

# Tidal Utilization of Nekton in Delaware Bay Restored and Reference Intertidal Salt Marsh Creeks

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**ABSTRACT:** Large-scale marsh restoration efforts were conducted to restore normal salt marsh structure and function to degraded marshes (i.e., former salt hay farms) in the mesohaline lower Delaware Bay. While nekton response has been previously evaluated for the marsh surface and subtidal creeks in these marshes, little effort has been focused on intertidal creeks. Nekton response in intertidal creeks was evaluated by sampling with seines to determine if restored (i.e., former salt hay farms restored in 1996) and reference (i.e., natural or relatively undisturbed) salt marshes were utilized by intertidal nekton in a similar manner. The overall nekton assemblage during June–October 2004–2005 was generally comprised of the same species in both the restored and reference marshes. Intertidal creek catches in both marsh types consisted primarily of *Fundulus heteroclitus* and *Menidia menidia*, with varying numbers of less abundant transient species present. Transient nekton were more abundant at restored marshes than reference marshes, but in insufficient numbers to cause differences in nekton assemblages. In both marsh types, low tide stages were characterized by resident nekton, dominated by *F. heteroclitus*, while high tide stages were characterized by a variable mix of transient and resident nekton. Assemblage level analyses indicated that intertidal creeks in restored and reference marshes were generally utilized in a similar manner by a similar nekton assemblage, so restoration efforts were deemed successful. This is in agreement with multiple comparative studies from the same marshes examining fish, invertebrates, and vegetation in different marsh habitats.

## Introduction

A large number of coastal and estuarine species depend on salt marsh habitats for critical functions such as refuge, reproduction, and foraging (Kneib 1997; Able and Fahay 1998; Cattrijsse and Hampel 2006). Among marsh habitats, intertidal creeks provide an extensive and direct interface with the marsh surface during periods of tidal inundation, and are of particular importance to the nekton community as they represent a critically important corridor between the marsh surface and subtidal habitats (McIvor and Odum 1988; Rozas et al. 1988; Weinstein et al. 1997; Rozas and Zimmerman 2000). Nekton utilization of intertidal creeks, with access to other intertidal habitats, is controlled by marsh hydroperiod and varies temporally and spatially according to physical and biological factors (Rozas 1995).

Anthropogenic disturbance to the salt marsh ecosystems, in the form of salt hay farming, has severely limited or eliminated access to intertidal habitats in Delaware Bay and other areas. Salt hay farming involved the construction of dikes to block tidal flow and ditches to drain large marsh areas (Philipp 2005). Isolation of the marshes from tidal flow eliminated use by all nekton, and over long periods of time transformed the marsh surface into

a smooth, compact plain, decreased overall marsh elevation, and filled in creeks (Philipp 2005; Weishar et al. 2005). To restore former salt hay farms to natural marsh form and function, ecological engineering principles were applied in an attempt to restore tidal flow, reconstruct (i.e., recreate) a natural tidal creek system, and ultimately create salt marsh habitats equivalent in ecological value to those in nearby natural marshes (Weishar et al. 2005).

While marsh surface and subtidal marsh creek nekton utilization patterns have been previously examined in these same restored and reference marshes, little effort has been focused solely on intertidal creeks, and no studies have examined nekton utilization patterns within tidal cycles. The movement and growth of the dominant salt marsh species, *Fundulus heteroclitus*, was documented for marsh surface habitats (Teo and Able 2003a,b), and the movement, growth, and diet of several species of larger transient nekton utilizing subtidal creeks were also examined (Tupper and Able 2000; Miller and Able 2002; Nemerson and Able 2005). Intertidal creek nekton assemblages were examined as one component of composite studies on multiple salt marsh habitats (Able et al. 2000, 2004), but these studies did not investigate intertidal creek tidal utilization patterns. Knowledge of the differential utility of marsh types during all stages throughout the tidal cycle is critical for determining the value of

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such habitats to nekton (Kimball and Able 2007). Relatively few studies have examined the distribution and habitat utilization of nekton in intertidal marsh areas on smaller temporal and spatial scales, such as those within individual tidal cycles (Kneib 1997; Bretsch and Allen 2006b; Cattrijsse and Hampel 2006), and even fewer have done so in the context of restored and natural marsh comparisons (Kimball and Able 2007).

To determine if restored and natural salt marshes were utilized in a similar manner, the nekton of intertidal creeks in restored (i.e., former salt hay farms) and reference (i.e., natural or relatively undisturbed) marshes were examined. Nekton were sampled during the daytime tidal cycle to discern small scale temporal and spatial movement patterns within tide stages in each marsh type (i.e., restored and reference marshes). It was hypothesized that nekton utilization of intertidal creeks would differ between marsh types, with greater utilization of the more established reference marshes over relatively newly created restored marshes, and between tide stages, with low tide stages and high tide stages consisting of different nekton assemblages. These results were used to determine overall nekton assemblage utilization patterns and to evaluate the success of marsh restoration efforts.

## Materials and Methods

### STUDY LOCATION

The restored and reference marshes were located in the mesohaline lower portion of the Delaware Bay estuary (39°12'N, 74°56'W). Construction of inlets and a tidal creek system at the former salt hay farm (i.e., the restored site, Dennis Township) began in early 1996 and marsh restoration efforts were completed in August of that year, after which the restored marsh (149 ha) was subject to normal daily tidal inundation and drainage (Hinkle and Mitsch 2005; Nemerson and Able 2005). The reference marsh (i.e., Moores Beach, 550 ha), small portions of which were formerly used for salt hay farming, has had continuous tidal flow since 1972 when storms breached perimeter dikes, ending all agricultural activities and permanently re-establishing natural marsh hydrologic conditions (Hinkle and Mitsch 2005). Both restored and reference marshes are currently characterized by a *Spartina alterniflora*-dominated vegetation community (Able et al. 2004; Hinkle and Mitsch 2005) typical of other U.S. Atlantic coast salt marshes (Kreeger and Newell 2000; Mendelssohn and Morris 2000). Intertidal creeks were approximately 2–3.5 m wide at the mouth and had soft mud substrate bottoms with little or no remaining pools of standing water when fully drained at low tide. Creeks in the reference

marsh had slightly sloping banks and creeks in the restored marsh had steep banks, approximately vertical. Due to limitations at the reference marsh, selecting intertidal creeks with a similar proximity to Delaware Bay was impracticable, so the reference marsh intertidal creeks are located somewhat farther inland (approximately 3 km) than the restored marsh intertidal creeks (approximately 1 km). Other site characteristics, such as creek width at the mouth, adjacency to a larger subtidal creek, and bottom topography and substrate, were similar for all intertidal creek sampling sites in restored and reference marshes.

### EXPERIMENTAL DESIGN

Two intertidal creeks were sampled in each marsh type (restored and reference marshes,  $n = 4$  creeks). Nekton were collected with a seine (3.5 × 1.5 m seine with a 1.5 × 1.5 × 1.5 m center bag, 3.2 mm mesh) in the section of the creek from the mouth to 30 m upstream (i.e., the first 30 m of the creek). The 30-m segment in each creek was sampled with three successive 10-m seine hauls: 0–10 m = mouth, 10–20 m = middle, 20–30 m = upstream. Sampling three discrete 10-m creek segments was preferred to sampling one segment three consecutive times to avoid problems associated with habitat disturbance and repetitive sampling (Kleypas and Dean 1983). For each haul, the seine was positioned so that it swept roughly the entire water column of each sampled creek segment, from bank to bank and top to bottom. In order to determine nekton use at different water depths and current directions associated with tidal fluctuations, each creek was sampled during four tide stages: Ebb 1 (high ebb), Ebb 2 (low ebb), Flood 1 (low flood), and Flood 2 (high flood). Sampling order was ebb then flood tides to reduce potential biases caused by catching and handling the same individuals migrating in and out of creeks. All seine hauls were against the dominant tide. Sampling occurred monthly from June through October in 2004 and 2005. Each marsh type was sampled completely (both creeks) in one day during daylight hours and both reference and restored marshes were sampled during two consecutive days each month.

All nekton were identified and enumerated, and the first 50 of each species were measured separately to the nearest millimeter. Fork length (FL) was recorded for fish species with forked tails; total lengths (TL) were recorded for all other fish. Carapace width (CW) was measured for crabs. Individuals not identifiable to species were preserved in 95% ethanol or 10% formalin and processed in the laboratory. All fishes and crabs not preserved for laboratory identification were returned to the water at the end of all sampling.

TABLE 1. Analysis of variance results (F statistics) for effect of marsh type, tide stage, and year on depth (m), salinity, temperature (°C), overall and individual species abundance (catch-per-unit-effort, CPUE), and overall species length (mm total length). Temperature and salinity were not recorded for some samples. Overall species CPUE included all species (n = 24) caught during this study. Individual species shown are those used in the principal component analysis (n = 7). Results are categorized as follows: \* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.001; ns = not significant (p > 0.05).

Dependent Variable	Error df	Marsh (df = 1)	Tide (df = 3)	Marsh × Tide (df = 3)	Marsh × Year (df = 1)
Depth	132	ns	44.91***	ns	ns
Temperature	109	11.83***	22.72***	ns	ns
Salinity	109	14.96***	ns	ns	ns
Overall species CPUE	132	65.69***	6.78***	ns	ns
Individual species CPUE					
<i>Alosa pseudoharengus</i>	132	10.16**	ns	ns	12.10***
<i>Brevoortia tyrannus</i>	132	7.95**	ns	ns	ns
<i>Callinectes sapidus</i>	132	ns	ns	2.99*	ns
<i>Cyprinodon variegatus</i>	132	25.39***	2.69*	2.73*	ns
<i>Fundulus heteroclitus</i>	132	24.61***	24.36***	2.73*	ns
<i>Menidia beryllina</i>	132	ns	ns	ns	ns
<i>Menidia menidia</i>	132	10.54**	25.55***	ns	ns
Overall species length	18,250	73.44***	39.42***	17.33***	ns

Physical and environmental parameters were measured when sampling individual creeks. Temperature and salinity were recorded once for each creek and tide stage combination and were measured with a handheld oxygen, conductivity, salinity, and temperature system (YSI Model 85, Yellow Springs, Ohio), by lowering the probe into the water and recording near-surface values. Creek channel depth (m) was measured at the start location of each 10-m seine haul prior to the beginning of the haul.

#### STATISTICAL ANALYSIS

Principal component analysis (PCA), a commonly used multivariate data reduction technique (McGarigal et al. 2000; Gotelli and Ellison 2004), was used to examine nekton assemblage variability. Only species with a total abundance greater than 100 individuals for both marshes combined were included in the PCA (n = 7; this included 99.3% of all individuals caught during the study period; see Tables 1 and 2). Since this study focused on summer and early fall months and a preliminary examination of principal component (PC) scores by month produced no patterns, month was not examined further. Individual species abundance (catch-per-unit-effort, CPUE) was used for this analysis and was calculated by first taking the mean of the catch of a given species across each set of creek seine hauls (n = 3) and then taking the mean of these values across marsh, tide, year, or a combination of variables (final sample size n = 152; due to unexpected circumstances some sampling events did not take place, making the actual sample size slightly lower than the balanced sample size of n = 160). Species abundance was natural log transformed (ln(1 + CPUE)) prior to analysis and all PCA were conducted using the PRINCOMP

procedure in SAS (SAS, version 9.1, Cary, North Carolina).

Abundance (CPUE) was compared among marsh types and tide stages for individual species and all species combined. Species abundance was natural log transformed (ln(1 + CPUE)) and analyzed with a randomized complete block (RCB) analysis of variance (ANOVA) with month as blocks and marsh, tide, and year as factors. Differences in treatment means were examined using the Tukey-Kramer test, a test that is preferred when sample sizes are unequal (Dunnett 1980; Day and Quinn 1989; Sokal and Rohlf 1997). To compare the relative abundance of different categories of estuarine nekton, individual species were assigned to an estuarine category (i.e., resident, transient, freshwater; Able and Fahay 1998; Arndt 2004).

Length (mean, range) was examined for all species collected. More extensive length analyses were conducted for *F. heteroclitus*, *Menidia menidia*, and *Callinectes sapidus*, the species with the largest number of individuals measured. Overall species length was examined by converting all FL species lengths possible to TL using the available length conversions calculated in Able and Fahay (1998). Overall and individual species lengths were analyzed with a RCB ANOVA with month as blocks and marsh, tide, and year as factors, and the Tukey-Kramer test was used for post hoc comparisons.

Physical and environmental variables were examined for all marsh types and tide stages. Since creek depth was recorded for each seine haul, depth was calculated as the mean of the depths across each set of creek seine hauls (n = 3) and then averaged across marsh type, tide stage, or both (in the same manner as for species CPUE). Depth was recorded for all samples (n = 152), but temperature and salinity were not recorded for some samples, so

TABLE 2. Intertidal creek species composition and abundance (catch-per-unit-effort, CPUE, with standard error), maximum catch, and total number caught for restored and reference marshes (all creeks, tide stages, months, and years combined). CPUE was calculated by first taking the mean of the catch of a given species across each set of creek seine hauls ( $n = 3$ ) and then taking the mean of these values across marsh type (final sample size: Restored,  $n = 75$ ; Reference,  $n = 77$ ). Combined total numbers indicate overall total abundance of all marsh types together. Each species was assigned to an estuarine category (EC): estuarine resident (R), estuarine transient (T), or freshwater (F). The relative abundance of estuarine resident and estuarine transient species is indicated as a percentage of the total abundance for restored, reference, and both marshes combined (percentages for freshwater species accounted for less than 0.05% in each marsh type and were not shown).

Species	EC	Restored				Reference				Combined
		CPUE	SE	Max	Total	CPUE	SE	Max	Total	Total
<i>Alosa aestivalis</i>	T	0.32	0.19	30	72	0	0	0	0	72
<i>Alosa mediocris</i>	T	0.10	0.10	22	22	0	0	0	0	22
<i>Alosa pseudoharengus</i>	T	1.02	0.45	71	229	0	0	0	0	229
<i>Ameiurus nebulosus</i>	F	0	0	0	0	0.01	0.01	1	1	1
<i>Anchoa mitchilli</i>	T	0.33	0.12	27	75	0	0	0	0	75
<i>Anguilla rostrata</i>	T	0.16	0.03	3	37	0.01	0.01	1	2	39
<i>Bairdiella chrysoura</i>	T	0.02	0.01	2	5	0	0	0	0	5
<i>Brevoortia tyrannus</i>	T	2.63	1.37	283	592	0.36	0.36	84	84	676
<i>Callinectes sapidus</i>	T	3.60	0.65	122	810	2.61	0.45	90	604	1,414
<i>Cynoscion regalis</i>	T	0.04	0.02	3	9	0	0	0	0	9
<i>Cyprinodon variegatus</i>	R	0.01	0.01	1	2	2.46	0.92	171	569	571
<i>Fundulus heteroclitus</i>	R	28.18	5.14	962	6,341	160.47	30.29	4,125	37,069	43,410
<i>Fundulus majalis</i>	R	0	0	0	0	0.01	0.01	1	2	2
<i>Gobiosoma bosc</i>	R	0.15	0.04	8	34	0	0	0	0	34
<i>Leiostomus xanthurus</i>	T	0.15	0.07	16	34	0.07	0.04	9	17	51
<i>Lucania parva</i>	R	0	0	0	0	0.01	0.01	1	1	1
<i>Menidia beryllina</i>	R	0.01	0.01	1	1	0.53	0.44	101	123	124
<i>Menidia menidia</i>	T	12.48	3.38	708	2,807	51.06	10.74	1,808	11,796	14,603
<i>Micropogonias undulatus</i>	T	0.13	0.08	22	30	0.01	0.01	1	1	31
<i>Morone americana</i>	R	0	0	0	0	0.02	0.01	2	4	4
<i>Morone saxatilis</i>	T	0.01	0.01	1	1	0.02	0.01	2	4	5
<i>Mugil curema</i>	T	0.01	0.01	1	2	0	0	0	0	2
<i>Pogonias cromis</i>	T	0.28	0.09	17	63	0.03	0.01	3	6	69
<i>Syngnathus fuscus</i>	T	0.01	0.01	1	1	0	0	0	0	1
All species combined		49.63	7.12	—	11,167	217.68	31.59	—	50,283	61,450
Resident species					57%				75%	72%
Transient species					43%				25%	28%

sample sizes vary:  $n = 125$  for temperature and salinity. Physical and environmental variables were analyzed with a RCB ANOVA with month as blocks and marsh, tide, and year as factors. Differences in treatment means were examined using the Tukey-Kramer test.

## Results

### PHYSICAL CHARACTERISTICS

Physical and environmental characteristics differed between restored and reference marshes and tide stages (Table 1). Salinity was significantly different between marshes, with restored marsh creeks reporting slightly higher salinities (mean salinity = 16.9, standard error [SE] = 0.32) than reference marsh creeks (mean salinity = 14.6, SE = 0.50) regardless of tide stage, presumably due to the closer proximity to Delaware Bay. Temperature varied significantly with both marsh type and tide stage. Restored marsh creeks had slightly higher temperatures (mean temperature = 24.1°C, SE = 0.62) than the reference marsh creeks (mean temperature = 23.5°C, SE = 0.46), while ebb tide

temperatures (Ebb 1: mean temperature = 22.3°C, SE = 0.68; Ebb 2 = 22.4°C, SE = 0.75) were lower than those in flood tide (Flood 1 = 25.4°C, SE = 0.71; Flood 2 = 24.9°C, SE = 0.77), but temperatures did not differ significantly within ebb or flood tides. As expected, depths at low tide stages (Ebb 2: mean depth = 0.6 m, SE = 0.02; Flood 1 = 0.5 m, SE = 0.02) were significantly different from those at high tide stages (Ebb 1 = 0.8 m, SE = 0.03; Flood 2 = 0.8 m, SE = 0.01) over all marsh types. Depth was not significantly different within low and high tide stages. There was no water in the sampled 30-m creek sections at the lowest tides, between Ebb 2 and Flood 1, but some creeks had pools of water within the creek beds farther upstream during this period.

### NEKTON ASSEMBLAGES

Fishes dominated the intertidal creek nekton with 23 species and 60,036 individuals out of an overall total of 24 species and 61,450 individuals collected (Tables 2 and 3). *C. sapidus* were also frequently caught throughout the study period. Resident



nekton species ( $n = 7$ ) accounted for 72% of the total catch and were dominated by *F. heteroclitus*, which alone accounted for 71% of the total individuals caught. Transient nekton species ( $n = 16$ ), primarily *M. menidia*, made up 28% of the total catch, while *Ameiurus nebulosus*, the only freshwater species collected, was only caught once and was represented by a single individual.

Multivariate analyses revealed that the nekton assemblage was similar for all intertidal marsh creek variables examined: marsh type, tide stage, year, and month. PCA identified two PCs that together explained 76% of the variance in the intertidal creek nekton assemblage: PC 1 accounted for 47% and PC 2 accounted for 29% of the variation. No nekton assemblage patterns were seen when PC scores were analyzed by marsh type, tide stage, year, or month (see Fig. 1 for marsh type). Species eigenvector loadings indicated that positive PC 1 and PC 2 scores were associated primarily with *F. heteroclitus* and that negative PC 1 and positive PC 2 scores were associated primarily with *M. menidia* (Fig. 1). The remaining five nekton species used in the PCA had low species eigenvector loadings that were near the origin and had little influence on the PCA. Together, site scores and species loadings indicated that samples from both restored and reference marshes were generally characterized by *F. heteroclitus*, *M. menidia*, or some combination of both along with less abundant species.

#### NEKTON SPECIES COMPOSITION, ABUNDANCE, AND SIZE

Species composition differed slightly between marshes, although overall abundance was much greater in the reference marsh than the restored marsh (Table 2). A total of 20 species were collected in the restored marsh, while 15 species were found in the reference marsh. The difference was largely due to the presence of transient nekton species in the restored marsh, some of which were absent from catches in the reference marsh (e.g., *Alosa aestivalis*, *Alosa mediocris*, *Alosa pseudoharengus*, *Anchoa mitchilli*, *Bairdiella chrysoura*, and *Cynoscion regalis*). Overall nekton abundance was significantly different between marsh types (Fig. 2 and Tables 1 and 2), with abundance an order of magnitude greater at the reference marsh (CPUE = 217.68, SE = 31.59) than the restored marsh (CPUE = 49.63, SE = 7.12). These differences were primarily due to greater abundances of *F. heteroclitus* and *M. menidia* in the reference marsh (Table 2).

The greater number of transient species in the restored marsh ( $n = 16$  versus  $n = 8$  for the reference marsh) was reflected in the greater relative abundance of transient species in the restored marsh (43%) as compared to the reference marsh (25%). Resident nekton dominated the catch

in the reference marsh (75%), but accounted for a smaller percentage in the restored marsh (57%). The abundance of individual species also differed between marsh types (Table 1). *Brevoortia tyrannus* abundance was significantly greater in the restored marsh than the reference marsh ( $p = 0.0055$ ), while the reverse was observed for *M. menidia* (Fig. 3) with greater abundance at the reference marsh than the restored marsh ( $p = 0.0015$ ). *A. pseudoharengus* was more abundant at the restored marsh, but this was the only species collected with an abundance trend that differed greatly with sampling year (Table 1). *F. heteroclitus* (Fig. 4), *C. sapidus* (Fig. 5), and *Cyprinodon variegatus* abundance differed between restored and reference marshes, but the relationships varied according to tide stage (Table 1). Despite the significant interaction between marsh type and tide stage, *C. variegatus* were collected almost exclusively at the reference marsh (Table 2).

Species composition and overall abundance also differed slightly between tide stages (Table 3). The number of species collected during each tide stage was similar: Ebb 1 = 18, Ebb 2 = 15, Flood 1 = 18, and Flood 2 = 17. Overall nekton abundance differed with tide stage (Fig. 2 and Tables 1 and 3), but the only significant difference in abundance was between Flood 1 (CPUE = 196.75, SE = 40.54) and Flood 2 (CPUE = 59.75, SE = 15.39;  $p < 0.0001$ ) despite the large difference in abundance between Ebb 2 (CPUE 148.69, SE = 39.07) and Flood 2 ( $p = 0.0554$ ). Overall nekton abundance at Ebb 1 (CPUE = 134.22, SE = 38.10) was not significantly different from any other tide stages. Resident nekton were the most abundant at low tide stages (Ebb 2 = 94%, Flood 1 = 80%), while at high tide stages resident and transient nekton abundance was mixed with a greater abundance of resident nekton (63%) at Ebb 1, and a greater abundance of transient nekton (88%) at Flood 2 (Table 3). The abundance of individual species differed between tide stages as well (Table 1). *M. menidia* abundance was greatest at Flood 2 (Table 3, Fig. 3), with significant differences between abundances at flood tide stages and ebb tide stages (Flood 1 versus Ebb 1,  $p = 0.0296$ ; Flood 1 versus Ebb 2,  $p < 0.0001$ ; Flood 2 versus Ebb 1,  $p = 0.0006$ ; Flood 2 versus Ebb 2,  $p < 0.0001$ ), but significant differences were only detected within ebb tide stages ( $p = 0.0003$ ) and not within flood tide stages ( $p = 0.6265$ ). *F. heteroclitus* (Fig. 4) and *C. variegatus* were generally more abundant at low tide stages than high tide stages (Table 3), but the relationships varied according to marsh type (Table 1). *C. sapidus* showed a trend towards steadily decreasing abundance from ebb to flood tides in the restored marsh, but abundance levels remained relatively constant in the reference marsh (Fig. 5 and Table 1).

TABLE 3. Intertidal creek species composition and abundance (catch-per-unit-effort, CPUE, with standard error), maximum catch, and total number caught for each tide stage (all creeks, marsh types, months, and years combined). CPUE was calculated by first taking the mean of the catch of a given species across each set of creek seine hauls (n = 3) and then taking the mean of these values across tide stage (final sample size: Ebb 1, n = 39; Ebb 2, n = 37; Flood 1, n = 38; Flood 2, n = 38). Combined total numbers indicate overall total abundance of all tide stages together. The relative abundance of estuarine resident and estuarine transient species is indicated as a percentage of the total abundance for all tide stages separately and combined (percentages for freshwater species accounted for less than 0.05% in each tide stage and were not shown).

Species	Ebb 1				Ebb 2				Flood 1				Flood 2				Combined	
	CPUE	SE	Max	Total	CPUE	SE	Max	Total	CPUE	SE	Max	Total	CPUE	SE	Max	Total	Total	Total
<i>Alosa aestivalis</i>	0.58	0.36	30	68	0.03	0.03	3	3	0.01	0.01	1	1	0	0	0	0	0	72
<i>Alosa mediocris</i>	0.19	0.19	22	22	0	0	0	0	0	0	0	0	0	0	0	0	0	22
<i>Alosa pseudoharengus</i>	1.41	0.84	71	165	0.09	0.14	9	15	0.13	0.13	15	15	0.30	0.21	18	34	229	
<i>Ameiurus nebulosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.01	1	1	1	
<i>Anchoa mitchilli</i>	0.31	0.19	27	36	0.02	0.01	1	2	0.19	0.10	10	22	0.13	0.08	12	15	75	
<i>Anguilla rostrata</i>	0.09	0.04	3	11	0.07	0.03	3	8	0.06	0.02	3	7	0.11	0.04	3	13	39	
<i>Bairdiella chrysoura</i>	0.01	0.01	1	1	0	0	0	0	0.03	0.02	2	2	0.01	0.01	1	1	5	
<i>Brevoortia tyrannus</i>	3.87	2.58	283	453	0.47	0.75	44	83	0.14	0.12	14	16	1.09	0.77	84	124	676	
<i>Callinectes sapidus</i>	4.66	1.22	122	545	3.15	0.70	78	350	2.52	0.53	50	287	2.04	0.34	44	232	1,414	
<i>Cynoscion regalis</i>	0.01	0.01	1	1	0.06	0.04	3	7	0.01	0.01	1	1	0	0	0	0	9	
<i>Cyprinodon variegatus</i>	0.65	0.43	70	76	2.30	1.54	171	255	2.00	1.08	140	228	0.11	0.06	6	12	571	
<i>Fundulus heteroclitus</i>	82.79	30.83	3,261	9,686	137.68	39.15	4,125	15,282	154.79	39.80	3,473	17,646	6.98	1.12	93	796	43,410	
<i>Fundulus majalis</i>	0	0	0	0	0	0	0	0	0.01	0.01	1	1	0.01	0.01	1	1	2	
<i>Gobiosoma bosc</i>	0.10	0.06	8	12	0.12	0.05	5	13	0.07	0.03	3	8	0.01	0.01	1	1	34	
<i>Leiostomus xanthurus</i>	0.17	0.14	16	20	0.06	0.03	3	7	0.10	0.04	2	11	0.11	0.08	9	13	51	
<i>Lucania parva</i>	0	0	0	0	0.01	0.01	1	1	0	0	0	0	0	0	0	0	1	
<i>Menidia beryllina</i>	0.99	0.87	101	116	0.07	0.05	5	8	0	0	0	0	0	0	0	0	124	
<i>Menidia menidia</i>	38.26	13.07	994	4,476	3.97	1.93	205	441	36.50	10.87	1,390	4,161	48.46	15.29	1,808	5,525	14,603	
<i>Microponogonius undulatus</i>	0	0	0	0	0	0	0	0	0.05	0.03	3	6	0.22	0.16	22	25	31	
<i>Morone americana</i>	0	0	0	0	0	0	0	0	0.01	0.01	1	1	0.03	0.02	2	3	4	
<i>Morone saxatilis</i>	0.03	0.02	2	4	0	0	0	0	0.01	0.01	1	1	0	0	0	0	5	
<i>Mugil curema</i>	0.02	0.01	1	2	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Pogonias cromis</i>	0.09	0.04	5	10	0.27	0.17	17	30	0.13	0.08	8	15	0.12	0.05	5	14	69	
<i>Syngnathus fuscus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.01	1	1	1	
All species combined	134.22	38.10	—	15,704	148.69	39.07	—	16,505	196.75	40.54	—	22,430	59.75	15.39	—	6,811	61,450	
Resident species				63%				94%				80%				12%	72%	
Transient species				37%			6%					20%				88%	28%	

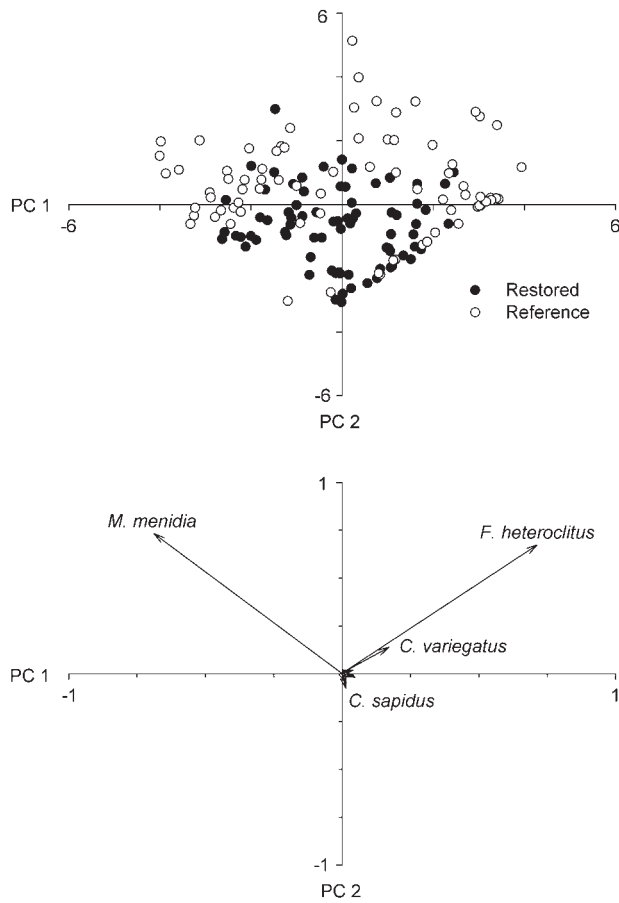


Fig. 1. Principal component analysis of intertidal creek nekton assemblage. Principal component 1 (PC 1) explained 47% of the variation and principal component 2 (PC 2) explained 29%. Species eigenvector loadings are plotted on PC 1 and PC 2 (scores for *Alosa pseudoharengus*, *Brevoortia tyrannus*, and *Menidia beryllina* were close to the origin and are not shown).

Size ranges (n = 19,677 total measured) indicated that intertidal creeks were utilized primarily by juveniles of transient nekton and both juveniles and adults of resident nekton (Table 4). Overall species length (all lengths TL, n = 18,270) varied with both marsh type and tide stage together (Fig. 2 and Table 1). Nekton were generally larger in the restored marsh for the majority of tide stages. This was likely due to the lower abundance of resident species and the presence of more transient species (Table 2), that were on average larger (Table 4), in the restored marsh as compared to the reference marsh. *F. heteroclitus* (n = 10,003) length declined from ebb to flood tide in the restored marsh, but showed the opposite trend in the reference marsh and increased from ebb to flood tide (Fig. 4). An opposing trend was observed for *M. menidia* (n = 6,671), with generally larger individuals collected in the restored marsh for all tide stages except Ebb 2

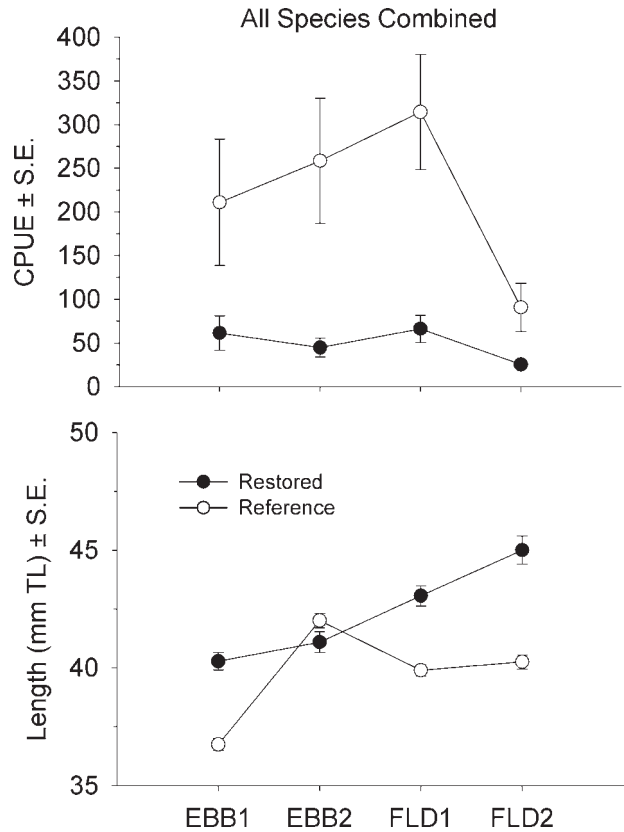


Fig. 2. Catch-per-unit-effort (n = 61,450) and mean length (n = 18,270) by marsh type and tide stage for all species combined.

(Fig. 3). An increase in the length of *C. sapidus* (n = 1,403) from ebb to flood tides was observed in both marshes, but individuals were larger in the reference marsh for all tide stages (Fig. 5). A length-frequency analysis showed a bimodal distribution for *C. sapidus* around 15 and 65 mm, with a much greater number of smaller individuals (5–40 mm) in the restored marsh and a greater number of larger individuals (45–115 mm) in the reference marsh (Fig. 5).

**Discussion**

**NEKTON ASSEMBLAGES**

The nekton assemblage was generally comprised of the same species in both the restored and reference marsh intertidal creeks, with *F. heteroclitus* and *M. menidia* dominating the catches in both marsh types. Although the abundance of *F. heteroclitus* and *M. menidia* was much greater in the reference marsh, both species were consistently present in restored and reference marsh intertidal creeks throughout the study period. A greater number of transient species were present in the restored marsh, but these species were observed in

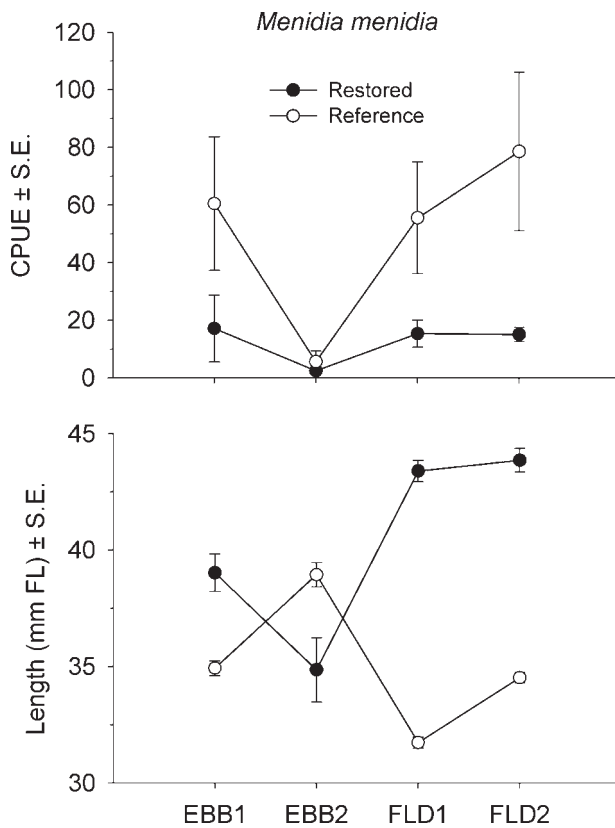


Fig. 3. Catch-per-unit-effort ( $n = 14,603$ ) and mean length ( $n = 6,671$ ) by marsh type and tide stage for *Menidia menidia*.

insufficient numbers to cause assemblage differences. Similar assemblage structures were also observed in these same Delaware Bay marshes during examinations of the intertidal creek nekton assemblages using weirs in the years immediately following marsh restoration efforts (Able et al. 2000, 2004). Interestingly, these studies conducted in April–November 1997 and 1998 had catches dominated by *F. heteroclitus* and *M. menidia* in both restored and reference marshes, but unlike the present study, abundances of both species were greater in the restored marsh than the reference marsh (Able et al. 2000, 2004). Analysis of a longer time series of intertidal creek nekton weir data from the same sites, collected annually over a 9-yr period (1996–2004), showed that the nekton assemblage converged over time to a similar assemblage in both marsh types by 2004, primarily due to steadily decreasing abundances of once highly abundant transient species in restored marshes (Able et al. in press). In combination, prior studies using weirs and the results from recent seine collections suggest that the species composition of nekton utilizing the restored and reference marsh intertidal creeks has remained largely unchanged during the 10-yr

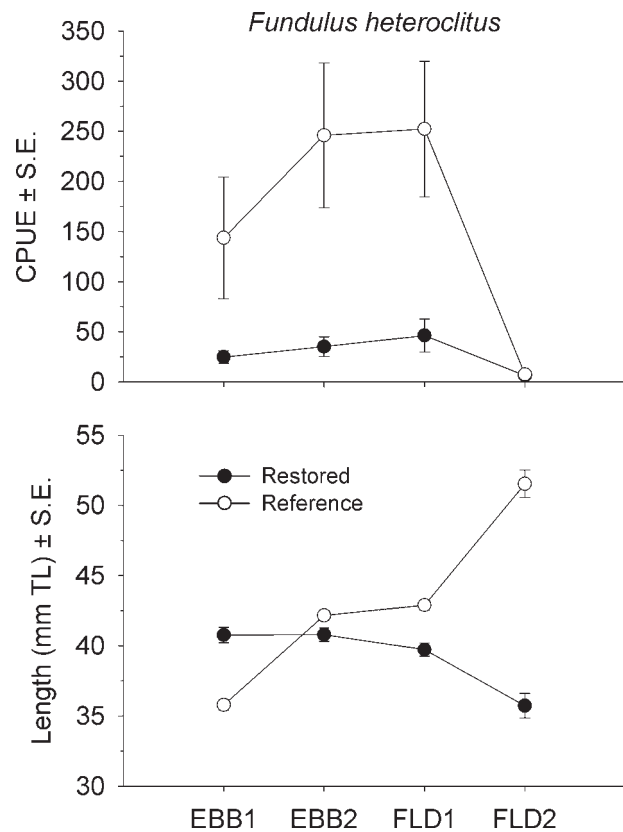


Fig. 4. Catch-per-unit-effort ( $n = 43,410$ ) and mean length ( $n = 10,003$ ) by marsh type and tide stage for *Fundulus heteroclitus*.

period (1996–2005) since marsh restoration efforts took place, but the relative abundances of the dominant species within each marsh type have changed over time. *F. heteroclitus* and *M. menidia* abundances are now relatively greater in the reference marsh than the restored marsh. Despite the agreement between studies examining intertidal creek nekton assemblages with seines and weirs, it should be noted that biases associated with each sampling method could potentially influence individual results and hinder comparisons.

Some components of the nekton assemblage displayed different tidal utilization patterns for low and high tide stages, despite the lack of detection of such patterns in the multivariate analyses. Low tide stages were characterized largely by resident nekton. High tide stages consisted of a mix of transient and resident nekton. The flood high tide stage (Flood 2) consisted almost exclusively of transient nekton and the ebb high tide stage (Ebb 1) was comprised of a much larger percentage of resident nekton. The greater abundance of transients during greater water depths of late flood tide may indicate an optimal utilization period, as has been demonstrated in intertidal creeks elsewhere (Bretsch and Allen



TABLE 4. Mean (with standard error), minimum, and maximum length (mm) and total number measured for species collected during the study period (all creeks, marsh types, tide stages, months, and years combined). Fishes and invertebrates were measured either in fork length (\*), total length (†), or carapace width (‡).

Species	Mean	SE	Min	Max	Total
<i>Alosa aestivalis</i> *	29	0.64	21	37	72
<i>Alosa mediocris</i> *	20	0.25	18	22	22
<i>Alosa pseudoharengus</i> *	29	0.37	18	37	221
<i>Ameiurus nebulosus</i> †	131	—	—	—	1
<i>Anchoa mitchilli</i> *	37	1.14	18	73	75
<i>Anguilla rostrata</i> †	130	11.45	55	420	39
<i>Bairdiella chrysoura</i> †	82	4.88	66	95	5
<i>Brevoortia tyrannus</i> *	36	0.22	11	57	440
<i>Callinectes sapidus</i> ‡	40	0.76	5	160	1,403
<i>Cynoscion regalis</i> †	84	5.25	61	109	9
<i>Cyprinodon variegatus</i> †	41	0.40	18	62	512
<i>Fundulus heteroclitus</i> †	41	0.17	10	117	10,003
<i>Fundulus majalis</i> †	67	3.00	64	70	2
<i>Gobiosoma bosc</i> †	31	1.07	18	42	33
<i>Leiostomus xanthurus</i> †	62	4.12	27	130	51
<i>Lucania parva</i> †	37	—	—	—	1
<i>Menidia menidia</i> *	36	0.15	10	95	6,671
<i>Micropogonias undulatus</i> †	44	1.60	20	62	31
<i>Morone americana</i> *	128	16.21	85	157	4
<i>Morone saxatilis</i> *	123	25.78	70	220	5
<i>Mugil curema</i> *	78	12.50	65	90	2
<i>Pogonias cromis</i> †	69	4.02	25	160	74
<i>Syngnathus fuscus</i> †	83	—	—	—	1

2006b). The lower abundance of transient nekton at both early and late ebb tide stages may be due to those species exiting intertidal creeks earlier in the ebb tide, prior to the ebb tide sampling periods in the present study. A general pattern of juveniles and adults of resident nekton dominating low tide stages and primarily juveniles of transient nekton abundant at high tide stages has been observed in other marshes in North America (Kneib 1997; Bretsch and Allen 2006b; Kimball and Able 2007) and Europe (Hampel et al. 2003; Cattrijsse and Hampel 2006). This response may possibly be due to a number of factors such as refuge from predators, foraging, and nursery functions. Studies examining the depth preferences of common intertidal marsh creek nekton found that many species exhibited preferences for either shallow or deep waters (Davis 1988; Ruiz et al. 1993; Bretsch and Allen 2006a), indicating that low tide and high tide assemblages should be different and distinguishable. The large differences in transient and resident nekton relative abundances within high tide stages and the overwhelming dominance by large numbers of relatively few species for all tide stages may have made distinct tidal nekton assemblages difficult to distinguish in some prior analyses.

#### NEKTON SPECIES COMPOSITION, ABUNDANCE, AND SIZE

Individual nekton species exhibited variable habitat and tidal utilization patterns in restored and reference marsh intertidal creeks, including some of the most abundant and ubiquitous inter-

tidal salt marsh resident and transient species. Intertidal nekton were predicted to follow a tidal utilization pattern based on estuarine classifications, with resident species more abundant at low tide stages and transient species more abundant at high tide stages in intertidal creeks. *F. heteroclitus* utilized intertidal creeks in much greater abundances during low tide stages than high tide stages in reference marsh creeks, but did not adhere to this pattern in restored marsh creeks. The lack of a consistent tidal utilization pattern for both marsh types was unexpected since *F. heteroclitus* have been documented following a similar uniform intertidal creek utilization pattern in other salt marsh systems (Bretsch and Allen 2006b; Kimball and Able 2007). Lower marsh surface elevation in former salt hay farms (Weishar et al. 2005; Philipp 2005) may cause deeper water on the marsh surface for longer periods of time during tidal inundations (Teo and Able 2003b). Longer inundation of the marsh surface could result in more extensive tidal migrations for *F. heteroclitus* in restored marshes, such as former salt hay farms (Teo and Able 2003b), which may influence tidal utilization patterns. The greater abundance and variable tidal utilization pattern of *F. heteroclitus* in reference marsh creeks could possibly account for the greater size variation observed in reference marsh creeks as compared to restored marsh creeks.

The overall tidal utilization pattern of *M. menidia* was also highly variable, but did not differ between restored and reference marshes, even though

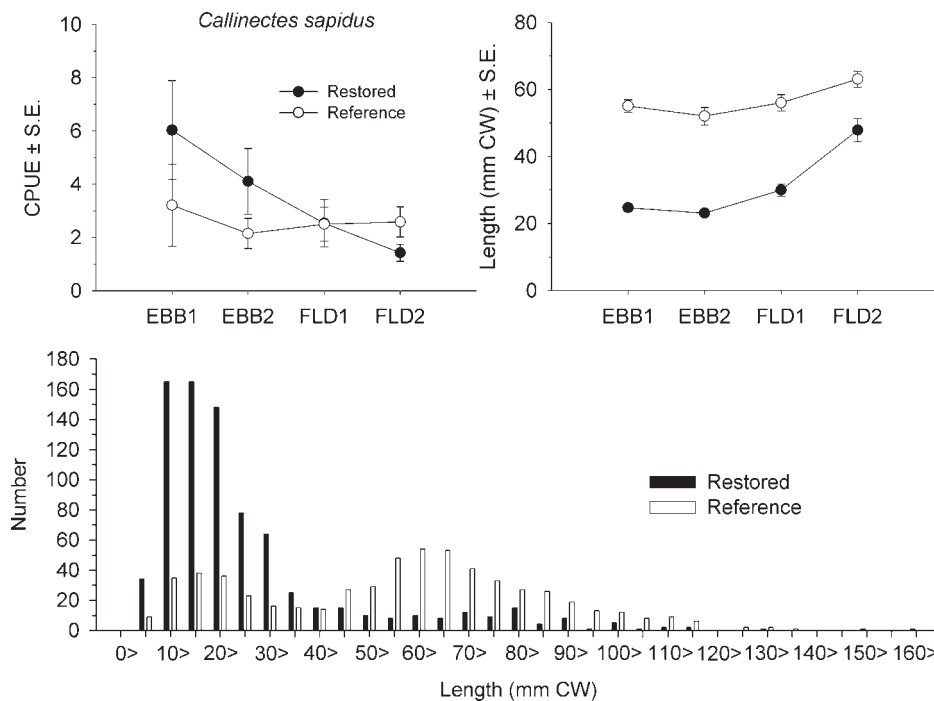


Fig. 5. Catch-per-unit-effort ( $n = 1,414$ ) and mean length ( $n = 1,403$ ) by marsh type and tide stage for *Callinectes sapidus*. Length-frequency distribution for *C. sapidus* sorted into 5-mm groups (0–160 mm) for each marsh type.

abundances were much greater in the reference marsh. Depths of peak migration between 50–80 cm water depth were observed for *M. menidia* entering and exiting intertidal creeks in a South Carolina salt marsh (Bretsch and Allen 2006b), which coincides with the water depth range examined in this study. The much lower abundance of *M. menidia* at late ebb tide in the present study may indicate that emigration from intertidal creeks occurs at a greater water depth in Delaware Bay marshes. The variation in *M. menidia* average size was potentially an artifact of the large sample size.

Overall abundance of *C. sapidus*, another abundant species in this study, steadily decreased from ebb to flood tide stages, but this pattern was only consistent in the restored marsh. A similar tidal abundance pattern was seen for *C. sapidus* in intertidal creeks in oligohaline Delaware Bay salt marshes and was consistent across all marsh types sampled (Kimball and Able 2007). Salt marsh creek feeding patterns for *C. sapidus* have been linked to tidal cycles with gut fullness greatest at high tide then decreasing to lows just prior to the next high tide (Ryer 1987). *C. sapidus* have also been observed to remain on the creek bottom during low and intermediate tides, and forage primarily at high tide levels (Ryer 1987). Steadily decreasing gut fullness from a high tide maximum could indicate foraging activity at only the highest water levels, which

coincides with *C. sapidus* utilizing creeks or the marsh surface (possibly to forage) at the highest water levels (slack high tide) then exiting creeks or remaining relatively inactive in pools (and potentially unavailable to creek seines) until the following high tide. Together, *C. sapidus* tidal behavioral patterns and associated feeding periodicity could account for the decreasing abundances from ebb to flood tides seen in restored and reference marshes, but these factors were not examined in this study.

Analysis of *C. sapidus* size indicated that the restored marsh had greater number of smaller crabs while the reference marsh had a greater number of larger crabs, a pattern that was constant over all tide stages. Comparison of nekton utilization of marsh surface habitats in created and natural marshes in a Texas estuary also found smaller *C. sapidus* in greater numbers in the created marsh and larger individuals more numerous in the natural marsh (Zeug et al. 2007). In a Texas coast-wide comparison of nekton marsh surface utilization, crab sizes and abundances were similar in both created and natural marshes (Minello and Zimmerman 1992). Studies in oligohaline Delaware Bay salt marshes also found that *C. sapidus* sizes and abundances were similar in restored and natural marsh subtidal creeks (Jivoff and Able 2003). Inconsistent relationships in *C. sapidus* abundance and size between intertidal creek, marsh surface, and subtidal creek

habitats illustrate the complexity of utilization patterns within these interconnected salt marsh habitats.

Differences in creek geomorphology may explain some of the observed nekton utilization differences between restored and reference marsh intertidal creeks. Typical intertidal creeks in the reference marsh had gently sloping banks, which have been associated with slower flow (McIvor and Odum 1988; Allen et al. 2007), while restored marsh creeks typically had steeper banks that were nearly vertical or concave, which tended to concentrate water in the creek and potentially increase flow rate. Since *F. heteroclitus* favors intertidal creeks with low flow (Allen et al. 2007), creek geomorphology may explain the much greater abundance of *F. heteroclitus* at the reference marsh as compared with the restored marsh. Creeks with gently sloped banks have also been reported to support higher nekton use (Allen et al. 2007), provide better refuges (McIvor and Odum 1988; Hettler 1989), and facilitate movement between creeks and the marsh surface (Rozas et al. 1988). Steep banks have been shown to negatively affect fish through increased predation (McIvor and Odum 1988), which is particularly important since many of the nekton that utilize intertidal creeks are common prey for larger transient nekton in Delaware Bay salt marshes (Tupper and Able 2000; Nemerson and Able 2003, 2005). Creeks with steep banks may also negatively affect nekton through reduced access to marsh surface habitats (McIvor and Odum 1988), which could potentially affect all nekton and especially marsh surface users, such as *F. heteroclitus*. Creek geomorphology may be especially important for resident species, such as *F. heteroclitus*, that have relatively small home ranges (Lotrich 1975; Teo and Able 2003b) and spend their entire life cycle in marsh habitats, and have a greater opportunity to be affected (positively or negatively) by intertidal creek geomorphologies. Transient species that are highly mobile and only spend a portion of their life cycle in salt marshes (Kneib 1997; Able and Fahay 1998) may be less affected. Although geomorphological characteristics may not explain abundance differences observed for all intertidal creek nekton (Allen et al. 2007), creek geomorphology is important to measure, especially in the context of marsh restorations (Desmond et al. 2000), and should be incorporated into salt marsh habitat sampling protocols (Williams and Zedler 1999; Neckles et al. 2002; Kneib 2003; Visintainer et al. 2006).

A plausible explanation for the observed differences in the relative abundance of transient nekton between restored and reference marshes may be the differences in proximity to Delaware Bay. The restored marsh was closer to the mouth of Delaware

Bay and the two intertidal creeks sampled in this marsh were closer to the bay (approximately 1 km versus 3 km for the reference marsh creeks). This equates to less distance between larval supply points and intertidal marsh habitats, which might contribute to increased numbers and abundances of transient species at the restored marsh compared to the reference marsh. Differences in proximity to an adjoining bay was proposed to explain species richness differences between a created marsh and a natural marsh in the Guadalupe Estuary, Texas (Zeug et al. 2007). Studies focusing on nekton utilization of subtidal creeks within these same Delaware Bay salt marshes observed that differences in distance did not bias abundance comparisons of three common transient species in subtidal creeks (Nemerson and Able 2005). Perhaps, the larger average size and greater mobility of subtidal nekton may lessen (or eliminate) any effects of distance from the bay.

The results of this study address the need for more research focusing on spatial and temporal salt marsh habitat utilization patterns within tidal cycles (Rountree and Able 2007) and illustrate the importance of including tide stage in the experimental protocol when sampling intertidal habitats (Kimball and Able 2007). Since subtidal creek and marsh surface habitats serve as nekton sources for intertidal creeks and nekton size along with the source habitat (i.e., subtidal creek or marsh surface) influence intertidal tidal migration patterns (Kneib and Wagner 1994), the timing of intertidal creek sampling during the tidal cycle may determine the nekton assemblage (Kimball and Able 2007). Because of the intermediate position of intertidal creeks (i.e., corridors), a better understanding of utilization patterns in intertidal creeks will also provide insight on tidal utilization patterns in subtidal creeks and on the marsh surface. Examining habitat use patterns within tidal cycles will greatly improve our knowledge of nekton habitat utilization throughout all salt marsh habitats (Rountree and Able 2007; Kimball and Able 2007).

#### IMPLICATIONS FOR MARSH RESTORATIONS

Assemblage level analyses indicated that restored and reference marshes were generally utilized in a similar manner by a similar assemblage of nekton species. These assemblages were dominated by a small subset of ubiquitous salt marsh species, despite some individual nekton species metrics (i.e., species abundance, size) differing between marshes. The opportunistic nature and broad environmental tolerances of estuarine nekton (Kneib 1997; Able and Fahay 1998; Nordlie 2003) often make marsh-scale comparisons difficult and it should be noted that similarities and differences

between restored and reference marsh intertidal creek nekton may be due to influential factors other than marsh restoration efforts (e.g., creek geomorphology, site differences, species annual variation). The species comprising intertidal creek nekton come from both marsh surface and subtidal habitats, so varying responses to some metrics may be attributed to this combination of both resident and transient nekton species from different sources. Within these same Delaware Bay marshes, studies examining nekton use of intertidal creek (Able et al. 2000, 2004), marsh surface (Teo and Able 2003a,b), and subtidal creek (Tupper and Able 2000; Miller and Able 2002; Nemerson and Able 2005) habitats also found restored and reference marshes utilized in a similar manner. A synthesis combining novel studies and previous work from the same Delaware Bay marshes examined the response of fishes, invertebrates, and vegetation and concluded that restoration efforts were successful (Able et al. in press). Although the nekton utilization of restored and reference marshes observed in multiple salt marsh habitats was generally similar for former salt hay farms in the mesohaline portion of the Delaware Bay estuary, this is not always the case. For example, in *Phragmites*-invaded oligohaline salt marshes nekton utilization patterns were different for intertidal creek, marsh surface, and subtidal creek habitats (Kimball and Able 2007), so the evaluation of restoration success should incorporate the nekton response in multiple marsh habitats.

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