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Tidal Migrations of Nekton in Salt Marsh Intertidal Creeks

KURT BRETSCH[1,]* and DENNIS M. ALLEN[1]

[1] *Belle W. Baruch Institute for Marine and Coastal Sciences, University of South Carolina, P. O. Box 1630, Georgetown, South Carolina 29442*

ABSTRACT: Salt marsh intertidal creeks are important habitats for dozens of species of nekton, but few studies have attempted to quantify patterns of tidal movement. We used the sweep flume, a new sampling device, to investigate relationships between depth and movements of nekton inside the mouths of intertidal creeks. Sweep flumes located in three creek beds were used to collect nekton at 10 cm increments (10–100 cm of water depth) during flood and ebb tides in the North Inlet, South Carolina, salt marsh. Of the 37 taxa collected, 13 comprised >99.5% of the total catch and were the focus of the analysis. A nonlinear mixed modeling procedure was used to determine the depth at which each major taxon reached peak abundance during flood tides. With high degrees of spatial and temporal consistency, resident taxa entered early on the rising tide and transient taxa entered during mid to late tide. Depths of peak migrations varied among taxa and were consistent between creeks, days (within months), and years. As summer progressed, depths of peak migration increased for young-of-the-year *Leiostomus xanthurus*, *Lagodon rhomboides*, *Mugil curema*, *Eucinostomus argenteus*, and *Litopenaeus setiferus* as their median sizes increased. Within tides, depths of migration increased as a function of size for *L. xanthurus* and *M. curema*. Comparisons between flood and ebb tides indicated that most taxa exited the creeks at approximately the same depths at which they entered. Relationships between major taxa pairs suggested that biotic interactions may have contributed to the structure of the migrations observed in this study. Our results are the first to demonstrate quantitatively that the migrations of nektonic taxa into intertidal creeks are structured and related to depth.

Introduction

Shallow, structurally complex, and highly productive salt marshes provide commercially and ecologically important nektonic species with an abundance of food and protection from predators (Weinstein 1979; Miller and Dunn 1980; Hettler 1989; Catrijsse et al. 1994; Kneib and Wagner 1994). Access to temporarily flooded intertidal salt marsh habitats is important for small nektonic species that remain in the marsh throughout their entire life cycle (resident species), as well as for early life stages of fishes and crustaceans that occupy salt marshes for only part of their lives (transient species). Tidal migratory nekton use flooding tides to move from permanently submerged areas into intertidal areas. In mesotidal and macrotidal systems, intertidal creeks provide major routes for tidal migratory nekton to move from subtidal channels into salt marshes. Intertidal creeks contain mud flats, sand and shelly bottoms, oyster reefs, and other features that are inundated for longer periods than the marsh surface. Some nekton may use intertidal creeks as flood tide destinations or as corridors for movement to the vegetated marsh (Rozas et al. 1988; Hettler 1989). Tidal migrations are thought to support survival and growth functions, such as feeding, reproduction, and predator avoidance (Gibson 2003), and ecosystem functions, such as nutrient (Haertel-Borer et al. 2004) and trophic (Kneib 2000; Deegan et al. 2000) transfers.

High densities and dozens of nektonic species have been reported for intertidal creeks in many temperate marshes (Cain and Dean 1976; Weinstein et al. 1980; Rogers et al. 1984; Rozas et al. 1988; Sogard and Able 1991). Knowledge regarding the use of intertidal creeks by nekton has been based almost entirely on integrative collections of animals retreating toward subtidal refuges with the ebbing tide. Passive collection devices, such as block nets, provide information about the general occupation of a creek at high tide but not the timing and structure of movements of nekton within the creek. Our objective in the present study was to describe species and life stage specific movements of tidal migrants inside the mouths of intertidal creeks. Flume studies on the flooded marsh surface have indicated that movements of species and life stages occur at different times as a function of depth and other factors (Kneib and Wagner 1994; Peterson and Turner 1994), but we are not aware of any previous efforts to characterize nekton migrations into intertidal creeks. In this study we used a sweep flume, a new sampling device, to address the general hypotheses that depths of migration vary among taxa and size classes within taxa and patterns of movement are similar among intertidal creeks, months, and years.

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* Corresponding author; tele: 843/546-6219 ext. 223; fax: 843/546-1632; e-mail: kbretsch@belle.baruch.sc.edu

Materials and Methods

STUDY SITE AND SAMPLING FREQUENCY

The study was conducted at the North Inlet Estuary (approximately 33°19′N, 79°09′W), a relatively undisturbed 28 km^2 salt marsh-dominated system within the North Inlet–Winyah Bay National Estuarine Research Reserve located about 6 km east of Georgetown, South Carolina. At mean low tide, the estuary consists of exposed *Spartina alterniflora* (71%), open water (including subtidal creeks; 16%), and unvegetated intertidal habitats including mudflats, oyster reefs, and intertidal creeks (13%; Potthoff and Allen 2003). Based on results from Novakowski et al. (2004), we estimate there are >1,000 intertidal creeks within the system. The intertidal zone is flooded by semidiurnal tides, the mean tidal range is 1.4 m, and throughout most of the year, the major waterways have salinities of 30 to 35 psu (Ogburn et al. 1988). North Inlet is occupied by more than 160 ecologically and economically important species of fishes, shrimps, and crabs, most of which are represented by early stages in their life cycle (Ogburn et al. 1988; Allen et al. 1992).

We collected nekton at different stages of the tide using a new sampling device, the sweep flume. One flume was constructed just inside the mouth of each of three intertidal creeks. Each sweep flume was located in the center of an intertidal creek channel approximately 40 m from the creek's confluence with a larger, permanently flooded (subtidal) channel, and at a location within each creek where the banks narrowed to a width comparable to that of the flume. Elevations of the creek beds at the flume installations were comparable so that the same depths occurred at all three sites at the same stage of the tide. The three creeks were located within several hundred meters of each other, and each was 6–8 m wide at the mouth and 200–300 m long. The substratum graded from a firm mix of sand, shell rubble, and mud near the mouth to soft mud in the upper reaches.

SWEEP FLUME STRUCTURE

The fixed infrastructure of each sweep flume consisted of two permanent, black plastic mesh walls parallel to the main axis of the creek and 2 m apart (Fig. 1). Each flume wall was 15 m long, 1.5 m high, and supported by vertical posts (5.1 cm × 5.1 cm × 1.5 m) driven into the substrate (to 0.5 m) approximately every 1.2 m. The mesh was stapled to the inside of all posts, and the bottom edges of the walls were buried (15 cm deep) to prevent animals from entering or exiting the sample area from the sides of the flumes. Larger posts (10.2 cm × 10.2 cm × 1.5 m) at the ends of the walls added stability and allowed nets to be secured to the ends of the flume during sampling. At the front of the flume (the end first encountered by nekton moving with the tide), wing walls (plastic mesh panels) extended from the end posts to the creek banks.

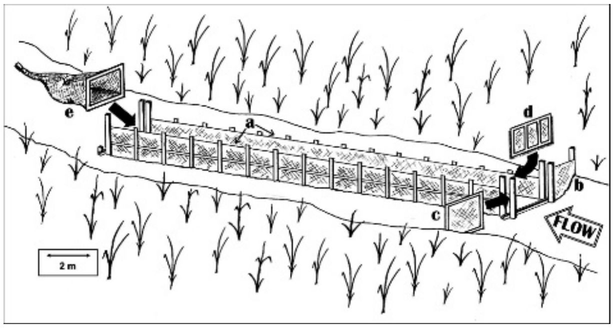

Fig. 1. Diagram showing placement of a sweep flume in the center of a salt marsh intertidal creek. Components are labeled as follows: fixed walls (a), wing wall (b), end panel (c), one of two sweep panels (d), and collection net (e). Block arrows indicate direction of movement for moveable components as well as the direction of water flow.

The movable components of the sweep flume consisted of an end panel constructed of plastic netting stretched over a 2.0 × 1.5 m PVC rectangular frame, a funnel shaped nylon collection net (1.2 × 2 m mouth, 3 m long) mounted on a 2.0 × 1.5 m PVC rectangular frame, and two sweep panels constructed of PVC frames (1.5 × 1.5 m) covered with plastic netting. Flexible plastic broom bristles (c. 10 cm long) secured to the bottom and sides of the sweep panels (8–12 bristles cm^{-1}) ensured a flexible seal between the sweep frames and both the substrate and the flume walls, preventing nekton from swimming around the sweep or through gaps created by irregularities in the creek bottom or flume walls. The mesh size in all walls, nets, and panels was 3 mm.

SAMPLING PROCEDURE

To determine differences in migration patterns between creeks, sampling occurred during daytime flooding tide on each of three consecutive days in July 2001. All three creeks were sampled simultaneously. We also sampled for 3 d each in May, July, and September 2002 to determine if migration patterns changed within season. To avoid potential oversampling effects within creeks during the multi-month sampling effort in 2002, a different creek (determined by lottery) was sampled on each of three consecutive days within each month.

Collections were made at each water depth by first securing the collection net at the back end of the flume and then securing the end panel at the front, effectively sealing the sampling area. Immediately before securing the end panel, a sweep panel was placed inside the front of the flume, perpendicular to the creek bottom and in contact with the substrate and walls. Two people then walked the sweep the length of the flume, pushing organisms into the collection net. After the first sweep panel was secured at the mouth of the collection net, the procedure was repeated with the second sweep. Once the second sweep reached the collection net, the first sweep was lifted out and replaced with the second sweep. The sample was then removed from the collection net and the two end nets and sweeps were removed, reestablishing the unobstructed passage of water and nekton through the flume until the next sample was taken (10 min later). In this study, a sample was collected every 10 cm starting at 10 cm and ending at 100 cm when the water level reached the lower edge of the vegetated creek bank. About 20 min elapsed between each 10 cm water depth. After each 10 cm collection, temperature, salinity, and surface current velocity within the flume were determined.

Sample Processing and Data Analysis

Within each sample, all individuals were identified (lowest possible taxon) and measured (mm: standard length [SL] for fishes, carapace length [CL] for shrimps). Wet weight biomass (g) was also determined for each taxon.

For many taxa, the total number and total biomass of individuals migrating during a tidal event varied with creek and month. To allow comparisons within a single taxon between different creeks and months, we determined the total abundance (sum of abundances from 10 to 100 cm) of the target taxon migrating during a tidal event (about 3 h) and calculated the proportion of the total abundance collected in each 10 cm sample. Monthly mean percentages and error terms (±1 standard error) at each depth were derived from all dates and creeks sampled within that month ($n = 3$ in 2002, $n = 9$ in 2001).

The depth of peak migration (an estimate of the depth at which the highest proportion of individuals migrated) was determined for each taxon during each month of occurrence. A nonlinear mixed procedure in SAS (Wolfinger 1999) was used to generate a monthly value and associated confidence interval (based on $\alpha = 0.05$) for the depth of peak migration by determining the depth at which the maximum slope occurred on the best-fit curve of the cumulative mean proportional abundance of all three creeks or days versus depth. Within each month, each creek or day was treated as a replicate ($n = 9$ in July 2001 and $n = 3$ in May, July, and September 2002). If <5 individuals of a taxon were collected from a creek, the data were not included in the analysis.

To explore how changing animal size might have affected migration patterns, median size was compared to the depth of peak migration for each taxon during May, July, and September 2002. In some months, multiple size classes of *Fundulus heteroclitus*, *Mugil cephalus*, *Mugil curema*, and *Eucinostomus argenteus* were present, and depth of peak migration was determined for each size class.

To compare patterns of immigration and emigration in the intertidal creeks, samples were collected during consecutive daytime flood and ebb tides over 3 d in July 2002. During ebb tide collections, the end panel and the collection net were reversed. Because a tear in the flume wall in one creek precluded quantitative sample comparisons among all three creeks, we were only able to describe the general emigration pattern using samples from two creeks.

We examined co-occurrence between pairs of the major (13 most abundant) taxa to explore the possibility that interactions between taxa might have contributed to the observed migration patterns. Because the abundance data did not meet the assumptions of a normal distribution, Spearman rank correlation analysis ($\alpha = 0.05$) was used to determine if the rank abundance of one taxon was linearly related to the rank abundance of another taxon. The magnitude and direction of association for pairs of taxa based on presence-absence data were explored with 2×2 contingency tables and Fisher's exact tests (Ogburn-Matthews and Allen 1993). In the association analysis, a taxon was considered present during a tidal stage only if ≥ 5 individuals were collected. Because sizes of individuals of many taxa changed during the season, correlation and association analyses were conducted for pairs of taxa in each sampling month.

Sweep Flume Recovery Efficiency

To determine the recovery efficiency of the sweep flume, we used a mark-recapture technique (Kneib 1991). *F. heteroclitus*, *Lagodon rhomboides*, *Leiostomus xanthurus*, *Mugil* spp., *Litopenaeus setiferus*, and *Palaemonetes* spp. were collected from adjacent subtidal areas prior to the tests and held in large, aerated, plastic tubs at the site. Fish ≥ 35 mm SL were marked by clipping a portion of the dorsal lobe of the caudal fin. *Palaemonetes* spp. were ≥ 10 mm CL, *L. setiferus* were ≥ 20 mm CL, and both were marked by clipping the tip of a uropod. Animals were marked immediately before release into the flume. Due to time and handling constraints, neither *Palaemonetes* spp. nor *Mugil* spp. were identified to the species level. We used 10 individuals of each taxon at each sampling depth

TABLE 1. Total abundance and total biomass (g) of the 13 most abundant species which composed >99.5% of the total catch of nekton collected during flood tides in July 2001 and May, July (both flood and ebb tide samples are included), and September 2002. Rankings are based on the total number of individuals collected for each species. Status indicates if species are resident (R) or transient (T) within North Inlet, SC.

Rank	Scientific Name	Common Name	Status	Total Abundance	% of Catch	Total Biomass
1	*Palaemonetes pugio*	daggerblade grass shrimp	R	26,643	29.8	6,918
2	*Fundulus heteroclitus*	mummichog	R	16,220	18.1	21,272
3	*Anchoa mitchilli*	bay anchovy	R	14,470	16.2	8,071
4	*Leiostomus xanthurus*	spot	T	10,953	12.2	22,037
5	*Mugil curema*	white mullet	T	7,761	8.7	26,756
6	*Menidia menidia*	Atlantic silverside	R	3,600	4.0	3,436
7	*Anchoa hepsetus*	striped anchovy	T	2,512	2.8	2,000
8	*Mugil cephalus*	striped mullet	R	2,391	2.7	12,451
9	*Lagodon rhomboides*	pinfish	T	2,184	2.4	15,583
10	*Fundulus majalis*	striped killifish	R	798	0.9	716
11	*Eucinostomus argenteus*	spotfin mojarra	T	753	0.8	2,712
12	*Palaemonetes vulgaris*	marsh grass shrimp	R	702	0.8	130
13	*Litopenaeus setiferus*	white shrimp	T	229	0.3	815
		Other[a]		316	0.3	8,296
		Total		89,532		131,193

[a] *Farfantepenaeus duorarum, Callinectes sapidus, Farfantepenaeus aztecus, Orthopristis chrysoptera, Gobiosoma bosc, Opsanus tau, Symphurus* sp., *Cyprinodon variegatus, Dorosoma petenense, Paralichthys lethostigma, Lolliguncula brevis, Stephanolepis hispidus, Chasmodes bosquianus, Sphoeroides maculatus, Brevoortia tyrannus, Strongylura marina, Chloroscombrus chrysurus, Ctenogobius boleosoma, Chilomycterus schoepfi, Alpheus* sp., *Hypsoblennius hentz, Syngnathus fuscus, Pomatomus saltatrix, Scomberomorus maculatus* (in order of decreasing abundance).

tested. Tests were conducted at low depths (10, 20, 30, and 40 cm) and high depths (60, 70, 80, and 90 cm) to measure whether differences in water volume and current speed affected recovery efficiencies. At each target depth, marked animals were released in the front half of the closed flume. After 1 min, the flume was swept twice according to standard sampling protocol. Once samples were secured and the flume was reopened, a third sweep was conducted to flush out any marked animals that the first two sweeps may have missed. The procedure was repeated using a new set of animals at each depth interval. To determine if recovery efficiencies for each taxon differed between low and high depths, the mean number recovered at pooled low depths and pooled high depths was compared using Wilcoxon Mann-Whitney U tests ($\alpha = 0.05$). The null hypothesis was that for each taxon there was no significant difference between mean percentage recovered at low depth and high depth.

Results

PHYSICAL VARIABLES

Water temperatures were lowest in May (21–22°C) and highest in July (28–30°C). Variations among consecutive days within creeks during July 2001 were 1–3°C, but differences among creeks on the same day were negligible. Within creeks, water temperature generally varied by <2°C during the flooding cycle. Salinity was typically greater than 30 psu (low of 28 psu in September) and varied by ≤3 psu during the flooding period. During all months, flood tide surface current velocity in all three creeks was generally stable at 15 cm s^{-1} until water depth reached 50 cm. Typically, flood tide surface current velocity increased to 40 cm s^{-1} by 80–90 cm depth, and slowed to 30 cm s^{-1} between 90 and 100 cm. Ebb surface current velocities were 20–40 cm s^{-1} from 100 to 80 cm depth, 40 cm s^{-1} from 80 to 60 cm depth, and 15 cm s^{-1} from 40 to 10 cm depth. Depth-related changes in surface current velocities were similar in all three creeks.

ASSEMBLAGE LEVEL ANALYSIS

A total of 89,532 individuals weighing >131 kg and comprising at least 37 species of nekton were collected in 180 flood and 20 ebb samples during July 2001 and May, July, and September 2002. The 13 most abundant taxa (Table 1) comprised >99.5% of the total catch and dominated the collections in all creeks during the 2 yr of sampling. Total abundance and total biomass of each major taxon varied between month and year (Table 2). All 13 were present in July and September, but only 10 were present in May. Most resident (e.g., *Palaemonetes pugio, F. heteroclitus, Fundulus majalis, Menidia menidia*) and local (resident during most of the year, but shifted to nearby coastal waters during colder months; e.g., *Anchoa mitchilli*) species were at peak abundances in September and dominated the assemblage at that time. Most young-of-the-year transients (e.g., *L. xanthurus, L. rhomboides, M. curema*) and *M. cephalus* (a resident species) were at highest abundances in May and at lowest levels in September; they were the numerically dominant taxa early in the season.

P. pugio was the most abundant species and occurred on every date and in 68% of all samples.

TABLE 2. Total abundance, total biomass (g; includes all size classes), and median length (mm) of the 13 major taxa collected each month. July 2002 values are flood samples only. Dashes indicate that data were not available.

	July 01			May 02			July 02			September 02		
Species	Abundance	Biomass	Length	Abundance	Biomass	Length	Abundance	Biomass	Length	Abundance	Biomass	Length
P. pugio	17,605	4,027	10	861	182	10	395	75	10	12,537	2,223	9
F. heteroclitus $>$ 28 mm	1,390	5,635	46	1,364	3,881	44	858	2,710	44	1,666	8,774	38
F. heteroclitus $\leq$ 28 mm	2,482	—	28	0	0	—	283	—	27	7,187	—	28
A. mitchilli	2,207	984	32	2,526	2,198	41	11	5	31	9,737	3,271	29
L. xanthurus	3,836	11,332	49	3,421	3,478	34	726	1,927	43	932	5,008	55
M. curema $>$ 50 mm	887	7,575	74	1,980	871	26	1,123	5,323	56	1,139	9,439	70
M. curema $\leq$ 50 mm	0	0	—	0	0	—	372	—	35	0	0	—
M. menidia	415	364	40	21	43	62	595	472	39	2,664	2,535	41
A. hepsetus	868	1,269	40	0	0	—	68	43	35	1,574	671	49
M. cephalus $>$ 100 mm	9	5,305	141	7	2,604	192	6	2,327	106	2	2,004	103
M. cephalus $\leq$ 100 mm	912	—	60	762	—	40	436	—	54	1,138	—	70
L. rhomboides	743	7,109	64	473	1,511	40	434	3,392	59	132	2,735	77
F. majalis	209	167	34	15	80	44	17	34	30	570	402	28
E. argenteus (one size class)	27	117	55	0	0	—	0	0	—	0	0	—
E. argenteus $>$ 36 mm (July 02), $>$ 50 (Sept 02)	0	0	—	0	0	—	351	1,200	49	100	1,016	61
E. argenteus $\leq$ 36 mm (July 02), $\leq$ 50 (Sept 02)	0	0	—	0	0	—	197	—	22	98	—	38
P. vulgaris	18	14	10	179	48	10	74	11	9	476	45	9
L. setiferus	16	38	24	0	0	—	70	110	21	142	477	28

F. heteroclitus was the most abundant fish, occurring in 77% of all samples. *F. heteroclitus* was more abundant than any other fish species in July 2001 and September 2002, second highest in July 2002, and fourth highest (after the very abundant small, young-of-the-year taxa) in May 2002 (Table 2). *F. heteroclitus* contributed the highest percentage to the total biomass in May 2002, and was among the top 4 in all other months (Table 2). The next 7 most abundant species were mostly young-of-the-year transient fish species that typically reached peak abundances in spring or summer (Table 1). The economically important macroinvertebrates *L. setiferus*, *Farfantepenaeus duorarum*, and *Callinectes sapidus* ranked 13–15 in abundance.

Almost all of the fishes and crustaceans were $<$100 mm in length, but some large mullets ($>$150 mm; $n = 21$), flounders ($>$150 mm; $n = 4$), and rays (to 15 kg; $n = 3$) were captured. The median sizes of most young-of-the-year transient species increased with month during 2002, while the median sizes of the resident species remained stable (Table 2).

NEKTON VARIABILITY BETWEEN CREEKS

The proportion that each species contributed to the total abundance and total biomass of the migrating assemblage varied between creeks and months, but within each creek, the assemblage composition was similar over the 3 d of sampling in July 2001. *L. xanthurus* and *F. heteroclitus* had highest abundances in creek 3 during all sampling months (often 2 orders of magnitude higher than in creeks 1 or 2), but other taxa were not consistently more abundant in any creek.

Within-taxon comparisons of median lengths (mm) in July 2001 using Mann-Whitney U tests indicated similarity among creeks for *Palaemonetes* spp., *Fundulus* spp., *L. xanthurus*, *M. cephalus*, and *M. menidia*. Median length of *L. rhomboides* was larger in creek 2 than in creeks 1 ($U = 29{,}385$, $p < 0.0001$) and 3 ($U = 31{,}151$, $p < 0.0001$). Median length of *M. curema* was larger in creek 1 than in creeks 2 ($U = 79{,}306$, $p < 0.0001$) and 3 ($U = 52{,}037$, $p < 0.0001$). *Anchoa hepsetus* was larger in creek 3 than in creeks 1 ($U = 83{,}343$, $p < 0.0001$) and 2 ($U = 23{,}488$, $p < 0.0001$) and larger in creek 2 than creek 1 ($U = 35{,}597$, $p = 0.0004$). *A. mitchilli* was smaller in creek 2 than in creeks 1 ($U = 21{,}864$, $p = 0.0019$) and 3 ($U = 493{,}778$, $p < 0.0001$). Although statistically significant differences in median size were observed for *L. rhomboides*, *M. curema*, and both *Anchoa* spp. between creeks, the range in median lengths within each taxon was small (typically 3 mm).

DEPTHS OF MIGRATION

Depths of peak migration were determined for each of the major taxa (and size classes within taxa) migrating into flooding intertidal creeks during most months. Both the general tidal migration pattern and the depth of peak migration were

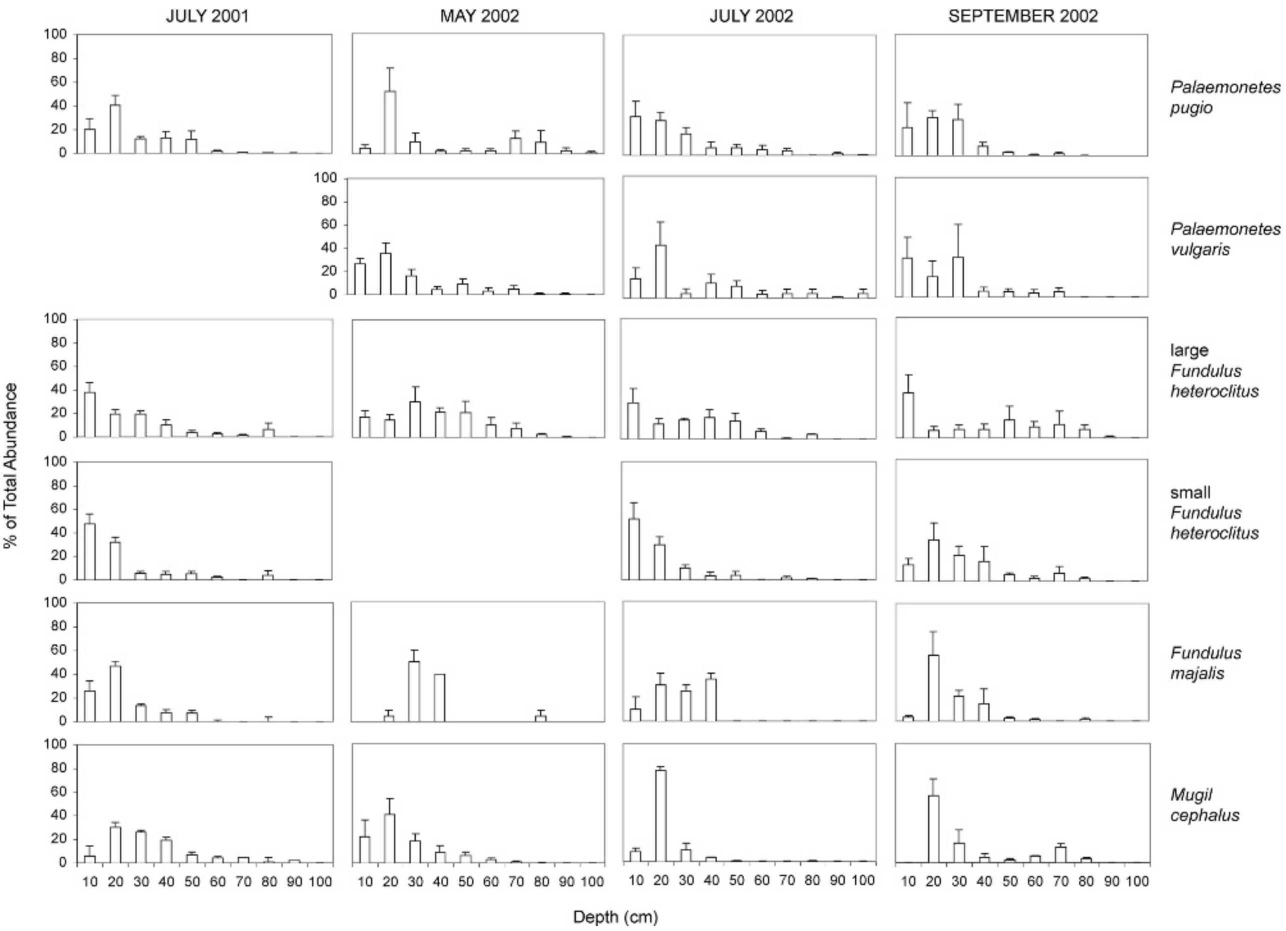

Fig. 2. Monthly variation in the flood migration patterns of resident taxa. For each taxon, bars indicate the mean proportion of the total catch entering the creeks (n = 3 tides in 2002 and 9 in 2001). Error bars are 1 standard error.

consistent between months for most major taxa. With the exception of *M. menidia*, all resident taxa entered the creeks early in the tide during all months; >90% of the total abundance entered when the water depth was ≤50 cm and peak depths of migration occurred in <40 cm water depth (Figs. 2 and 3). Transient taxa typically entered throughout the tide each month (Fig. 4), with depths of peak migration occurring between mid (40–60 cm water depth) and late tide (Fig. 3). Exceptions among transients to the mid-late tidal migration pattern included *M. curema*, which displayed a depth of peak migration during the first half of the tide in May 2002 and just before mid tide in July 2001, and *L. setiferus*, which entered early in July 2002 (depth of peak migration = 17–26; Figs. 3 and 4). The resident *M. menidia* displayed a migration pattern similar to that of the transient taxa, with depths of peak migration consistently occurring between 50 and 80 cm water depth (Figs. 3 and 4). Although the migration pattern of *A. mitchilli* (the only local species among the major taxa) was also similar to that of the transients, we were unable to determine a depth of peak migration for *A. mitchilli* during September 2002, likely due to the high variability associated with the proportions present at 30 and 80 cm water depth (Fig. 4).

For most taxa, the depths at which the highest proportions of individuals entered the creeks during flood tide mirrored the depths at which they exited during ebb tide (Fig. 5). *P. pugio* and *F. heteroclitus* (large and small sizes) entered the creeks early in the flood tide and exited late in the ebb tide. Although *L. setiferus* also entered early in the tide, the largest proportion exited between 70 and 50 cm water depth. *L. xanthurus, M. curema,* and *M. menidia* entered the creeks around mid tide. While *M. menidia* exited around mid tide, *L. xanthurus* and *M. curema* exited between mid and late ebb tide. Both *L. rhomboides* and *A. hepsetus* entered the creeks from mid to late flood tide, but nearly all of them had exited the creeks by 50 cm during the ebb tide. *E. argenteus* entered around

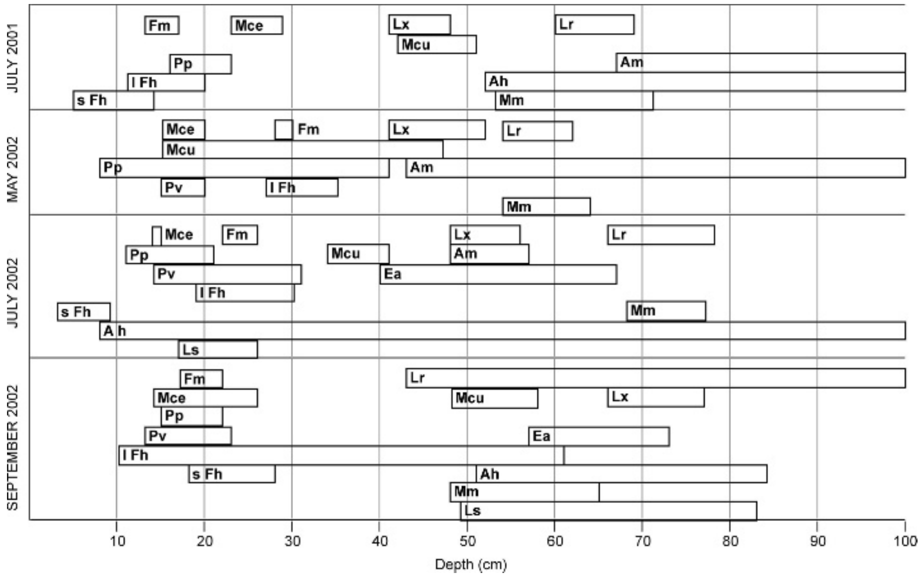

Fig. 3. Depths of peak flood migration for *Leiostomus xanthurus* (Lx), *Lagodon rhomboides* (Lr), *Mugil cephalus* (Mce), *Mugil curema* (Mcu), *Palaemonetes pugio* (Pp), *Palaemonetes vulgaris* (Pv), large *Fundulus heteroclitus* (l Fh), small *Fundulus heteroclitus* (s Fh), *Fundulus majalis* (Fm), *Litopenaeus setiferus* (Ls), and *Eucinostomus argenteus* (Ea). Blocks indicate 95% upper and lower confidence intervals.

mid flood tide, but exited throughout the ebbing tide.

A positive relationship was observed between size of individuals and depth of migration for most taxa, especially the transients. Depth of peak flood migration increased with monthly median size of individuals for *L. xanthurus*, *L. rhomboides*, *M. curema*, and *L. setiferus* during the summer of 2002 (Fig. 3, Table 2). There was a tendency for larger individuals of *L. xanthurus* and *M. curema* to enter the creeks later during the flood tide within each month and to exit the creeks earlier during the July 2002 ebb tide than smaller individuals (Fig. 6). Although *L. setiferus* and *E. argenteus* were only present during two sampling months, we observed a similar positive relationship between size of individuals and depth of flood and ebb migrations.

COOCCURRENCE OF TAXA

Overall, about 82% of the abundance correlations and 48% of the associations examined were significant. All significant relationships (abundance correlations and presence-absence associations) between pairs of congeners during months of cooccurrence were positive. Abundances of *P. pugio* and *Palaemonetes vulgaris* were always positively correlated, but the only positive association occurred during September 2002. Both relationships were always positive between large *F. heteroclitus* and *F. majalis* and between small *F. heteroclitus* and *F. majalis* except in September 2002 when there was no significant association between the second pair. Abundance correlations between the two *Mugil* spp. were positive each month, but the only significant association occurred in May 2002 (positive). The only significant relationships between *A. mitchilli* and *A. hepsetus* occurred during July 2001 when both abundance correlations and associations were positive.

Significant relationships between size classes of conspecifics were always positive. Large and small *F. heteroclitus* exhibited positive relationships during all months of cooccurrence. When two size classes of *M. curema* were present during July 2002, both relationships were positive. The two size classes of *E. argenteus* exhibited positive abundance correlations during both months of cooccurrence, but a positive association only occurred in July 2002.

Other positive relationships included consistently positive abundance correlations between *P. pugio* and large *F. heteroclitus*, small *F. heteroclitus*, and *M. cephalus*. Most associations between *P. pugio* and these taxa were also positive. Abundances of *L. xanthurus* and *L. rhomboides* were positively correlated every month, but the only positive association occurred in July 2001. Positive relationships were almost always observed during months of cooccurrence between the large size class of *E. argenteus* and both *L. rhomboides* and *A. mitchilli*. *A. hepsetus* and *M. menidia* were positively related nearly every month.

Although significant negative relationships were rare, all relationships between *L. rhomboides* and *P.*

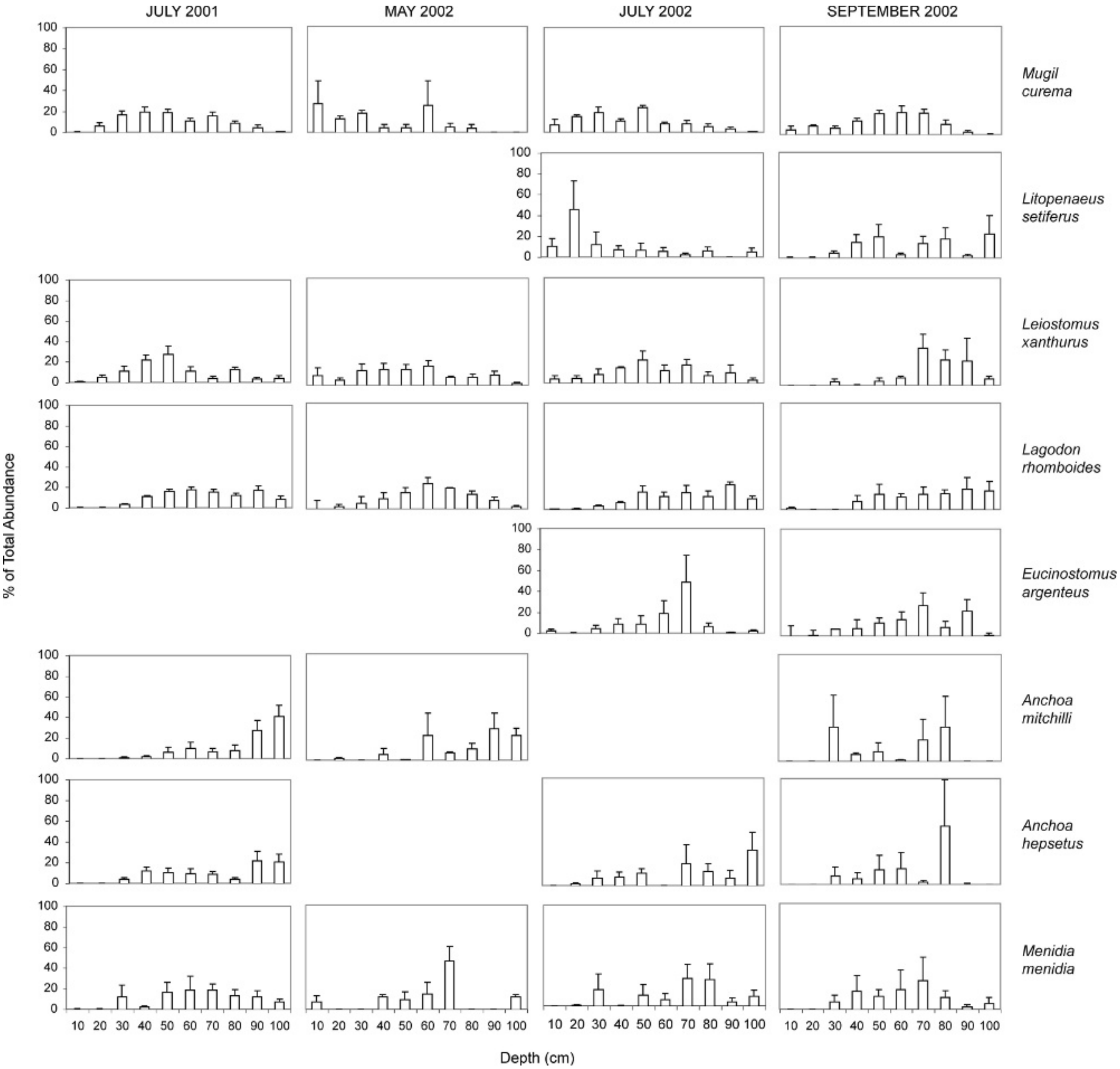

Fig. 4. Monthly variation in the flood migration patterns of transient taxa (and one resident *Menidia menidia*). For each taxon, bars indicate the mean proportion of the total catch entering the creeks (n = 3 tides in 2002 and 9 in 2001). Error bars are 1 standard error.

pugio were negative except during May 2002 when neither abundance correlations nor associations were significant, and during July 2002 when the association between the two was not significant. Both relationships between *L. rhomboides* and large *F. heteroclitus* were negative in July of both years. Abundances of the large *E. argenteus* and both large and small *F. heteroclitus* were negatively related during both months. Large *E. argenteus* was negatively associated with both size classes of *F. heteroclitus* in July 2002, but was positively associated with large *F. heteroclitus* in September 2002.

Recovery Efficiency Estimates

Efficiency estimates for the sweep flume were high for all fish taxa and low for both shrimp taxa at both high and low depths (Table 3). The device was most efficient at recovering *F. heteroclitus* (83–94%) and *L. xanthurus* (84–93%) and least efficient at recovering *L. setiferus* (27–44%). Although recovery efficiencies were generally greater at high than low depth, there were no significant differences between recovery efficiencies at high and low water depths for any taxon.

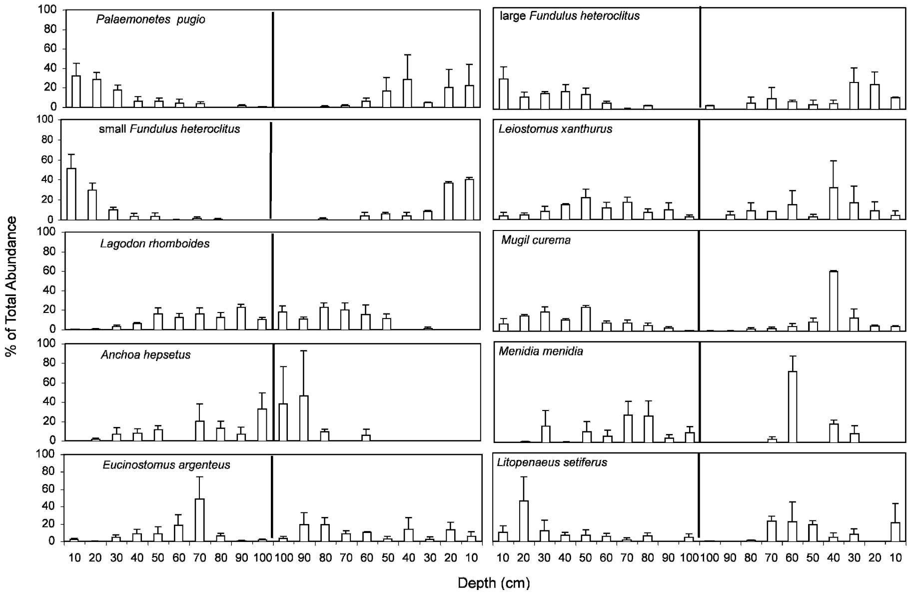

Fig. 5. Comparisons of July 2002 flood (left of solid vertical line) and ebb (right of solid vertical line) tide migration patterns for major taxa; 3 flood and 2 ebb tides were sampled. Error bars are 1 standard error.

Discussion

This study provides the first evidence that dominant species of nekton exhibit nonrandom movements into and out of salt marsh intertidal creeks. With high degrees of spatial and temporal consistency, resident taxa entered early on the rising tide (at shallow depths) and transient taxa entered during mid to late tide (at deeper depths). Depths of peak migration varied among major taxa. Our discovery that patterns of movement were consistent among creeks and between consecutive days, months (for the same size class), and years suggests that taxon-specific migratory behavior was strongly influenced by water depth. This conclusion was reinforced by our observation that depths of migration increased for most taxa as they grew during the summer season. Although we observed depths of peak movement for most major taxa, it is important to note that their migrations extended over much of the tide. Individual variation in depth of movement probably provides an increased likelihood that some of the population will encounter optimum conditions during migrations.

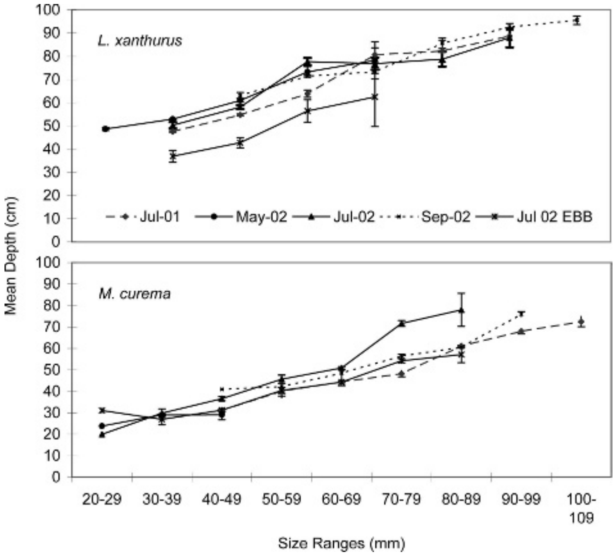

Fig. 6. Size segregated mean depths of migration (during 4 flood and 1 ebb tides) for *Leiostomus xanthurus* and *Mugil curema* (only size classes with >3 individuals per depth were included). Nine means were used in July 2001, 3 in May, July, and September 2002, and 2 in July 2002 ebb. Error bars are 1 standard error.

Migrations of nekton are controlled by both abiotic and biotic factors and their relative roles have been the subject of considerable discussion in the literature (see Craig and Crowder 2000 for review). Gibson (1973) suggested that maintaining a constant depth was a primary mechanism for tidal movements in some fishes. Our results demonstrated that the depth of ebb tide migration mirrored the depth of flood tide migration for most taxa, supporting both Gibson's hypothesis, as well as our own conclusion that depth may have influenced the structure of tidal migrations. In our placement of the sweep flumes in the three creeks, we standardized distance from the mouth of the creek, elevation, and broad physical characteristics of the creeks (e.g., width and substrate) in an effort to reduce the between-creek variability of factors

TABLE 3. Sweep flume recovery efficiency estimates. Size range and mean (mm; fish: standard length, shrimp: carapace length), number of tests (N), and mean efficiency [% recovered (±SD)] are given at both low water and high water for each species tested. Two-tailed p values were generated using Wilcoxon Mann-Whitney tests designed to test the hypothesis that there is no difference between the mean at low water depth and the mean at high water depth for each species ($\alpha = 0.05$).

Species	Size Range (mean)	Low Water Depth N	Low Water Depth Efficiency	High Water Depth N	High Water Depth Efficiency	p Values
F. heteroclitus	38–50 (44)	7	0.83 (0.17)	8	0.94 (0.11)	0.18
L. xanthurus	48–76 (55)	7	0.84 (0.11)	8	0.93 (0.08)	0.18
Mugil spp.	61–76 (67)	7	0.75 (0.18)	4	0.90 (0.08)	0.27
L. rhomboides	63–84 (70)	6	0.70 (0.25)	5	0.84 (0.11)	0.38
L. setiferus	20–38 (26)	3	0.27 (0.21)	5	0.44 (0.27)	0.48
Palaemonetes spp.	9–14 (12)	4	0.43 (0.05)	4	0.40 (0.22)	0.56

correlated with depth such as current velocity, time from slack low tide, time between depths, and depth at stage of tide. We could not separate the effects of individual factors associated with depth, so in this study, depth serves as a proxy for these factors. Although temperature and salinity can affect nekton distributions, in this study, neither varied significantly between depths. Spatial and temporal differences in turbulence, turbidity, dissolved oxygen, light, and other physical conditions might also have affected migrations on multiple scales. Most estuarine animals (especially the residents *Fundulus* spp. and *Palaemonetes* spp.) tolerate a wide range of environmental conditions and their movements may have been less sensitive to changing abiotic conditions in the creeks than changes in biotic factors, such as prey distribution or high densities of competitors or predators (Craig and Crowder 2000).

Our work indicates that biotic factors might have affected nekton movements into intertidal creeks. Predation by large, aquatic predators (e.g., *Sciaenops ocellatus*, *Cynoscion nebulosus*, *Paralichthys* spp.) did not appear to be a major threat to small fishes and shrimps within the creeks. *Paralichthys dentatus*, the only large predator collected in our study, preys on *M. menidia*, *F. heteroclitus*, and *P. vulgaris* (Rountree and Able 1992), but only 4 flounders were collected inside the mouths of the intertidal creeks during the 2 yr of sampling. Although we did not make collections at the highest stage of the flooding tide (depths > 1 m), the scarcity of predators in our catch supports the assertion that intertidal creeks can serve as refuges from subtidal predation for many migrating taxa (Paterson and Whitfield 2000). The relative refuge value of creeks might change with increasing size of individuals. In a similar intertidal assemblage within the Chesapeake Bay estuary, there was a tendency for large species, as well as for larger individuals within species, to occupy deeper depths (Ruiz et al. 1993). Bishop and Khan (1991) have also shown that a positive relationship exists between size and depth for several species of shrimps. In our study, there was a tendency for *L. rhomboides*, *L. xanthurus*, *M. curema*, *E. argenteus*, and *L. setiferus* to enter creeks at later stages of the tide as they increased in size during the summer, and for larger individuals of *L. xanthurus* and *M. curema* to enter later within a single tide. This could be attributed to a lower risk from aquatic predators or a higher risk from terrestrial predators (e.g., birds) that generally accompany increasing size. The bigger fish-deeper habitat pattern has been supported by observations and experiments in freshwater streams (Power 1987; Harvey and Stewart 1991) and is based on the premise that larger fish are more susceptible to being targeted by wading or diving birds in the shallows than smaller fish, but are less susceptible to predation from gape-limited aquatic predators. The North Inlet Estuary is occupied by numerous piscivorous fishes and diving and wading birds (Bildstein et al. 1981), especially during the summer. The presence of these predators might be important in structuring patterns of habitat selection for small fishes (McIvor and Odum 1988), and their effect on the depth of migration of intertidal creek nekton warrants further investigation.

In our study, residents migrated into the intertidal creeks during early flood tide and exited during late stages of the ebb tide, suggesting that they took advantage of the potential refuge provided by shallow intertidal creeks. Ruiz et al. (1993) observed that *P. pugio* and *F. heteroclitus* were significantly more abundant in relatively shallow (<36 cm) than deep (>36 cm) habitats, and that mortality was significantly higher in deep than shallow water. Laboratory experiments demonstrated that *P. pugio* selected for shallow water in the presence of fish predators (Posey and Hines 1991). *Fundulus* spp. and *Palaemonetes* spp. feed in the intertidal area and may be consumed in the subtidal area at low tide by fishes, such as *Sciaenops ocellatus* and *Cynoscion nebulosus.* (Wenner 1992; Wenner and Archambault 1996). Kneib and Wagner (1994) observed that residents entered vegetated marsh as soon as it was inundated by the flooding tide. When flooded, the structure of *Spartina* may provide a predator refuge for *Palaemonetes* spp. and *Fundulus* spp. Entering intertidal creeks early could allow small resident taxa to minimize the risk of predation from large aquatic predators by occupying shallow waters until the structured refuge of the vegetated marsh becomes accessible during the flood tide.

Another reason *Fundulus* spp. and *Palaemonetes* spp. might have entered the creeks first is that they travel farther into the vegetated marsh at high tide than transient species, which typically remain within creeks or close to the edge of the vegetated marsh (often < 5 m; Kneib and Wagner 1994; Minello et al. 1994; Peterson and Turner 1994; Kneib 1997). The vegetated intertidal marsh is a profitable foraging area for many species of nekton (Coull and Feller 1988; Rozas and LaSalle 1990; Allen et al. 1994), and animals that enter intertidal areas early in the flood tide and leave late in the ebb tide maximize their foraging time and minimize encounters with subtidal predators. At low tide, residents such as *Palaemonetes* spp. and *Fundulus* spp. are commonly found in shallow pools and areas immediately adjacent to the vegetated marsh. Transient species typically occupy deeper areas in contiguous subtidal channels at low tide, likely because they are more susceptible to the risk of stranding in the intertidal area (Gibson 1987; Kneib 1995). Consequently, the general timing (early, mid, late tide) of the movements within the creeks may have been related to the distance that nekton move along the intertidal creek corridors between subtidal and high intertidal areas.

Interactions between migrating taxa may have influenced the tidal migration patterns observed in this study. Many pairs of species and size classes exhibited significant abundance correlations and presence-absence associations. One explanation for positive relationships is that multispecies schooling behavior is mutually beneficial, especially for the early migrants. Within North Inlet, nearly all of the dominant species form schools, and aggregations composed of multiple species are common (Ogburn-Matthews and Allen 1993). Similar sized animals can take advantage of the refuge from predation afforded by being part of a large group (Parrish 1989). Over time, relationships probably change with ontogenetic shifts in depth preferences, especially relationships involving rapidly growing transient taxa. Negative relationships occurred between *L. rhomboides* and *P. pugio* during summer and fall, but not during spring 2002. *L. rhomboides* was the only major transient in the migrating assemblage with the capacity to prey on the sizes of *Palaemonetes* spp. collected in our study (Stoner 1980; Montgomery and Targett 1992). Large *L. rhomboides* ($\geq$59 mm) present late in the summer were more likely to prey on 10 mm grass shrimp than were the 40 mm *L. rhomboides* present in spring. *P. pugio* was more likely to avoid depths where large *L. rhomboides* were present later in the year. Based on these results, as well as observations by Ruiz et al. (1993) that grass shrimp seasonally occupied deeper water when visual aquatic predators were absent, we predict that peak depths for resident taxa increase in winter when transient predators are absent. Our analyses of the relationships between taxa suggest that biotic interactions may have played a role in the depths of migration of intertidal creek taxa, but neither causes nor consequences of these relationships were explored in this study.

Recovery efficiency of the sweep flume was relatively high, especially considering that several of the species tested are widely recognized for their ability to evade capture by both active and passive sampling devices. Recovery efficiencies were comparable to or higher than those of other sampling methods (Weinstein and Davis 1980; Kushlan 1981; Kneib 1991; Rozas 1992; Lorenz et al. 1997). The relatively low and consistent variability associated with repeated tests of recovery at both high and low water depths suggests that the sweep flume is an effective device throughout the 1 m range of water depth sampled in this study. The sweep flume's main strengths lie in its ability to rapidly collect multiple samples from a large area (30 m^2 in this application) within a single tidal cycle. Most enclosure devices are based on one-time deployments; standard flume nets (McIvor and Odum 1986), lift nets (Rozas 1992; Wenner et al. 1996), flume weirs (Kneib 1991), and tide traps (Kneib 1984, 1997) depend on falling water levels for sample retrieval. Drop nets (Zimmerman et al. 1984) and throw samplers (Kushlan 1981) can be used repeatedly during a single tide, but they typically sample a smaller area and may undersample fast-swimming animals that are adept at avoiding active sampling gear. Large drop samplers must be deployed from a boat, restricting their use to deeper depths than sweep flumes, which we have demonstrated can be used in as little as 10 cm of water. Although the sweep flume has been tested only in salt marsh intertidal creeks, the device and procedure described here should be considered for use in studies designed to reveal spatial or temporal trends of nekton use in other shallow water habitats.

We have demonstrated that the depth of peak migration into intertidal creeks varies between nektonic taxa. Coastal resource management decisions that preserve the maximum range of intertidal creek depths are likely to result in the highest diversity and use of the habitat. This study lends support to the recommendation that mimicking natural intertidal creek morphology is important for the creation and restoration of salt marsh systems (Peterson and Turner 1994; West and Zedler 2000; Minello and Rozas 2002; Kneib 2003).

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Literature Cited

Allen, D. M., S. K. Service, and M. V. Ogburn-Matthews. 1992. Factors influencing the collection efficiency of estuarine fishes. *Transactions of the American Fisheries Society* 121:234–244.

Allen, E. A., P. E. Fell, M. A. Peck, J. A. Gieg, C. R. Guthke, and M. D. Newkirk. 1994. Gut contents of common mummichogs, *Fundulus heteroclitus* L., in a restored impounded marsh and in natural reference marshes. *Estuaries* 17:464–471.

Bildstein, K. L., B. Christy, and P. Decoursey. 1981. Behavior and behavioral ecology abstracts from Southeastern Coastal and Estuarine Birds: A Conference Workshop, Georgetown, South Carolina USA. *Bird Behavior* 4:50–53.

Bishop, J. M. and M. H. Khan. 1991. Depth as a factor in abundance and size of juvenile penaeid shrimps in the absence of estuaries and marshes. *Marine Biology* 109:103–114.

Cain, R. L. and J. M. Dean. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. *Marine Biology* 36:369–379.

Catrijsse, A., E. S. Makwaia, H. R. Dankwa, O. Hamerlynck, and M. A. Hemminga. 1994. Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Marine Ecology Progress Series* 109:195–208.

Coull, B. C. and R. J. Feller. 1988. Site-to-site variability in abundance of meiobenthic copepods along a tidal gradient over 24 hours. *Hydrobiologia* 167/168:477–483.

Craig, J. K. and L. B. Crowder. 2000. Factors influencing habitat selection in fishes with a review of marsh ecosystems, p. 241–266. *In* M. P. Weinstein and D. A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publications, Dordrecht, Netherlands.

Deegan, L. A., J. E. Hughes, and R. A. Rountree. 2000. Salt marsh ecosystem support of marine transient species, p. 333–365. *In* M. P. Weinstein and D. A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publications, Dordrecht, Netherlands.

Gibson, R. N. 1973. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *Journal of Experimental Marine Biology and Ecology* 12:79–102.

Gibson, R. N. 1987. Patterns of movement in intertidal fishes, p. 55–63. *In* G. Chelassi and M. Vannini (eds.), Behavioral Adaptation to Intertidal Life. Plenum Press, New York.

Gibson, R. N. 2003. Go with the flow: Tidal migrations of marine animals. *Hydrobiologia* 503:153–161.

Haertel-Borer, S. S., D. M. Allen, and R. F. Dame. 2004. Fishes and shrimps are significant sources of dissolved inorganic nutrients in intertidal salt marsh creeks. *Journal of Experimental Marine Biology and Ecology* 311:79–99.

Harvey, B. C. and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. *Oecologia* 87:336–342.

Hettler, W. F. 1989. Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. *Marine Ecology Progress Series* 56:111–118.

Kneib, R. T. 1984. Patterns in the utilization of the intertidal saltmarsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). *Journal of Experimental Marine Biology and Ecology* 83:41–51.

Kneib, R. T. 1991. Flume weir for quantitative collection of nekton from vegetated intertidal habitats. *Marine Ecology Progress Series* 75:29–38.

Kneib, R. T. 1995. Behavior separates potential and realized effects of decapod crustaceans in salt marsh communities. *Journal of Experimental Marine Biology and Ecology* 193:239–256.

Kneib, R. T. 1997. Early life stages of resident nekton in intertidal marshes. *Estuaries* 20:214–230.

Kneib, R. T. 2000. Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States, p. 267–291. *In* M. P. Weinstein and D. A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publications, Dordrecht, Netherlands.

Kneib, R. T. 2003. Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes. *Marine Ecology Progress Series* 264:279–296.

Kneib, R. T. and S. L. Wagner. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* 106:227–238.

Kushlan, J. A. 1981. Sampling characteristics of enclosure fish traps. *Transactions of the American Fisheries Society* 110:557–562.

Lorenz, J. J., C. C. McIvor, G. V. N. Powell, and P. C. Frederick. 1997. A drop net and removable walkway used to quantitatively sample fishes over wetland surfaces in the dwarf mangroves of the southern Everglades. *Wetlands* 17:346–359.

McIvor, C. C. and W. E. Odum. 1986. The flume net: A quantitative method for sampling fishes and macrocrustaceans on tidal marsh surfaces. *Estuaries* 9:219–224.

McIvor, C. C. and W. E. Odum. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69: 1341–1351.

Miller, J. M. and M. L. Dunn. 1980. Feeding strategies and patterns of movement in juvenile estuarine fishes, p. 437–448. *In* V. S. Kennedy (ed.), Estuarine Perspectives. Academic Press, New York.

Minello, T. J. and L. P. Rozas. 2002. Nekton in gulf coast wetlands: Fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12:441–455.

Minello, T. J., R. J. Zimmerman, and R. Medina. 1994. The importance of edge for natant macrofauna in a created saltmarsh. *Wetlands* 14:184–198.

Montgomery, J. L. M. and T. E. Targett. 1992. The nutritional role of seagrass in the diet of the omnivorous pinfish *Lagodon rhomboides* (L.). *Journal of Experimental Marine Biology and Ecology* 158:37–57.

Novakowski, K. I., R. Torres, L. R. Gardner, and G. Voulgaris. 2004. Geomorphic analysis of tidal creek networks. *Water Resources Research* 40, W05401, doi: 10.1029/2003WR002722.

Ogburn-Matthews, M. V. and D. M. Allen. 1993. Interactions among some dominant estuarine nekton species. *Estuaries* 16: 840–850.

Ogburn, M. V., D. M. Allen, and W. K. Michener. 1988. Fishes, shrimps, and crabs of the North Inlet Estuary, SC: A four-year seine and trawl survey. Baruch Institute Technical Report. No. 88-1. University of South Carolina, Columbia, South Carolina.

Parrish, J. K. 1989. Layering with depth in a heterospecific fish aggregation. *Environmental Biology of Fishes* 26:79–85.

Paterson, A. W. and A. K. Whitfield. 2000. Do shallow-water habitats function as refugia for juvenile fishes? *Estuarine Coastal and Shelf Science* 51:359–364.

Peterson, G. W. and R. E. Turner. 1994. The value of salt marsh edge vs. interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17:235–262.

Posey, M. H. and A. H. Hines. 1991. Complex predator-prey interactions within an estuarine benthic community. *Ecology* 72: 2155–2169.

Potthoff, M. T. and D. M. Allen. 2003. Site fidelity, home range, and tidal migrations of juvenile pinfish, *Lagodon rhomboides*, in salt marsh creeks. *Environmental Biology of Fishes* 67:231–240.

Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: Importance of stream depth and prey size, p. 333–351. *In* W. C. Kerfoot and A. Sih (eds.), Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover, New Hampshire.

Rogers, S. G., T. E. Targett, and S. B. Van Sant. 1984. Fish-nursery use in Georgia salt-marsh estuaries: The influence of springtime freshwater conditions. *Transactions of the American Fisheries Society* 113:595–606.

Rountree, R. A. and K. W. Able. 1992. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-the-year summer flounder in New Jersey. *Transactions of the American Fisheries Society* 121:765–776.

Rozas, L. P. 1992. Bottomless lift net for quantitatively sampling nekton on intertidal marshes. *Marine Ecology Progress Series* 89: 287–292.

Rozas, L. P. and M. W. Lasalle. 1990. A comparison of the diets of gulf killifish, *Fundulus grandis* Baird and Girard, entering and leaving a Mississippi brackish marsh. *Estuaries* 13:332–336.

Rozas, L. P., C. C. McIvor, and W. E. Odum. 1988. Intertidal rivulets and creekbanks: Corridors between tidal creeks and marshes. *Marine Ecology Progress Series* 47:303–307.

Ruiz, G. M., A. H. Hines, and M. H. Posey. 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.

Sogard, S. M. and K. W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine Coastal and Shelf Science* 33:501–519.

Stoner, A. W. 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae) variation and functional responses. *Fisheries Bulletin* 78:337–352.

Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fisheries Bulletin* 77:339–357.

Weinstein, M. P. and R. W. Davis. 1980. Collection efficiency of seine and rotenone samples from tidal creeks, Cape Fear River, North Carolina. *Estuaries* 3:98–105.

Weinstein, M. P., S. L. Weiss, and M. F. Walters. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River Estuary, North Carolina, USA. *Marine Biology* 58:227–243.

Wenner, C. 1992. Red drum: Natural history and fishing techniques in South Carolina. Educational Report No. 17, South Carolina Wildlife and Marine Resources Department, Charleston, South Carolina.

Wenner, C. and J. Archambault. 1996. Spotted seatrout: Natural history and fishing techniques in South Carolina. Educational Report No. 18, South Carolina Department of Natural Resources, Charleston, South Carolina.

Wenner, E., H. R. Beatty, and L. Coen. 1996. A method for quantitatively sampling nekton on intertidal oyster reefs. *Journal of Shellfish Research* 15:769–775.

West, J. M. and J. B. Zedler. 2000. Marsh-creek connectivity: Fish use of a tidal salt marsh in southern California. *Estuaries* 23:699–710.

Wolfinger, R. D. 1999. Fitting nonlinear mixed models with the new NLMIXED procedure. SAS Users Group International Proceedings. SAS Institute Inc., Cary, North Carolina.

Zimmerman, R. J., T. J. Minello, and J. Zamora, Jr. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. *Fishery Bulletin* 82:325–336.

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