, which tends to enhance residence time and density of juvenile shrimp, while providing sufficient intertidal foraging habitat and predator refugia at high tide to promote high rates of juvenile shrimp growth and survival. Spatially explicit information on growth rates and the extent to which individual shrimp move within their estuarine nurseries are necessary initial steps toward meeting the challenge of maintaining quality nursery habitat for a sustainable shrimp fishery and satisfying other demands associated with human development in and around estuarine watersheds.

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