HABITAT ECOLOGY OF INTERTIDAL NEKTON IN SOUTHERN NEW JERSEY SALT MARSHES: TIDAL INFLUENCES IN NATURAL AND RESTORED MARSHES

by

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ABSTRACT OF THE DISSERTATION

Habitat ecology of intertidal nekton in southern New Jersey salt marshes: Tidal influences in natural and restored marshes

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Intertidal creeks are of particular importance to the nekton community as they represent a critical corridor linking marsh surface and subtidal habitats during periods of tidal inundation. Nekton use of intertidal creeks is controlled by marsh hydroperiod and varies temporally and spatially according to multiple physical and biological factors. Many oligohaline and mesohaline southern New Jersey salt marshes have been altered through anthropogenic disturbance, in the form of salt hay farming, or the invasion and subsequent dominance of *Phragmites australis*. Intertidal creeks are especially vulnerable to marsh habitat alteration, which may affect creek structure and function, but may be mitigated (or reversed) through habitat restoration efforts. Intertidal creek nekton were sampled in multiple marsh types (i.e., natural, invasive-dominated, and marshes treated either to remove *Phragmites* or to restore tidal flow to former salt hay farms) using three different sampling gears (i.e., weirs, seines, and underwater video) to compare nekton utilization between marsh types, determine general nekton tidal use

patterns, and evaluate overall restoration success. Intertidal creek nekton collections in all marsh types consisted primarily of resident nekton and were dominated by a relatively low number of ubiquitous intertidal species, especially *Fundulus heteroclitus*. Low tide stages were characterized by resident nekton (dominated by *F. heteroclitus*), while high tide stages were characterized by a variable mix of transient (dominated by *Anchoa mitchilli*, *Menidia menidia*, and *Callinectes sapidus*) and resident nekton. Examination of intertidal creek nekton at multiple spatial and temporal scales within the tidal cycle (using seines and underwater video) generally found that the tidal use patterns of the most abundant nekton were similar in all marsh types. Most studies found that treated marsh creeks provided enhanced conditions for intertidal nekton, as evidenced by species abundances in treated marshes as compared to natural or invasive-dominated marshes. However, the short and long-term response of intertidal creek nekton suggests that the stage of the restoration may influence the results of comparisons between marsh types and should be considered when evaluating marsh restorations.

ACKNOWLEDGEMENTS

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GENERAL INTRODUCTION

Salt marshes have been shown to be critically important to many fisheries, providing essential habitat for single or multiple life history stages of a variety of species (Weinstein, 1979; Boesch and Turner, 1984; Rountree and Able, 1992; Kneib, 1997b). In general, salt marshes can be subdivided into irregularly flooded marsh surface, regularly flooded intertidal marsh surface, intertidal creek, subtidal creek, and open water-marsh fringe (Rountree and Able, 1992). Of the various salt marsh habitats, intertidal marsh creeks are of particular importance to the nekton community since they provide an extensive and direct interface with the marsh surface during periods of tidal inundation, and thus represent a critically important corridor (both physically and biologically) between the marsh surface and subtidal habitats (McIvor and Odum, 1988; Rozas et al., 1988; Weinstein et al., 1997; Rozas and Zimmerman, 2000). Nekton access to intertidal habitats is limited and varies spatially and temporally due to factors such as marsh hydroperiod (Rozas, 1995), life history stage, species-specific migration cycles (e.g., seasonal, diel, diurnal, etc.), and intra/interspecific interactions (McIvor and Odum, 1988; Kneib, 1997b). The limited availability of these temporary habitats, and their function as refuge, foraging, and reproduction habitats for numerous coastal and estuarine species (Kneib, 1997b; Able and Fahay, 1998; Cattrijsse and Hampel, 2006), makes continued access to intertidal creeks vital.

Utilization of intertidal creeks is primarily governed by tidal cycles (Rozas, 1995). The flood and ebb of the tides produce a predictable expansion and contraction of available intertidal habitat which dictates usage patterns by both marsh residents and transient species. Fishes generally migrate or follow the tide as it rises (i.e., floods) to

forage, for example, in these highly productive intertidal areas, then similarly follow the ebbing tide as waters recede into subtidal habitats (Cain and Dean, 1976). Beyond this widely accepted general pattern, however, there is insufficient evidence to definitively describe tidal utilization patterns for the majority of species commonly found in intertidal creek habitats. Some research has examined the small scale tidal movement patterns of nekton utilizing intertidal habitats, but 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, for example, in North American (Kneib, 1997b; Desmond et al., 2000; Bretsch and Allen, 2006b), New Zealand (Morrison et al., 2002), South African (Paterson and Whitfield, 1996, 2000, 2003), and European (Cattrijsse and Hampel, 2006) salt marshes.

Anthropogenic disturbances can transform salt marsh habitats, causing physical and functional habitat alterations potentially capable of affecting nekton utilization of intertidal creeks (Weinstein and Balletto, 1999; Adam, 2002; Able et al., 2003; Lotze et al., 2006). One of the most important factors determining the function of salt marsh habitats is the dominant vegetation (Weinstein et al., 1997). Salt marshes along the Atlantic and Gulf coasts of the U.S. are typically dominated by smooth cordgrass, *Spartina alterniflora* and other *Spartina* species (Kreeger and Newell, 2000; Mendelssohn and Morris, 2000). Over the last several decades, however, the invasion and subsequent dominance by the common reed (*Phragmites australis*, hereafter referred to as *Phragmites*), especially in the northeastern U.S., has occurred in anthropogenically disturbed marshes as well as some relatively undisturbed marsh areas (Chambers et al., 1999; Weinstein and Balletto, 1999; Windham and Lathrop, 1999; Bart and Hartman,

2000; Weinstein et al., 2000; Lathrop et al., 2003; Raichel et al., 2003). *Phragmites* can potentially alter intertidal creek function dependent upon the stage of invasion (Able et al., 2003; Hunter et al., 2006). As a *Phragmites* invasion progresses, localized sediment accumulation occurs which impedes tidal flow and slowly fills in smaller intertidal creeks, eventually resulting in creeks that are filled in during the late invasion stages (Teal and Weinstein, 2002; Able et al., 2003; Osgood et al., 2003). Similarly, larger intertidal creeks in *Phragmites* marshes are characterized by steep banks, which have been postulated to negatively affect fish through increased predation and reduced access to marsh surface habitats (McIvor and Odum, 1988; Teal and Weinstein, 2002). Large scale habitat restorations were conducted in multiple marshes throughout the Delaware Bay estuary to ameliorate the deleterious effects of *Phragmites* invasion in brackish marshes and restore marshes to pre-invasion form and function (Able et al., 2003; Balletto et al., 2005).

Salt marshes in the northeastern United States have also been subjected to anthropogenic disturbances in the form of agriculture, primarily salt hay farming. Marshes in the Delaware Bay estuary have a long history of salt hay farming spanning several centuries, with some farms operating until late in the twentieth century. 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 and decreased overall marsh elevation (Weishar et al., 2005; Philipp, 2005). Habitat restoration was proposed to restore marshes in former Delaware Bay salt hay farms to natural marsh form and function. Ecological engineering principles were

applied to restore tidal flow, reconstruct (i.e., re-create) a natural tidal creek system, and ultimately create salt marsh habitats equivalent in ecological value to those in nearby natural marshes (Weinstein et al., 1997; Weishar et al., 2005). Despite these impacts there has been little research to date comparing small scale tidal movement patterns of nekton utilizing intertidal creeks within natural and restored marshes, whether in marshes treated for *Phragmites* eradication (Able et al., 2001; Nemerson and Able, 2003) or in former salt hay farms (Able et al., 2000; Able et al., 2004).

The presence of thick vegetative cover and a soft substrate, coupled with nearly continuous changes in water depth, current speed, and flow direction, make intertidal marsh habitats some of the most difficult areas to sample nekton within a salt marsh system (Varnell and Havens, 1995; Kneib, 1997b). Basic issues of accessibility and operation are some of the most challenging to address. Access to sampling sites via boat, if possible at all, is often limited to favorable tidal conditions (i.e., high water). Even if water levels are high, tidal channels are usually narrow and often contain sunken debris (e.g., logs, stumps) that renders boat navigation impossible. If inaccessible by water, then sampling site selection must include access by other means, which can be equally difficult to achieve and further limits the area available for study. Moreover, sampling gear has to be easily transportable and manageable in the field, while also keeping habitat alteration to a minimum when in operation, and meeting both of these requirements can create catch biases and affect gear efficiency. Considering the difficulties associated with sampling intertidal marsh habitats as well as the limitations and biases of individual sampling methods (Connolly, 1999), an experimental design that employs multiple different sampling methods to examine the same intertidal marsh habitat is preferred.

Therefore, to discern small scale nekton movement patterns within tidal cycles and elucidate nekton habitat preferences, intertidal creek nekton were sampled at various tidal intervals in multiple natural and restored marshes using three different intertidal sampling gears (i.e., weirs, seines, and underwater video). Weirs or block nets function on a large spatial and temporal scale by passively sampling an entire intertidal creek drainage area over the entire ebb tide (approximately 6 hours). Seining multiple times during both flood and ebb tides in an intertidal creek actively samples the nekton community at distinct periods (hours) within the tidal cycle, and provides information on intermediate spatial and temporal scales. Underwater video is a passive method that continuously samples intertidal creek nekton (at the camera location) on smaller scales (minutes) throughout the entire tidal cycle at a single location. As each sampling method operates on a different spatial and temporal scale, the same intertidal nekton community was sampled at multiple scales, allowing for a more complete picture of nekton tidal and habitat utilization patterns. Differences and similarities in intertidal creek nekton assemblages as well as individual species composition, abundance, and length were investigated for each marsh type and tide stage sampled. It was hypothesized that nekton utilization of intertidal creeks would differ both between habitat types and tide stages. These results were also used to determine overall nekton assemblage preferences and to evaluate the success of marsh restoration efforts.

In an effort to thoroughly examine intertidal creek nekton utilization and movement patterns, studies were conducted in multiple natural and restored salt marshes throughout southern New Jersey (Fig. 1). The New Jersey portion of the Delaware Bay estuary encompasses a long coastline from the mesohaline lower bay close to the Atlantic

Ocean to the oligohaline upper bay at the mouth of the Delaware River. Several studies

took place at multiple marsh locations along this gradient. For Chapters 1 and 2, nekton

tidal utilization patterns were examined by sampling intertidal creek nekton using seines

multiple times during ebb and flood tides. Chapter 1 examined nekton utilization in three

marsh habitat types (natural *Spartina*-dominated, Treated and now dominated by

Spartina, and invasive *Phragmites*-dominated marshes) within the Alloway Creek

watershed located in the oligohaline upper Delaware Bay. Chapter 2 followed the same

seine sampling protocol in the mesohaline lower Delaware Bay marshes, where intertidal

creek nekton were examined in restored (i.e., former salt hay farms) and reference (i.e.,

natural) marshes. Chapter 3 examined long-term nekton habitat utilization patterns using

weirs (i.e., block nets) to sample intertidal creek nekton in *Spartina*, Treated, and

Phragmites marshes in the Alloway Creek watershed (different creeks than those

examined in Chapter 1). Underwater video sampling took place in the marshes of the

Jacques Cousteau National Estuarine Research Reserve which is comprised primarily of

the Great Bay-Mullica River estuary located on the southern New Jersey Atlantic coast.

A detailed comparison of nekton tidal utilization patterns in intertidal creeks using

underwater video in invasive *Phragmites*-dominated marshes and restored marshes

treated for *Phragmites* eradication in the oligohaline portion of the Great Bay-Mullica

River estuary was the focus of Chapter 4. Together, these studies will provide a more

complete picture of intertidal nekton habitat utilization and movement patterns within

tidal cycles in intertidal salt marsh creeks.
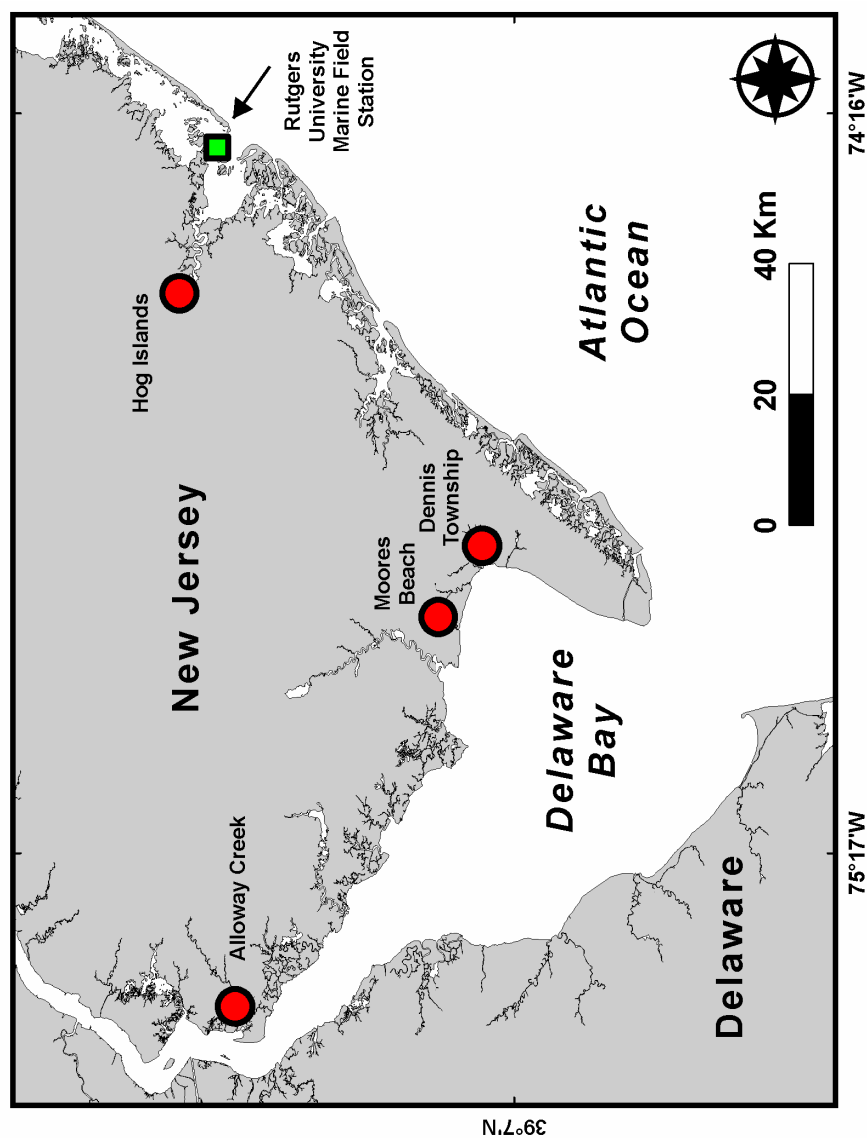
Figure 1. Study locations in the Delaware Bay estuary (i.e., Alloway Creek, Moores Beach, Dennis Township) and the Great Bay-Mullica River estuary (i.e., Hog Islands) of southern New Jersey.

CHAPTER 1

Nekton utilization of intertidal salt marsh creeks: Tidal influences in natural *Spartina*,

invasive *Phragmites*, and marshes treated for *Phragmites* removal

INTRODUCTION

Salt marsh habitats are thought to be critically important to coastal ecosystems,

operating as essential habitat for single or multiple life history stages of a variety of fish

and invertebrate species (Weinstein, 1979; Boesch and Turner, 1984; Rountree and Able,

1992; Kneib, 1997b). Of the various salt marsh habitats, intertidal marsh creeks are of

particular importance to the nekton community since they provide an extensive and direct

interface with the marsh surface during periods of tidal inundation, and thus 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 access to intertidal habitats is governed by marsh hydroperiod (Rozas, 1995) and

varies spatially and temporally due to factors such as life history stage, species-specific

migration cycles (e.g., seasonal, diel, diurnal, etc.), and intra/interspecific interactions

(McIvor and Odum, 1988; Kneib, 1997b). The limited availability of these temporary

habitats and their function as refuge, foraging, and reproduction habitats for numerous

coastal and estuarine species (Kneib, 1997b; Able and Fahay, 1998) makes continued

access to intertidal creeks vital.

One of the most important factors determining the function of salt marsh habitats

is the dominant vegetation (Weinstein et al., 1997). Salt marshes along the Atlantic and

Gulf coasts of the U.S. are typically dominated by smooth cordgrass, *Spartina*

alterniflora and other *Spartina* species (Kreeger and Newell, 2000; Mendelssohn and Morris, 2000). Over the last several decades, however, the invasion and subsequent dominance by the common reed (*Phragmites australis*), especially in the northeastern U.S., has occurred in anthropogenically disturbed marshes as well as relatively undisturbed marsh areas (Chambers et al., 1999; Weinstein and Balletto, 1999; Windham and Lathrop, 1999; Bart and Hartman, 2000; Weinstein et al., 2000; Lathrop et al., 2003; Raichel et al., 2003).

The alteration of marsh habitats through changes in vegetation type is especially important for intertidal creeks. *Phragmites* can potentially alter intertidal creek function dependent upon the stage of invasion (Able et al., 2003; Hunter et al., 2006). As the *Phragmites* invasion progresses, localized sediment accumulation occurs which impedes tidal flow and slowly fills in smaller intertidal creeks, eventually resulting in creeks that are filled in during the late invasion stages (Teal and Weinstein, 2002; Able et al., 2003; Osgood et al., 2003). Similarly, larger intertidal creeks in *Phragmites* marshes are characterized by steep banks, which have been shown to negatively affect fish through increased predation and reduced access to marsh surface habitats (McIvor and Odum, 1988; Teal and Weinstein, 2002). Habitat restoration has been proposed to ameliorate the deleterious effects of *Phragmites* invasion in brackish marshes and restore marshes to pre-invasion form and function (Able et al., 2003; Balletto et al., 2005).

Knowledge of the differential utility of marsh types during all tidal stages is critical for determining the value of such habitats to both the resident and transient nekton communities, assessing the risks that *Phragmites* invasions pose to such communities, and evaluating restoration success. Research has been conducted to examine the tidal

movement patterns of fish utilizing intertidal habitats, but relatively few studies have examined the distribution and habitat utilization of fishes in intertidal marsh areas on smaller temporal and spatial scales, such as those within individual tidal cycles (Kneib, 1997b; Desmond et al., 2000; Morrison et al., 2002; Speirs et al., 2002; Bretsch and Allen, 2006b; Cattrijsse and Hampel, 2006). Furthermore, there has been little research to date comparing small scale tidal movement patterns of fishes utilizing intertidal creeks within natural and restored marshes versus invasive *Phragmites* marshes.

Therefore, in order to discern the small scale temporal and spatial movement patterns within different marsh types and tidal stages, the nekton of intertidal creeks in representative natural *Spartina*-dominated, sites treated for *Phragmites* removal (hereafter called Treated), and invasive *Phragmites*-dominated marshes were examined. It was hypothesized that nekton utilization of intertidal creeks would differ (1) between the three marsh types, with *Spartina* and Treated creeks being utilized more than *Phragmites* creeks, and (2) between tide stages, with low tide stages and high tide stages consisting of unique nekton assemblages. These results were then used to determine overall nekton assemblage preferences and to identify possible effects of restoration efforts on intertidal nekton.

METHODS

Study area

The Alloway Creek watershed (Fig. 1-1), located in the oligohaline portion of the Delaware Bay estuary, has a long history of anthropogenic disturbance (Lotze et al., 2006), primarily in the form of agriculture, which has continued well into the 20th

century (Phillip, 2005). This consistent disturbance regime degraded the salt marshes and facilitated the invasion and establishment of *Phragmites* in this watershed (Weinstein and Balletto, 1999; Phillip and Field, 2005). Treatment for *Phragmites* removal (via herbicide and burning) in a 648 ha portion of the Alloway Creek watershed was undertaken for mitigation purposes by the Public Service Enterprise Group (PSEG) Estuarine Enhancement Program (EEP), with large scale efforts beginning in 1996 and reduced, concentrated efforts continuing on an as needed basis (Grothues and Able, 2003b; Balletto et al., 2005). These restoration efforts have resulted in three distinct marsh types of natural *Spartina*-dominated, Treated (and now dominated by *Spartina*), and invasive *Phragmites*-dominated marshes within the Alloway Creek watershed. Intertidal creeks were approximately 2 - 3.5 m wide at the mouth and had featureless, soft mud substrate bottoms with little or no remaining pools of standing water when fully drained at low tide. Creeks in the *Spartina* and Treated marshes had slightly sloping banks and creeks in *Phragmites* marsh had steep banks, approximately vertical or slightly concave. When selecting sampling sites, geographic proximity had to be partially sacrificed due to the locations of representative marshes of each type within the watershed, resulting in the *Spartina* and Treated sites being somewhat inland and approximately adjacent, while the *Phragmites* site was located closer to Delaware Bay (Fig. 1-1). Despite this difference, 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 sampling sites.

Field sampling

Two intertidal creeks were sampled in each marsh type (*Spartina*, Treated, and *Phragmites*; n = 6 creeks; Fig. 1-1). Nekton were collected with a seine (3.5 x 1.5 m seine with a 1.5 x 1.5 x1.5 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), 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-September 2004. Each marsh type was sampled completely (both creeks) in one day during daylight hours and all three marsh types were sampled during three 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. Individual fishes not identifiable to species were preserved in 95% ethanol or 10% formalin and processed in the laboratory. All nekton

not preserved for laboratory identification were returned to the water at the end of all sampling. Physical and environmental parameters were measured when sampling individual creeks. Temperature and salinity were recorded once for each creek and tide stage combination and measured with a hand-held oxygen, conductivity, salinity, and temperature system (YSI Model 85), 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.

Data analysis

Catch-per-unit-effort (CPUE) was used to compare the abundance of individual species among marsh types and tide stages. 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, marsh type, or both (final sample size n = 90, 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 = 96). Species abundance was then natural log transformed (ln (1 + CPUE)) and analyzed with a two factor analysis of variance (ANOVA) with tide and marsh 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). Where necessary, and 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).

Principal component analysis (PCA) was used to examine nekton assemblage variability. PCA is a commonly used multivariate data reduction technique that reduces

an original data set with a large number of correlated variables to a data set with a smaller

number of new, uncorrelated variables (or principal components) (Stauffer et al., 1985;

Bulger et al., 1993; Gotelli and Ellison, 2004). The principal components (PC) are linear

combinations of the original variables that explain most of the variation in the original

data set (McGarigal et al., 2000), and can be used in various other statistical techniques

(Gotelli and Ellison, 2004). Only species with a total abundance greater than 40

individuals for all marsh types combined were included in the PCA (n = 8, see Table 1).

For this analysis, CPUE was natural log transformed (ln (1 + CPUE)). All principal

component analyses were conducted using the PRINCOMP procedure in SAS (SAS,

Version 9.1). Treating the first principal component (PC1) as a proxy for nekton

assemblage, a simple linear regression was performed with mean depth and PC1 using

the REG procedure in SAS (SAS, Version 9.1).

Length (mean, range) was examined for all species collected. More extensive

length analyses were conducted with *F. heroclitus* and *M. americana*, the species with

the largest number of individuals measured. Overall length was examined by converting

all fork length species lengths possible to total length (TL) using the available length

conversions provided in Able and Fahay (1998). For the overall length, as well as the

two individual species, length was analyzed with a two factor ANOVA (with marsh and

tide 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). Temperature

and salinity were not recorded for some samples and were never recorded for Flood 2

samples at *Phragmites* creeks, thus sample sizes vary. Temperature (n = 62), salinity (n

= 62), and depth (n = 90) were then analyzed with a two factor ANOVA with marsh and

tide as factors. Differences in treatment means were examined using the Tukey-Kramer

test.

RESULTS

Physical characteristics

      Physical and environmental variables differed between marsh types and tide

stages (Fig. 1-2). Salinity was only significantly different between marshes, with

Phragmites creeks reporting slightly higher salinities (mean salinity = 2.8, SE = 0.43)

than the other sites (*Spartina* = 1.9, SE = 0.12; Treated = 1.8, SE = 0.15) regardless of

tide stage (Table 1-1), presumably due to the closer proximity to Delaware Bay (Fig. 1-

1). Temperature did not vary significantly between tide stages or marsh types. As

expected, depths at low tide stages (Ebb 2: mean depth = 0.5 m, SE = 0.02; Flood 1 = 0.5

m, SE = 0.03) were significantly different from those at high tide stages (Ebb 1 = 0.8 m,

SE = 0.05; Flood 2 = 0.9 m, SE = 0.03) 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 species composition, abundance, and size

      Fishes dominated the intertidal creek nekton, comprising 20 species and 5,248

individuals out of an overall total of 22 species and 5,456 individuals collected during the

duration of this study (Tables 1-2 and 1-3). Blue crab (*Callinectes sapidus*) were

frequently caught, while a snapping turtle (*Chelydra serpentina*) was caught only once.

Common resident nekton species (n = 4) were the dominant group (i.e., *F. heteroclitus,*

M. americana, Gobiosoma bosc, Trinectes maculatus) and made up 79% of the total

catch. *F. heteroclitus* alone accounted for 64% of the total indviduals caught. Transient

nekton species (n = 12) including *A. mitchilli, A. rostrata, C. sapidus*, and *M. saxatilis*

represented 20% of the total catch, with the remaining species (n = 6) from freshwater.

Species composition differed slightly between marsh types (Table 1-2). A total of

17 species were collected in *Spartina* and Treated marshes, while *Phragmites* marshes

had a slightly lower count of 13 species. These differences, however, were largely due to

the occurrence of species that were infrequently caught in all marshes. Overall nekton

abundance differed between marsh types (Tables 1-1 and 1-2), and was greatest in

Spartina marshes (CPUE = 25.78, SE = 3.96), followed by Treated (CPUE = 19.81, SE =

2.84) and *Phragmites* (CPUE = 14.32, SE = 2.00), but the only significant difference was

between *Spartina* and *Phragmites* marshes (p = 0.0138). Resident nekton dominated the

catch in *Spartina* (82%), Treated (72%), and *Phragmites* (82%) marshes, and transient

nekton had similar percentages in all three marsh types (Table 1-2). The abundance of

individual species differed between marsh types. *Ameiurus nebulosus, A. rostrata, G.*

bosc, and *M. saxatilis* showed significant differences (Table 1-1), and each species

exhibited a different abundance pattern across marshes (Fig. 1-3). *A. nebulosus* and *M.*

saxatilis were most abundant in Treated marshes and only showed a significant difference

between Treated and *Phragmites* marshes (*A. nebulosus*, p = 0.0066; *M. saxatilis*, p =

0.0413). The abundances of *A. rostrata* and *G. bosc* were significantly greater in

Phragmites than both *Spartina* and Treated marshes (*A. rostrata*: *Spartina, p* < 0.0001; Treated, *p* = 0.0006; *G. bosc*: *Spartina, p* = 0.0178; Treated, *p* = 0.0083). There were no significant differences between *Spartina* and Treated marshes for all four species with significant marsh effects. Although generally more *M. americana* were caught in *Spartina* marshes (Table 1-2), abundance did not vary between marsh types (*p* = 0.8303).

Species composition also differed slightly between tide stages, primarily due to the presence of a few infrequently caught species in some tide stages (Table 1-3). The number of species collected during each tide stage differed: Ebb 1 = 17, Ebb 2 = 12, Flood 1 = 11, and Flood 2 = 14. Total nekton abundance also differed between tides (Tables 1-1 and 1-3) and was greater for the low tide stages, Ebb 2 (CPUE = 25.68, SE = 4.27) and Flood 1 (CPUE = 26.17, SE = 4.41), than for the high tide stages, Ebb 1 (CPUE = 15.95, SE = 1.74) and Flood 2 (CPUE = 11.68, SE = 2.12), but the abundances at low tide stages were only significantly different from Flood 2 (Ebb 2, *p* = 0.0199; Flood 1, *p* = 0.0150). Resident nekton were by far the most abundant at low tide stages (Ebb 2 = 92%, Flood 1 = 90%), while resident and transient nekton abundance at high tide stages was mixed with a greater abundance of resident nekton (64%) at Ebb 1, and a greater abundance of transient nekton (60%) at Flood 2 (Table 1-3). The abundance of individual species also differed between tides. *A. mitchilli, A. rostrata, C. sapidus*, and *F. heteroclitus* all showed significant differences in abundance between tide stages (Table 1-1). *A. mitchilli* was significantly more abundant in Flood 2 (Fig. 1-4), with much lower abundance levels in all other tide stages (Ebb 1, *p* = 0.0478; Ebb 2, *p* < 0.0001; Flood 1, *p* = 0.0003). Conversely, *A. rostrata* had a significantly greater abundance in Ebb 1 than all other tide stages (Fig. 3; Ebb 2, *p* = 0.0019; Flood 1, *p* = 0.0055; Flood 2, *p* = 0.0008).

F. heteroclitus was the most abundant species overall and especially dominated the catch in the low tide stages (Table 1-3, Fig. 1-4), where significantly more were caught than in both of the high tide stages (Ebb 2 vs. Ebb 1 and Flood 2, $p < 0.0001$; Flood 1 vs. Ebb 1, $p = 0.0004$; Flood 1 vs. Flood 2, $p < 0.0001$). *C. sapidus* showed a trend towards steadily decreasing abundance from ebb to flood tides (Fig. 1-4), but abundance was only significantly different between Ebb 1 and Flood 2 ($p = 0.0059$). *M. americana* abundance did not vary statistically between tide stages ($p = 0.0766$), but the highest abundance was at the high tide stage Ebb 1 (CPUE = 3.95, S.E. = 0.93) and the lowest abundance was observed at the low tide stage Ebb 2 (CPUE = 1.82, S.E. = 0.65).

Size ranges (n = 4767 total measured) indicated that intertidal creeks were utilized primarily by juveniles of transient nekton and both juveniles and adults of resident nekton (Table 1-4). Overall length (across all species, all lengths TL, n = 4499) was not significantly different between marsh types, but differed between tide stages with some variation according to marsh type (ANOVA: tide, h*t $p < 0.0001$), however, larger fish were generally caught during Ebb 1 than all other tide stages (Fig. 1-5). The two intertidal nekton species with the most individuals measured, *F. heteroclitus* (n = 2848) and *M. americana* (n = 698), were examined individually. *F. heteroclitus* in both *Spartina* and Treated marshes were greater in size than those in *Phragmites* (Fig. 1-5), but this relationship varied with tide stage (ANOVA: marsh, tide, m*t $p < 0.0001$). Nevertheless, *F. heteroclitus* length in *Phragmites* was not affected by tide stage and fish in these creeks were consistently smaller. *M. americana* length followed a similar trend in *Phragmites* and Treated marshes, but fish size in *Spartina* marshes was more variable (Fig. 1-5), causing length to vary with both marsh type and tide stage (ANOVA: marsh,

tide $p < 0.0001$; m*t $p = 0.0002$). *M. americana* were largest during Ebb 1 in *Phragmites*, and fish were generally larger in *Phragmites* than both *Spartina* and Treated marshes for all tide stages except Flood 1.

Nekton assemblages

The nekton assemblage was characterized by two principal components, which together explained 73% of the variation in the original data set. PC1 explained 54% of the variation, apparently due to water depth, with samples from low tide stages (Ebb 2, Flood 1) associated with positive PC1 scores and samples from high tide stages (Ebb1, Flood 2) associated with negative scores (Fig. 1-6). The separation along PC2, while not quite as pronounced (19% of the variation), was most likely due to slight changes in the nekton assemblage from early to late summer, however sample dates were well mixed and no distinct patterns were seen when PC1 versus PC2 was plotted by month. Since this study focused only on one season, summer, and an examination of PCA scores by month revealed no patterns, PC2 was not examined further. The nekton assemblage did not differ between marsh types, therefore the assemblage analysis focused on tide stage differences. The prevailing species composition of the low and high tide groupings was determined by a plot of the species eigenvector loadings (Fig. 1-6). *F. heroclitus* primarily characterized low tide stages, whereas *A. mitchilli* and *M. americana* characterized high tide stages. *M. saxatilis*, *A. nebulosus*, and *A. rostrata* exhibited a minor trend towards high tide stages, while *G. bosc* and *C. sapidus* displayed a very minor trend towards low tide stages.

Since PCA revealed that nekton assemblage structure was largely dictated by water depth, it is not surprising that simple linear regression yielded an inverse

relationship between mean depth and PC1 (PC1 = 2.83 – 4.33*Mean Depth; R^2 = 0.60), with low and high tide assemblages distributed according to depth (Fig. 1-7). Some mixing occurred where tide stage depth ranges overlapped due to artifacts in the sampling procedure on particular days (i.e., delays caused by storm events). Excluding these exceptions, however, two distinct nekton assemblages can be identified within the tidal cycle of intertidal creeks: a low tide assemblage dominated by resident nekton and a high tide assemblage consisting of a mix of transient and resident nekton.

DISCUSSION

Nekton species composition, abundance, and size

Marsh type, generally, did not influence nekton intertidal creek utilization preferences based on comparison of species composition and abundance. However, two less abundant species preferred *Phragmites* creeks. *A. rostrata* abundance was consistently greater in *Phragmites* creeks for all tide stages. A similar preference for *Phragmites* marshes has also been observed on the marsh surface (Warren et al., 2001). *G. bosc* was also most abundant in *Phragmites* creeks, however, studies conducted in other New Jersey estuaries found that *G. bosc* were common in subtidal and intertidal creeks and displayed no distinct preferences for particular creek characteristics (Sogard and Able, 1991; Able et al., 1996; Able and Fahay, 1998, Rountree and Able, 1992).

Two other less abundant species, *M. saxatilis* and *A. nebulosus*, had greater abundance in Treated intertidal creeks than either *Spartina* or *Phragmites* creeks. A similar pattern for both species was found in subtidal creeks treated for *Phragmites* removal compared to a reference *Spartina* marsh (Grothues and Able, 2003a). In both

studies *A. nebulosus* abundance was greater in lower salinity waters, which is not surprising since *A. nebulosus* is characterized as a freshwater species (Arndt, 2004; see also Able et al., 2001). However, salinity was not significantly different between *Spartina* and Treated marshes in the present study, indicating that lower abundances in *Spartina* marshes may be attributed to other factors. Young-of-the-year (YOY) *M. saxatilis* (size groupings determined from Able and Fahay, 1998; Nemerson and Able, 2003; the size most often captured in the present study) have been observed at greater abundances in lower salinity subtidal marsh creeks (Grothues and Able, 2003a; Nemerson and Able, 2003), but they are just as likely to be equally abundant in creeks with higher salinities and varying dominant marsh vegetation (Able et al., 2001).

Greater abundances of smaller *F. heteroclitus* in *Spartina* versus *Phragmites* marshes have been observed in studies comparing marsh surface habitats (Able and Hagan, 2000; Able and Hagan, 2003; Able et al., 2003; Hunter et al., 2006; Hagan et al., 2007). The lack of smaller *F. heteroclitus* in *Spartina* and Treated intertidal creeks compared to *Phragmites* creeks in the present study is consistent with the above results because the smaller individuals in *Spartina* and Treated marshes utilize the available marsh surface (Able et al., 2003). The loss of such surface habitats in *Phragmites* marshes (see Hagan et al., 2007, for detailed descriptions of marsh surface habitats at these sites) would likely force smaller individuals to move to subtidal or other less suitable habitats during low tides (Able and Hagan, 2003).

Individual nekton species were predicted to follow a tidal migration pattern in intertidal creeks based upon their size and classification as either residents or transients, with resident species more abundant at low tide stages and in shallower water and

transient species more abundant at high tide stages and in deeper water in intertidal creeks. *F. heteroclitus* was the only resident nekton species to consistently adhere to this pattern and was the overwhelmingly dominant species in low tide stages. This same pattern was reported for *F. heteroclitus* in South Carolina salt marsh intertidal creeks (Bretsch and Allen, 2006b). Thus, the results of the present study are not surprising since *F. heteroclitus* is a ubiquitous and abundant species that utilizes intertidal marsh surface habitats extensively while they are submerged during high tide stages (Kneib, 1984, 1986; Able, 2002; Teo and Able, 2003b). Moreover, *F. heteroclitus* is a common prey item of piscivores (Kneib, 1997a, b; Tupper and Able, 2000; Nemerson and Able, 2003) and could find refuge by maintaining a position in the shallow, often turbid waters of intertidal habitats throughout the tidal cycle (i.e., following the edge of the tide and moving on to the marsh surface) (Cain and Dean, 1976; Cattrijsse et al., 1994; Kneib and Wagner, 1994; Rozas, 1995; Baltz et al., 1998; Franco et al., 2006), especially at smaller sizes.

Common transient nekton were most abundant when tides were high and water depths were greatest, but did not exhibit a symmetrical tidal migration pattern. This is likely due to transient nekton using intertidal creeks for shorter periods, migrating into creeks later and returning to subtidal habitats earlier (e.g., *A. rostrata*, *C. sapidus*, and *A. mitchilli* in the present study), presumably to feed, seek refuge from larger predators, or possibly to avoid stranding in unsuitable intertidal habitats (Kneib and Wagner, 1994; Kneib, 1995; Salgado et al., 2004a, b). *M. americana*, a large estuarine resident species, displayed an analogous intertidal creek utilization pattern (although not statistically significant). Juvenile *M. saxatilis* (Tupper and Able, 2000; Nemerson and Able, 2003),

M. undulatus (Nemerson and Able, 2005), and *M. americana* (Jones, Fox, and Able, unpublished data) have been observed using tidal creeks in Delaware Bay marshes to feed on many of the abundant nekton species caught in intertidal creeks in the present study including *F. heteroclitus*, *A. mitchilli*, *Menidia menidia*, and *C. sapidus*. Bretsch and Allen (2006b) observed that the highest proportion of individuals of most nekton taxa entered and exited South Carolina intertidal creeks at approximately the same depths during flood and ebb tides, but that some taxa did not display such symmetry. In the present study most nekton species did not migrate at similar depths during ebb and flood tides (see Table 1-3, Fig. 1-4 except *F. heteroclitus*). The asymmetrical abundance pattern is presumably not an artifact of sampling bias since varying tidal utilization patterns were observed as sampling occurred at approximately the same water depths for both low and both high tide stages (see Fig. 1-2 for water depths). For example, *C. sapidus* were captured frequently during the Ebb 1 high tide stage, but were rarely caught during the Flood 2 high tide stage at a similar water depth, possibly indicating that the sampling frequency might have only overlapped with nekton as they were either entering or leaving the marsh creeks, but not during both migrations.

Nekton assemblages

The nekton assemblage was generally comprised of the same species for all three marsh types. Assemblage structures were also found to be similar for marsh surface and intertidal and subtidal creeks in *Phragmite*s and non-*Phragmites* marshes within multiple US east coast salt marshes (Fell et al., 1998; Able et al., 2000; Able et al., 2001; Meyer et al., 2001; Fell et al., 2003; for marsh surface exceptions see Able and Hagan, 2000; Able et al., 2003). This indicates that each marsh type examined provides some base level of

resources allowing at least a small number of individuals to survive in each. Where differences occurred they were attributed to the presence of less abundant species. Therefore assemblage structure similarities alone may mask important differences in individual nekton movement and utilization patterns and should not be the sole metric relied upon for comparisons between marshes.

Nekton utilizing intertidal creeks in the Alloway Creek watershed showed a pattern of smaller, primarily resident marsh nekton dominating shallow water at low tide stages, and larger marsh nekton, including both transient and resident species, dominating deep water at high tide stages. A similar nekton assemblage pattern was observed in tidal creeks in Florida, with low tide catches of predominately juvenile and adult resident fishes, and high tide catches of mainly juveniles of transient species (Subrahmayman and Drake, 1975; Subrahmayman and Coultas, 1980). Studies in European intertidal salt marsh creeks revealed similar nekton assemblage patterns with *Pomatoschistus microps*, a species occupying a niche similar to *F. heteroclitus* in North American marshes (Cattrijsse et al., 1994), dominating low tide stages and a mix of species present at high tide stages (Hampel et al., 2003). Species identified with low or high tide assemblages may seek similar benefits and incur similar costs associated with their particular migration pattern, resulting in a predictable and routine tidal assemblage structure in intertidal creeks. Refuge from predators (both aquatic and non-aquatic), foraging, and nursery functions have been postulated as possible reasons for such tidal preferences in these Delaware Bay (Tupper and Able, 2000; Nemerson and Able, 2003, 2005) and other marshes (Baltz et al., 1993; Peterson and Turner, 1994; Kneib, 1997b; Salgado et al., 2004a, b; Bretsch and Allen, 2006b), and likely contribute to the tidal assemblage

differences observed in the present study. Water depth has been shown to be an important factor contributing to nekton habitat utilization and movement patterns (Davis, 1988; Ruiz et al., 1993; Krumme et al., 2004; Bretsch and Allen, 2006a), and the separation of low and high tide assemblages dominated by different species supports this concept.

The results of this study illustrate the importance of including tide stage in the experimental protocol when sampling intertidal habitats. Intertidal creeks serve as a tide-stage dependent corridor linking marsh surface and subtidal habitats (McIvor and Odum, 1988), both of which act as nekton sources for intertidal creeks. Smaller nekton may come off of the marsh surface into creeks during periods of inundation or as the tide is dropping, while larger nekton that are found in subtidal habitats during low tide periods (i.e., when intertidal creeks are drained) migrate into intertidal creeks on the incoming flood tide (Kneib and Wagner, 1994), thus the timing of sampling during the tidal cycle would determine the nekton assemblage. Conversely, information on nekton utilization patterns in intertidal creeks will aid in explaining observed tidal utilization patterns on the marsh surface and in subtidal creeks. Thus, examining habitat use patterns within tidal cycles provides valuable information on species and size composition of nekton utilizing intertidal habitats, as well as timing and duration of tidal migrations, all of which are critical to gain a complete picture of nekton habitat utilization throughout interconnected salt marsh habitats.

Implications for marsh restorations

The effect of marsh restoration efforts on intertidal nekton in the Alloway Creek watershed was inconsistent and varied according to the metric under consideration (i.e.,

species composition, abundance, size, nekton assemblage). *Spartina* and Treated

intertidal creeks supported a greater number of species than *Phragmites* creeks, but these

differences were due to the occurrence of a small number of infrequently caught species.

Spartina intertidal creeks had greater overall nekton abundance than *Phragmites* creeks

but Treated creeks had an intermediate abundance, possibly suggesting that they have not

yet converged on the values observed for natural reference (i.e., *Spartina*) creeks. All

three marsh types were similarly dominated by resident nekton. Two species were more

abundant in *Phragmites* intertidal creeks, which suggests that some species may benefit

from utilizing invasive *Phragmites* intertidal creeks. Two species were more abundant in

Treated creeks indicating that, for these two species, Treated creeks were functioning

similar to natural *Spartina* creeks. However, the majority of individual species showed

no significant differences in abundance by marsh type. Furthermore, the overall nekton

assemblage did not differ between marsh types. It is important to note that similarities

and differences between *Spartina*, Treated, and *Phragmites* intertidal creek nekton may

be attributable to influential factors other than marsh restoration efforts (e.g., site

differences, species annual variation), but based on the multiple intertidal creek nekton

metrics examined in this study, it appears that *Spartina*, Treated, and *Phragmites*

intertidal creeks were functioning similarly and restoration efforts had little impact on

intertidal creek nekton utilization patterns.

The effect of salt marsh restoration differs relative to the marsh habitat examined.

Within similar salt marsh systems, studies found that marsh surface resident fishes were

negatively affected by invasive *Phragmites* (Able and Hagan, 2000, 2003; Hunter et al.,

2006), while studies on subtidal creeks found no differences (although this is scale

dependent, Grothues and Able, 2003a, b). Detection of a definitive nekton response to

invasive *Phragmites* in marsh surface habitats is more likely since small fishes and crabs

utilizing marsh surface habitats are less mobile and dependent on the same habitat for

long periods of time (e.g., days or weeks). Nekton responses in subtidal habitats are

more difficult to detect because nekton utilizing these habitats are highly mobile and not

bound to specific habitats, therefore possibly lessening exposure time to invasive

Phragmites marshes and diminishing any potential negative effects. Since the species

comprising intertidal creek nekton come from both marsh surface and subtidal habitats,

the varying responses to each metric evaluated are not surprising and can presumably be

attributed to this combination of both resident and transient nekton species. A number of

previous studies observed similarities in nekton species composition and abundance when

comparing *Spartina* (or mixed non-*Phragmites* vegetation) and *Phragmites* intertidal

marsh surface and creek edge habitats (Fell et al., 1998; Meyer et al., 2001; Warren et al.,

2001; Fell et al., 2003; Osgood et al., 2003; Osgood et al., 2006), and several also

reported size differences between marshes (Able and Hagan, 2000; Meyer et al., 2001;

Osgood et al., 2003). Such varying results illustrate that the specific salt marsh habitat

examined will greatly influence the restoration evaluation outcome, and therefore an

evaluation approach synthesizing the response in multiple habitats is preferred (see Able

et al., 2008).

Table 1-1. Analysis of variance results (F statistics) for effect of marsh type and tide stage on depth (m), salinity, temperature (°C), and overall and individual species CPUE. Temperature and salinity were not recorded for some samples and were never recorded for Flood 2 samples at *Phragmites* marshes. Overall species CPUE included all species (n = 22) caught during this study. Individual species (n = 8) shown are those used in the PCA. Marsh*Tide interactions were rarely significant (only once) and are not shown. 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 = 2)	Tide (df = 3)
Physical Characteristics			
Depth	78	ns	48.21***
Salinity	51	4.65*	ns
Temperature	51	ns	ns
Nekton			
Overall Species CPUE	78	4.18*	4.70**
Individual Species CPUE			
Ameiurus nebulosus	78	5.04**	ns
Anchoa mitchilli	78	ns	10.62***
Anguilla rostrata	78	17.85***	6.80***
Callinectes sapidus	78	ns	4.58**
Fundulus heteroclitus	78	ns	22.14***
Gobiosoma bosc	78	5.65**	ns
Morone americana	78	ns	ns
Morone saxatilis	78	3.60*	ns

Table 1-2. Alloway Creek watershed intertidal creek tidal seining species composition and abundance (catch-per-unit-effort, CPUE, with standard error), and total number caught for each marsh type (all creeks, tide stages, and months 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: *Spartina*, n = 32; Treated, n = 30; *Phragmites*, n= 28). 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 each marsh type separately and combined (percentages for freshwater species accounted for 2% or less in each marsh type and were not shown).

Species	EC	*Spartina*			Treated			*Phragmites*			Combined
		CPUE	SE	Total	CPUE	SE	Total	CPUE	SE	Total	Total
Alosa aestivalis	T	0.01	0.01	1	0	0	0	0.04	0.03	3	4
Ameiurus nebulosus	F	0.18	0.06	17	0.29	0.11	26	0.01	0.01	1	44
Anchoa mitchilli	T	2.95	0.94	283	3.66	1.40	329	0.79	0.15	66	678
Anguilla rostrata	T	0.19	0.06	18	0.36	0.08	32	0.80	0.14	67	117
Brevoortia tyrannus	T	0.17	0.16	16	0	0	0	0	0	0	16
Callinectes sapidus	T	0.78	0.24	74	0.78	0.31	70	0.75	0.17	63	207
Chelydra serpentina	F	0.01	0.01	1	0	0	0	0	0	0	1
Clupea harengus	T	0.01	0.01	1	0.01	0.01	1	0	0	0	2
Cynoscion regalis	T	0.01	0.01	1	0.01	0.01	1	0.01	0.01	1	3
Fundulus heteroclitus	R	17.74	4.39	1702	11.92	3.06	1073	8.35	1.76	701	3476
Gobiosoma bosc	R	0.30	0.12	28	0.26	0.12	23	0.88	0.22	74	125
Lepomis gibbosus	F	0	0	0	0.01	0.01	1	0	0	0	1
Lepomis macrochirus	F	0.01	0.01	1	0.01	0.01	1	0.05	0.05	4	6
Menidia menidia	T	0	0	0	0.03	0.02	3	0.04	0.02	3	6
Micropogonias undulatus	T	0.09	0.08	9	0.03	0.02	3	0	0	0	12
Morone americana	R	3.18	0.82	303	2.07	0.44	186	2.49	0.55	209	698
Morone saxatilis	T	0.14	0.04	13	0.34	0.10	31	0.12	0.05	10	54
Notemigonus crysoleucas	F	0.01	0.01	1	0	0	0	0	0	0	1
Perca flavescens	F	0	0	0	0	0	0	0.01	0.01	1	1
Strongylura marina	T	0	0	0	0.01	0.01	1	0	0	0	1
Syngnathus fuscus	T	0.01	0.01	1	0.01	0.01	1	0	0	0	2
Trinectes maculatus	R	0	0	0	0.01	0.01	1	0	0	0	1
All Species Combined		25.78	3.96	2470	19.81	2.84	1783	14.32	2.00	1203	5456
Resident Species				82%			72%			82%	79%
Transient Species				17%			26%			18%	20%

Table 1-3. Alloway Creek watershed intertidal creek tidal seining species composition and abundance (catch-per-unit-effort, CPUE, with standard error), and total number caught for each tide stage (all creeks, marsh types, and months 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 (final sample size: Ebb 1, n = 20; Ebb 2, n = 24; Flood 1, n = 24; Flood 2, n = 22). The relative abundance of estuarine resident and estuarine transient species is indicated as a percentage of the total abundance for each tide stage separately and combined (percentages for freshwater species accounted for 3% or less in each tide stage and were not shown).

Species	EBB 1			EBB 2			FLOOD 1			FLOOD 2		
	CPUE	SE	Total	CPUE	SE	Total	CPUE	SE	Total	CPUE	SE	Total
Alosa aestivalis	0	0	0	0.06	0.03	4	0	0	0	0	0	0
Ameiurus nebulosus	0.38	0.17	23	0.10	0.05	7	0.08	0.05	6	0.12	0.06	8
Anchoa mitchilli	2.27	0.85	136	0.40	0.14	29	1.39	0.85	100	6.27	1.86	413
Anguilla rostrata	0.87	0.22	52	0.31	0.06	22	0.38	0.10	27	0.24	0.06	16
Brevoortia tyrannus	0.27	0.25	16	0	0	0	0	0	0	0	0	0
Callinectes sapidus	1.40	0.38	84	1.06	0.34	76	0.53	0.20	38	0.14	0.05	9
Chelydra serpentina	0.02	0.02	1	0	0	0	0	0	0	0	0	0
Clupea harengus	0.02	0.02	1	0	0	0	0	0	0	0.02	0.02	1
Cynoscion regalis	0.03	0.02	2	0	0	0	0	0	0	0.02	0.02	1
Fundulus heteroclitus	5.77	1.73	346	20.94	4.52	1508	21.10	4.56	1519	1.58	0.33	103
Gobiosoma bosc	0.45	0.19	27	0.75	0.26	54	0.35	0.15	25	0.30	0.10	19
Lepomis gibbosus	0.02	0.02	1	0	0	0	0	0	0	0	0	0
Lepomis macrochirus	0.02	0.02	1	0.07	0.06	5	0	0	0	0	0	0
Menidia menidia	0.05	0.04	3	0.01	0.01	1	0.01	0.01	1	0.02	0.02	1
Micropogonias undulatus	0.13	0.12	8	0.04	0.03	3	0.01	0.01	1	0	0	0
Morone americana	3.95	0.93	237	1.82	0.65	131	2.17	0.69	156	2.67	0.68	174
Morone saxatilis	0.30	0.09	18	0.13	0.06	9	0.14	0.06	10	0.26	0.11	17
Notemigonus crysoleucas	0	0	0	0	0	0	0.01	0.01	1	0	0	0
Perca flavescens	0.02	0.02	1	0	0	0	0	0	0	0	0	0
Strongylura marina	0	0	0	0	0	0	0	0	0	0.02	0.02	1
Syngnathus fuscus	0	0	0	0	0	0	0	0	0	0.03	0.02	2
Trinectes maculatus	0	0	0	0	0	0	0	0	0	0.02	0.02	1
All Species Combined	15.95	1.74	957	25.68	4.27	1849	26.17	4.41	1884	11.68	2.12	766
Resident Species			64%			92%			90%			39%
Transient Species			33%			8%			9%			60%

Table 1-4. 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, and months combined). Fishes and
invertebrates were measured either in fork length (*), total length (†), carapace
width (‡), or standard straight carapace length (§).

Species	Mean	SE	Min	Max	Total
Alosa aestivalis *	49	--	--	--	1
Ameiurus nebulosus [†]	196	9.01	110	310	44
Anchoa mitchilli *	27	0.30	11	68	633
Anguilla rostrata [†]	168	9.33	69	530	113
Brevoortia tyrannus *	53	2.78	40	91	16
Callinectes sapidus [‡]	36	1.74	5	143	205
Chelydra serpentina [§]	350	--	--	--	1
Clupea harengus *	36	0.50	35	36	2
Cynoscion regalis [†]	29	14.90	12	59	3
Fundulus heteroclitus [†]	51	0.44	12	122	2848
Gobiosoma bosc [†]	24	0.43	13	40	125
Lepomis gibbosus *	50	--	--	--	1
Lepomis macrochirus *	39	2.00	32	44	5
Menidia menidia *	41	3.53	30	50	6
Micropogonias undulatus [†]	22	0.95	19	29	12
Morone americana *	93	0.95	20	259	692
Morone saxatilis *	83	6.59	22	190	54
Notemigonus crysoleucas *	99	--	--	--	1
Perca flavescens *	155	--	--	--	1
Strongylura marina [†]	93	--	--	--	1
Syngnathus fuscus [†]	49	2.00	47	51	2
Trinectes maculatus [†]	61	--	--	--	1
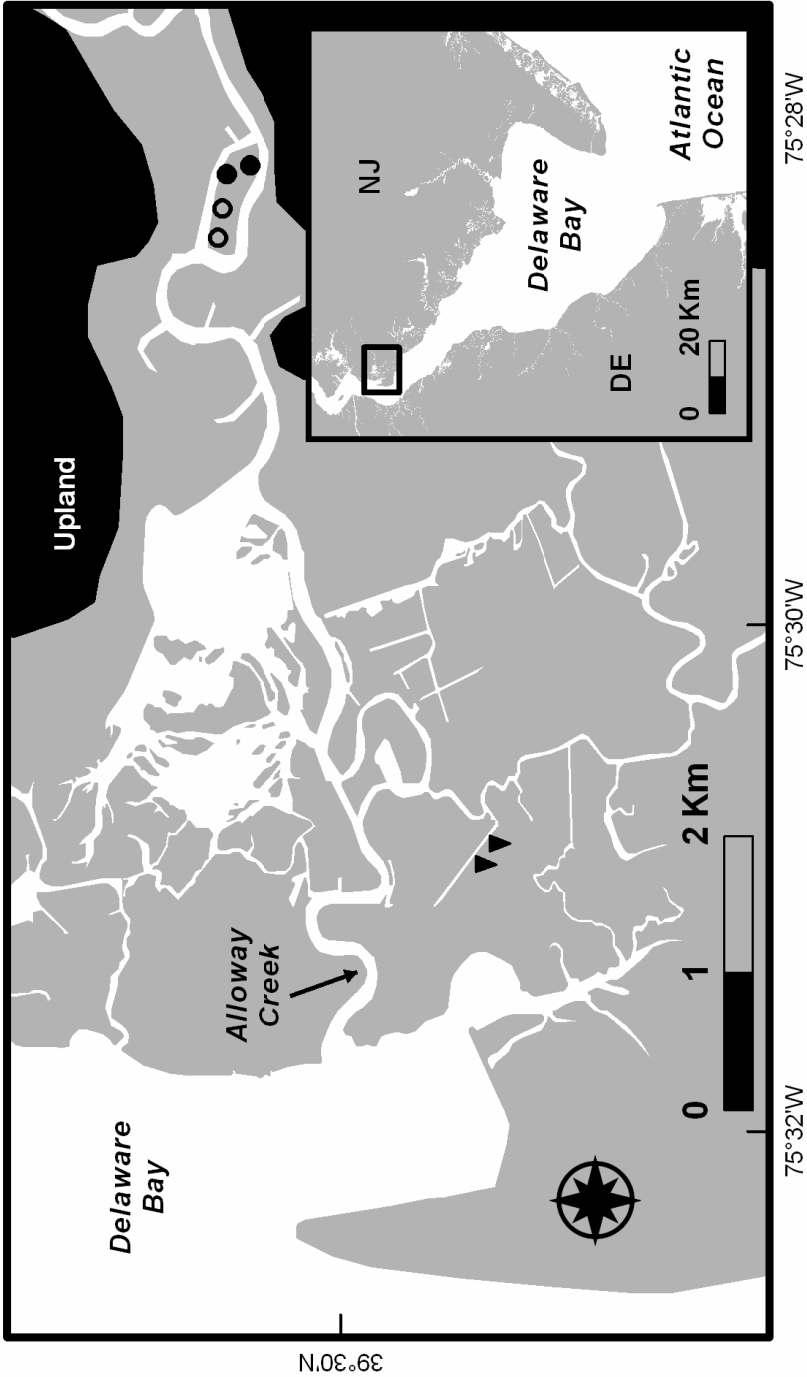
Figure 1-1. The Alloway Creek watershed in the oligohaline upper Delaware Bay estuary of New Jersey (NJ), USA. Intertidal creek seine sampling sites are shown for *Spartina* (closed circles), Treated (open circles), and *Phragmites* (closed triangles) marshes.
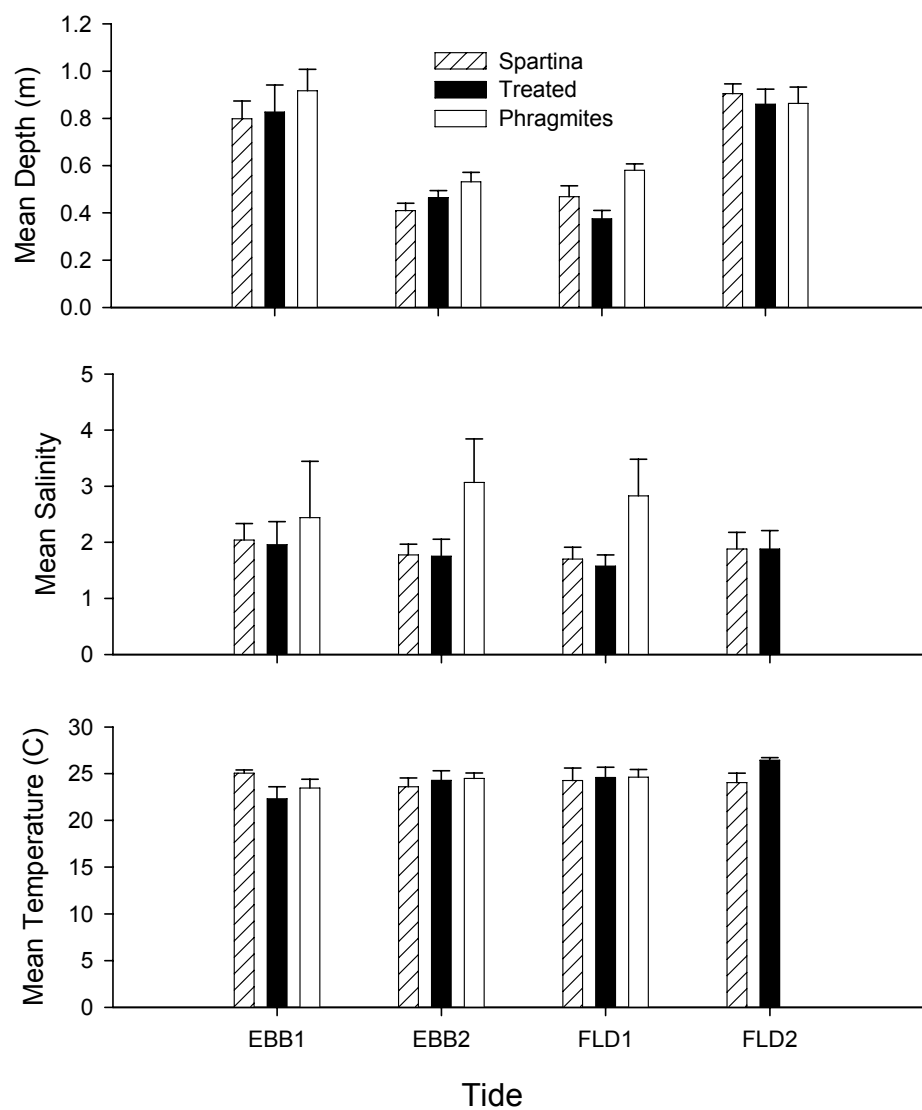
Figure 1-2. Mean depth, salinity, and temperature for all marsh types and tide stages. Temperature and salinity were not recorded for Flood 2 at *Phragmites* marshes.
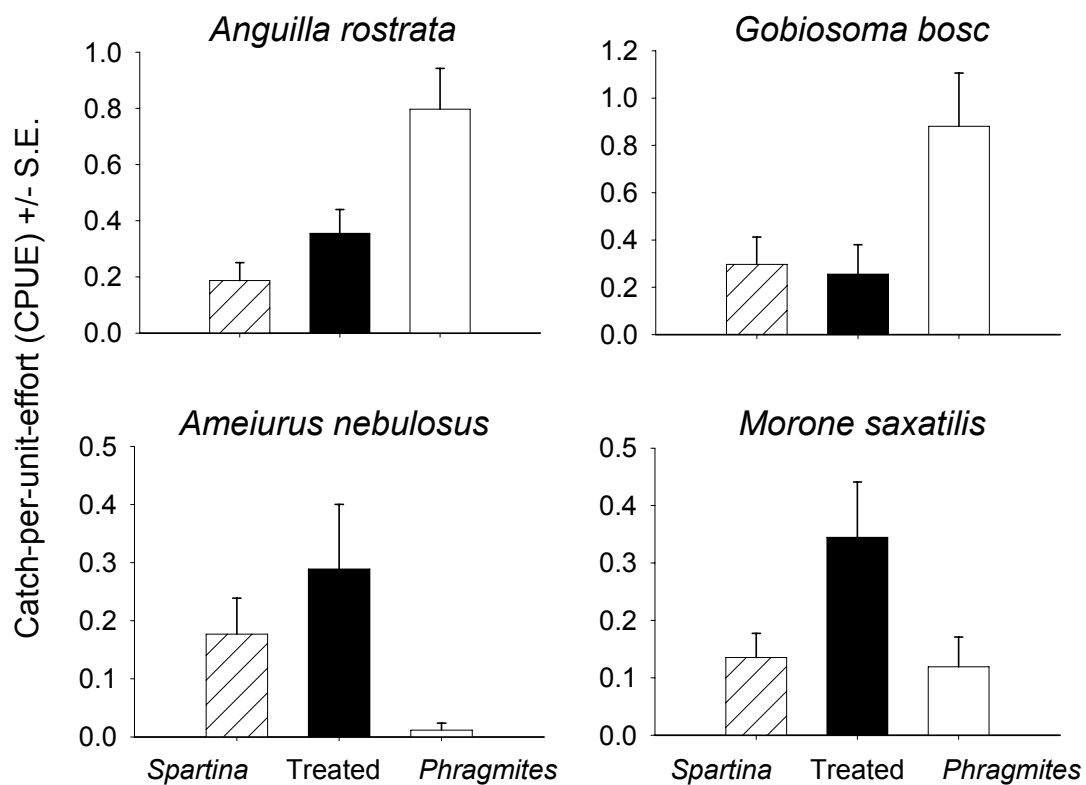
Figure 1-3. Catch-per-unit-effort (CPUE) by marsh type for species where marsh type (*Spartina*, Treated, *Phragmites*) was found to have a significant effect on abundance.
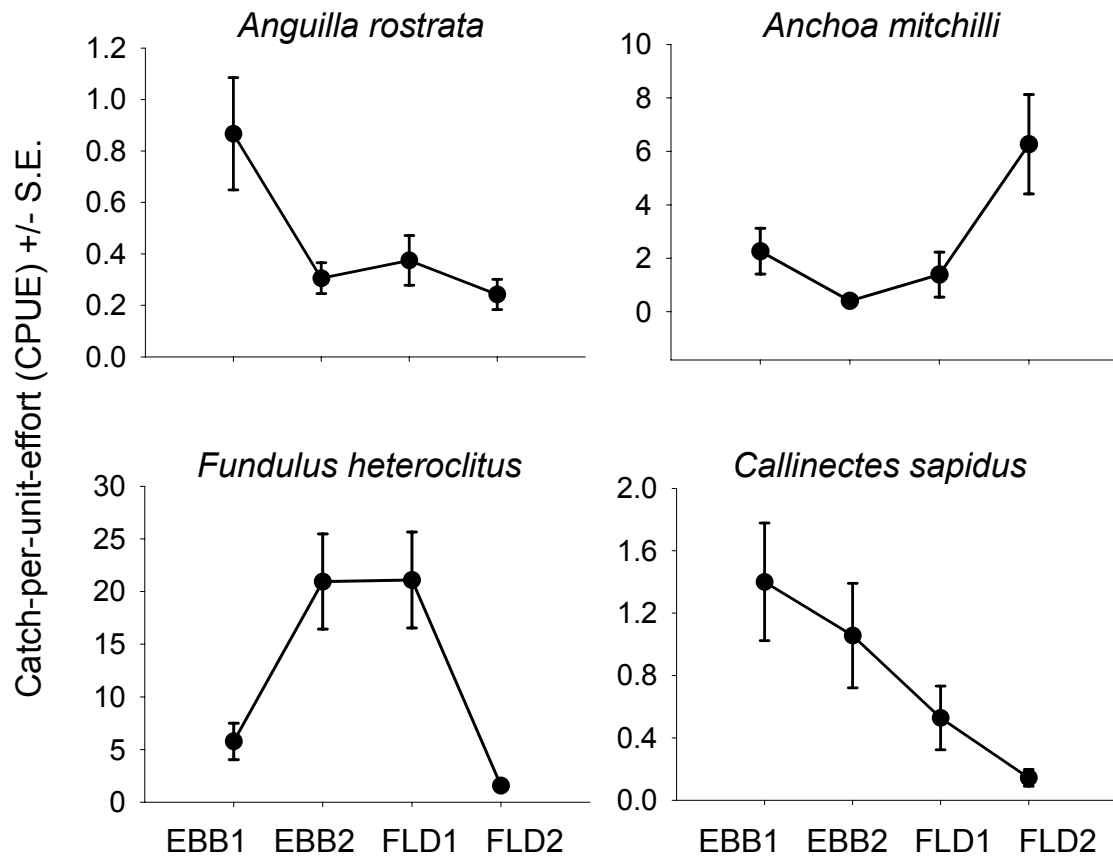
Figure 1-4. Catch-per-unit-effort (CPUE) by tide stage for species where tide stage (Ebb 1, Ebb 2, Flood 1, Flood 2) was found to have a significant effect on abundance.
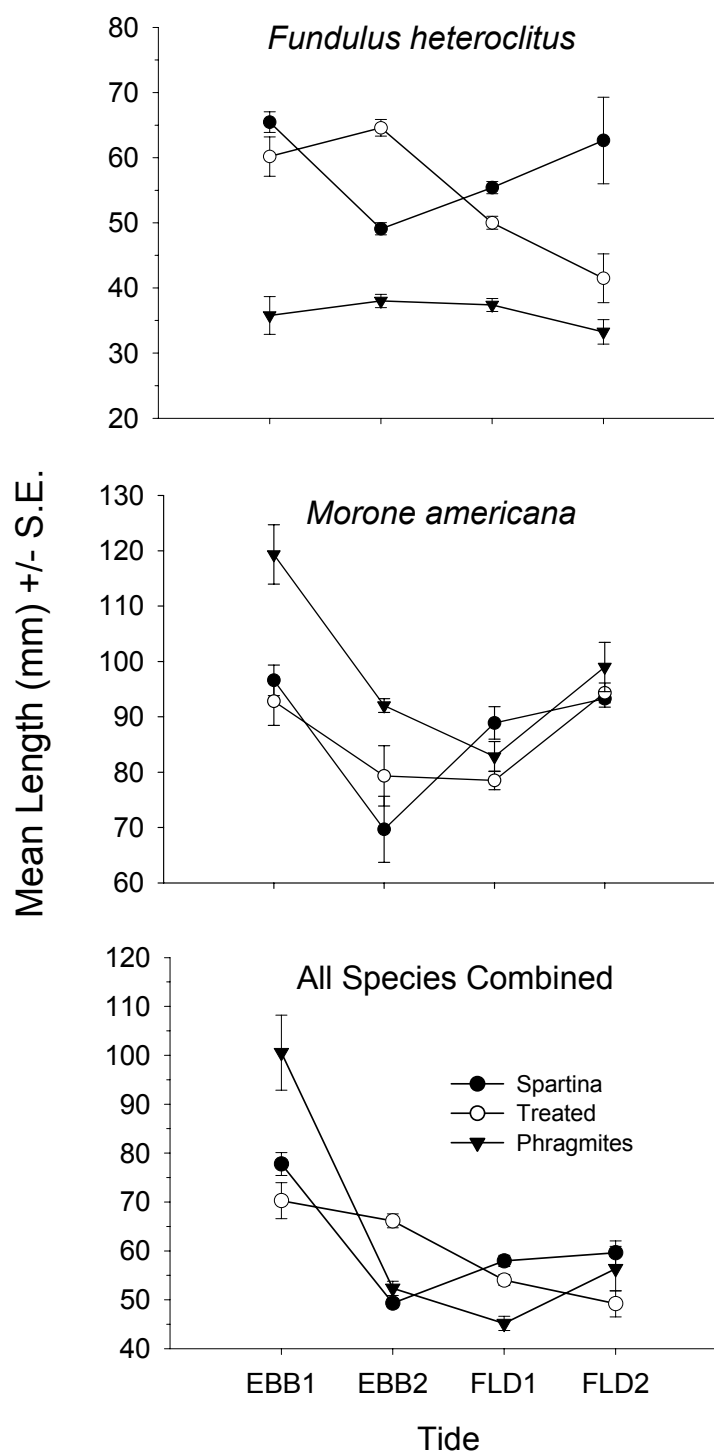
Figure 1-5. Mean length by marsh type and tide stage for *F. heteroclitus* (n = 2,848), *M. americana* (n = 692), and all species combined (n = 4,499).
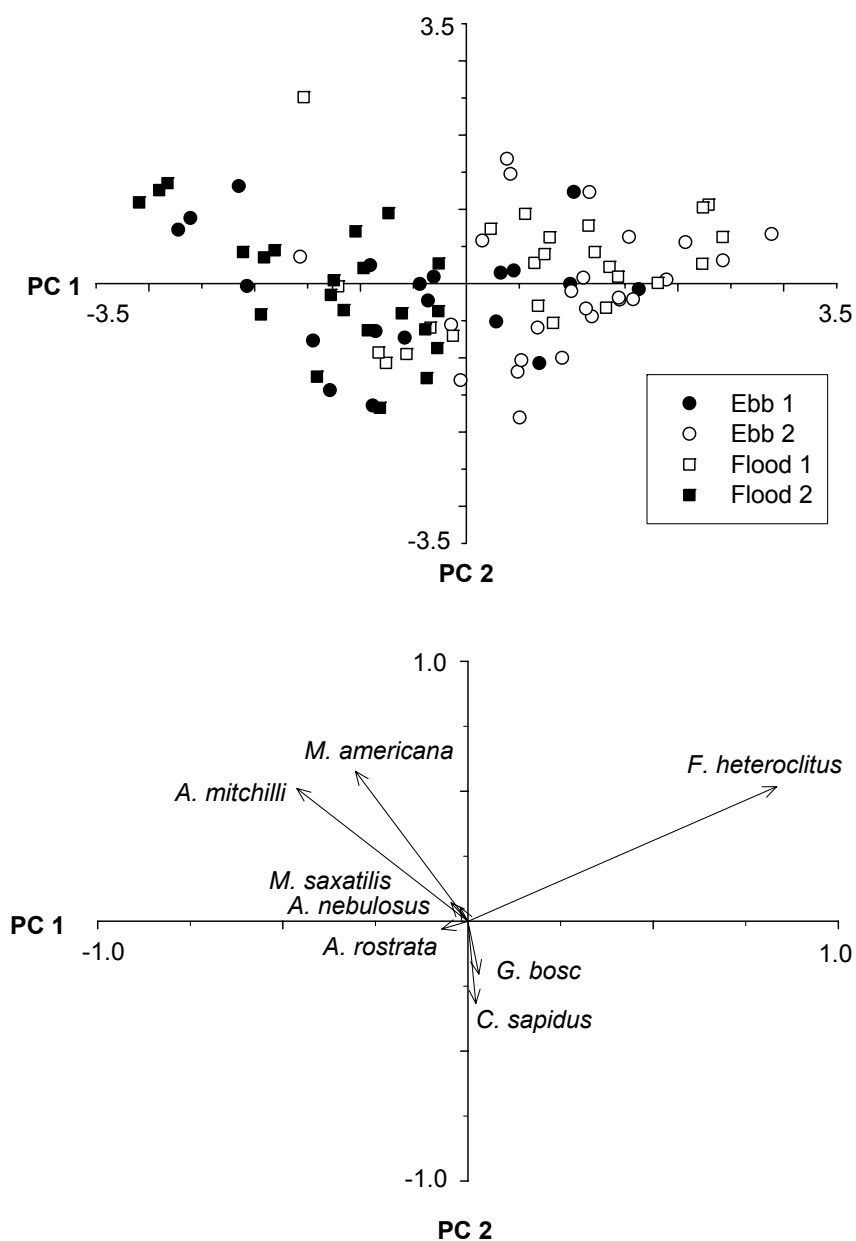
Figure 1-6. Principal component analysis of intertidal nekton assemblage. Principal component 1 (PC1) explained 54% of the variation and principal component 2 (PC2) explained 19%. Species eigenvector loadings are plotted on PC1 and PC2.
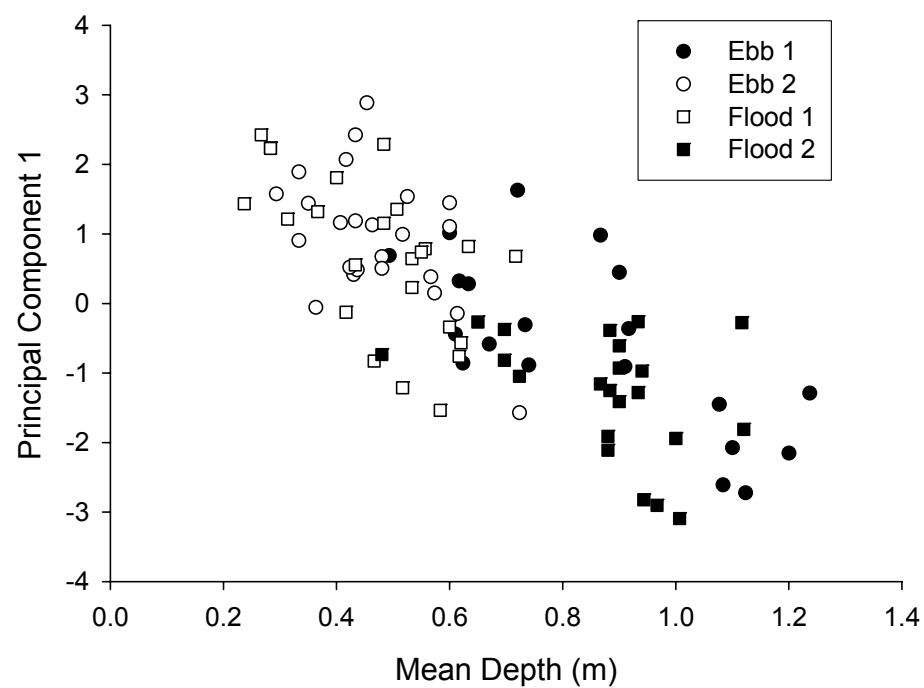
Figure 1-7. Simple linear regression of mean water depth and PC1 for the intertidal nekton assemblage across all marsh types.

CHAPTER 2

Tidal utilization of nekton in Delaware Bay restored and reference intertidal salt marsh

creeks

INTRODUCTION

A large number of coastal and estuarine species depend on salt marsh habitats for

such critical functions as refuge, reproduction, and foraging (Kneib, 1997b; 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, and therefore access to other intertidal habitats, is

controlled by marsh hydroperiod and varies temporally and spatially according to

physical and biological factors (Rozas, 1995).

Anthropogenic disturbances to the salt marsh ecosystem, 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 (Weishar et al., 2005; Philipp, 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., re-create) 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 such habitats to nekton (Kimball and Able, 2007a). Relatively few studies, however, 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, 1997b; 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, 2007a).

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 then used to determine overall nekton assemblage utilization patterns and to evaluate the success of marsh restoration efforts.

METHODS

Study Area

The restored and reference marshes were located in the mesohaline lower portion of the Delaware Bay estuary (Fig. 2-1). 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 references marshes are currently characterized by a *Spartina alterniflora*-dominated vegetation community (Able et al., 2004; Hinkle and Mitsch, 2005) typical of other US 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, thus the

reference marsh intertidal creeks are located somewhat farther inland (approximately 3

km) than the restored marsh intertidal creeks (approximately 1 km; Fig. 2-1). Other site

characteristics, however, 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.

Field Sampling

Two intertidal creeks were sampled in each marsh type (restored and reference

marshes, n = 4 creeks; Fig. 2-1). Nekton were collected with a seine (3.5 x 1.5 m seine

with a 1.5 x 1.5 x 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), 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. Physical and environmental parameters were measured when sampling individual creeks. Temperature and salinity were recorded once for each creek and tide stage combination and measured with a hand-held oxygen, conductivity, salinity, and temperature system (YSI Model 85), 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.

Data 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 2-1 and 2-2).

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 principal

component analyses were conducted using the PRINCOMP procedure in SAS (SAS,

Version 9.1).

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 fork length species lengths possible to total length (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 tides 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 and therefore sample sizes vary: temperature, n = 125; salinity, n = 125. 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 2-1). Salinity was significantly different between marshes, with restored marsh creeks reporting slightly higher salinities (mean salinity = 16.9, 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 (Fig. 2-1). Temperature varied significantly with both marsh type and tide stage. Restored marsh creeks had slightly higher temperatures (mean temperature = 24.1, SE = 0.62) than the reference marsh creeks (mean temperature = 23.5, SE = 0.46), while ebb tide temperatures (Ebb 1: mean temperature = 22.3, SE = 0.68; Ebb 2 = 22.4, SE = 0.75) were lower than those in flood tide (Flood 1 = 25.4, SE = 0.71; Flood 2 = 24.9, 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 2-2 and 2-3). Blue Crab (*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 principal components (PC) 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 respectively. No nekton assemblage patterns were seen when PC scores were analyzed by marsh type, tide stage, year, or month (see Fig. 2 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. 2-2). The remaining five nekton species used in the PCA had low species eigenvector loadings that were near the origin, and therefore 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 2-2). A total of 20 species were collected in the restored marsh while the reference marsh had fewer with 15 species. 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 (Tables 2-1 and 2-2, Fig. 2-3), 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 2-2).

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 2-1). *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. 2-4) with greater abundance at the reference marsh than the restored marsh ($p = 0.0015$). *A. pseudoharengus* was more abundant at the restored marsh, however, this was the only species collected with an abundance trend that differed greatly with sampling year (Table 2-1). *F. heteroclitus* (Fig. 2-5), *C. sapidus* (Fig. 2-6), 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 2-2).

Species composition and overall abundance also differed slightly between tide stages (Table 2-3). 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 (Tables 2-1 and 2-3, Fig. 2-3), 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 2-3). The abundance of individual species

differed between tide stages as well (Table 2-1). *M. menidia* abundance was greatest at

Flood 2 (Table 2-3, Fig. 2-4), with significant differences between abundances at flood

tide stages and ebb tide stages (Flood 1 vs. Ebb 1, $p = 0.0296$; Flood 1 vs. Ebb 2, $p <$

0.0001; Flood 2 vs. Ebb 1, $p = 0.0006$; Flood 2 vs. 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. 2-5) and *C. variegatus* were generally more

abundant at low tide stages than high tide stages (Table 2-3), but the relationships varied

according to marsh type (Table 2-1). *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 (Table 2-1, Fig. 2-6).

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 2-4). Overall species length (all lengths TL, n = 18,270) varied

with both marsh type and tide stage together (Table 2-1, Fig. 2-3). However, 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 2-2), that were on average larger (Table 2-4), 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. 2-5). 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. 2-4). 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. 2-6). A length-frequency analysis showed a bimodal distribution for *C. sapidus* around 15 mm 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. 2-6).

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 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.

heroclitus* 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 year 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., 2008). 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 year period (1996 – 2005) since marsh

restoration efforts took place. However, the relative abundances of the dominant species

within each marsh type have changed over time. *F. heteroclitus* and *M. menidia*

abundances, for example, 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 documented by 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, 2006b). Similarly, 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, 1997b; Bretsch and Allen, 2006b; Kimball and Able, 2007a) 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. Furthermore, 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), thus 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, however, 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 intertidal 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, 2007a). 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 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. However, 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, 2007a). 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 thus 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, however, 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 blue crabs

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, however, 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*. In addition, 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 therefore have a greater opportunity to be affected (positively or negatively) by intertidal creek geomorphologies. In contrast, transient species that are highly mobile and only spend a portion of their life cycle in salt marshes (Kneib, 1997b; 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; Fig. 2-1). 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). However, 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, 2007a). 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, 2007a). 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. Therefore examining habitat use patterns within tidal cycles will greatly improve our knowledge of nekton habitat utilization throughout all salt marsh habitats (Kimball and Able, 2007a; Rountree 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, 1997b; 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). Furthermore, the species comprising intertidal creek nekton come from both marsh surface and subtidal habitats, thus varying responses to some metrics may be attributed to this combination of both resident and transient nekton species from different sources. Nevertheless, within these same Delaware Bay marshes studies examining nekton use of intertidal creeks (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. Additionally, 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., 2008). 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, 2007a), therefore the evaluation of restoration success should incorporate the nekton response in multiple marsh habitats.

Table 2-1. 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 (n = 7) shown are those used in the principal component analysis. 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 x Tide (df = 3)	Marsh x 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
Nekton					
Overall Species CPUE	132	65.69***	6.78***	ns	ns
Individual Species CPUE					
Alosa pseudoharengus	132	10.16**	ns	ns	12.10***
Brevoortia tyrannus	132	7.95**	ns	ns	ns
Callinectes sapidus	132	ns	ns	2.99*	ns
Cyprinodon variegatus	132	25.39***	2.69*	2.73*	ns
Fundulus heteroclitus	132	24.61***	24.36***	2.73*	ns
Menidia beryllina	132	ns	ns	ns	ns
Menidia menidia	132	10.54**	25.55***	ns	ns
Overall Species Length	18250	73.44***	39.42***	17.33***	ns

Table 2-2. 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 0.5% in each marsh type and were not shown).

Species	EC	Restored			Reference			Combined
		CPUE	SE	Total	CPUE	SE	Total	Total
Alosa aestivalis	T	0.32	0.19	72	0	0	0	72
Alosa mediocris	T	0.10	0.10	22	0	0	0	22
Alosa pseudoharengus	T	1.02	0.45	229	0	0	0	229
Ameiurus nebulosus	F	0	0	0	0.01	0.01	1	1
Anchoa mitchilli	T	0.33	0.12	75	0	0	0	75
Anguilla rostrata	T	0.16	0.03	37	0.01	0.01	2	39
Bairdiella chrysoura	T	0.02	0.01	5	0	0	0	5
Brevoortia tyrannus	T	2.63	1.37	592	0.36	0.36	84	676
Callinectes sapidus	T	3.60	0.65	810	2.61	0.45	604	1414
Cynoscion regalis	T	0.04	0.02	9	0	0	0	9
Cyprinodon variegatus	R	0.01	0.01	2	2.46	0.92	569	571
Fundulus heteroclitus	R	28.18	5.14	6341	160.47	30.29	37069	43410
Fundulus majalis	R	0	0	0	0.01	0.01	2	2
Gobiosoma bosc	R	0.15	0.04	34	0	0	0	34
Leiostomus xanthurus	T	0.15	0.07	34	0.07	0.04	17	51
Lucania parva	R	0	0	0	0.01	0.01	1	1
Menidia beryllina	R	0.01	0.01	1	0.53	0.44	123	124
Menidia menidia	T	12.48	3.38	2807	51.06	10.74	11796	14603
Micropogonias undulatus	T	0.13	0.08	30	0.01	0.01	1	31
Morone americana	R	0	0	0	0.02	0.01	4	4
Morone saxatilis	T	0.01	0.01	1	0.02	0.01	4	5
Mugil curema	T	0.01	0.01	2	0	0	0	2
Pogonias cromis	T	0.28	0.09	63	0.03	0.01	6	69
Syngnathus fuscus	T	0.01	0.01	1	0	0	0	1
All Species Combined		49.63	7.12	11167	217.68	31.59	50283	61450
Resident Species				57%			75%	72%
Transient Species				43%			25%	28%

Table 2-3. 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). 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 0.5% in each tide stage and were not shown).

Species	EBB 1			EBB 2			FLOOD 1			FLOOD 2		
	CPUE	SE	Total	CPUE	SE	Total	CPUE	SE	Total	CPUE	SE	Total
Alosa aestivalis	0.58	0.36	68	0.03	0.03	3	0.01	0.01	1	0	0	0
Alosa mediocris	0.19	0.19	22	0	0	0	0	0	0	0	0	0
Alosa pseudoharengus	1.41	0.84	165	0.14	0.09	15	0.13	0.13	15	0.30	0.21	34
Ameiurus nebulosus	0	0	0	0	0	0	0	0	0	0.01	0.01	1
Anchoa mitchilli	0.31	0.19	36	0.02	0.01	2	0.19	0.10	22	0.13	0.08	15
Anguilla rostrata	0.09	0.04	11	0.07	0.03	8	0.06	0.02	7	0.11	0.04	13
Bairdiella chrysoura	0.01	0.01	1	0	0	0	0.03	0.02	3	0.01	0.01	1
Brevoortia tyrannus	3.87	2.58	453	0.75	0.47	83	0.14	0.12	16	1.09	0.77	124
Callinectes sapidus	4.66	1.22	545	3.15	0.70	350	2.52	0.53	287	2.04	0.34	232
Cynoscion regalis	0.01	0.01	1	0.06	0.04	7	0.01	0.01	1	0	0	0
Cyprinodon variegatus	0.65	0.43	76	2.30	1.54	255	2.00	1.08	228	0.11	0.06	12
Fundulus heteroclitus	82.79	30.83	9686	137.68	39.15	15282	154.79	39.80	17646	6.98	1.12	796
Fundulus majalis	0	0	0	0	0	0	0.01	0.01	1	0.01	0.01	1
Gobiosoma bosc	0.10	0.06	12	0.12	0.05	13	0.07	0.03	8	0.01	0.01	1
Leiostomus xanthurus	0.17	0.14	20	0.06	0.03	7	0.10	0.04	11	0.11	0.08	13
Lucania parva	0	0	0	0.01	0.01	1	0	0	0	0	0	0
Menidia beryllina	0.99	0.87	116	0.07	0.05	8	0	0	0	0	0	0
Menidia menidia	38.26	13.07	4476	3.97	1.93	441	36.50	10.87	4161	48.46	15.29	5525
Micropogonias undulatus	0	0	0	0	0	0	0.05	0.03	6	0.22	0.16	25
Morone americana	0	0	0	0	0	0	0.01	0.01	1	0.03	0.02	3
Morone saxatilis	0.03	0.02	4	0	0	0	0.01	0.01	1	0	0	0
Mugil curema	0.02	0.01	2	0	0	0	0	0	0	0	0	0
Pogonias cromis	0.09	0.04	10	0.27	0.17	30	0.13	0.08	15	0.12	0.05	14
Syngnathus fuscus	0	0	0	0	0	0	0	0	0	0.01	0.01	1
All Species Combined	134.22	38.10	15704	148.69	39.07	16505	196.75	40.54	22430	59.75	15.39	6811
Resident Species			63%			94%			80%			12%
Transient Species			37%			6%			20%			88%

Table 2-4. 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
Alosa aestivalis *	29	0.64	21	37	72
Alosa mediocris *	20	0.25	18	22	22
Alosa pseudoharengus *	29	0.37	18	37	221
Ameiurus nebulosus †	131	--	--	--	1
Anchoa mitchilli *	37	1.14	18	73	75
Anguilla rostrata †	130	11.45	55	420	39
Bairdiella chrysoura †	82	4.88	66	95	5
Brevoortia tyrannus *	36	0.22	11	57	440
Callinectes sapidus ‡	40	0.76	5	160	1403
Cynoscion regalis †	84	5.25	61	109	9
Cyprinodon variegatus †	41	0.40	18	62	512
Fundulus heteroclitus †	41	0.17	10	117	10003
Fundulus majalis †	67	3.00	64	70	2
Gobiosoma bosc †	31	1.07	18	42	33
Leiostomus xanthurus †	62	4.12	27	130	51
Lucania parva †	37	--	--	--	1
Menidia menidia *	36	0.15	10	95	6671
Micropogonias undulatus †	44	1.60	20	62	31
Morone americana *	128	16.21	85	157	4
Morone saxatilis *	123	25.78	70	220	5
Mugil curema *	78	12.50	65	90	2
Pogonias cromis †	69	4.02	25	160	74
Syngnathus fuscus †	83	--	--	--	1
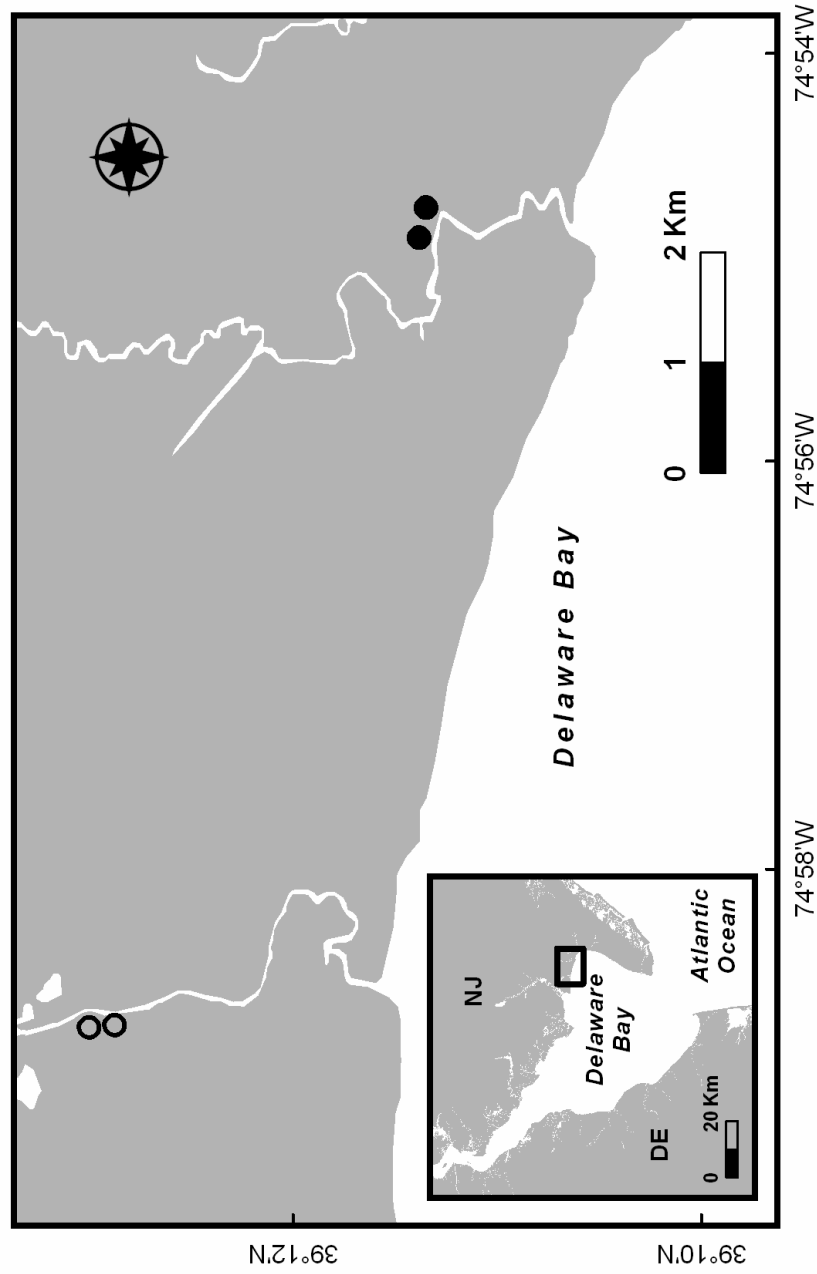
Figure 2-1. The lower Delaware Bay Estuary of New Jersey (NJ), USA. Intertidal creek seine sampling sites are shown for restored (closed circles) and reference (open circles) marshes.
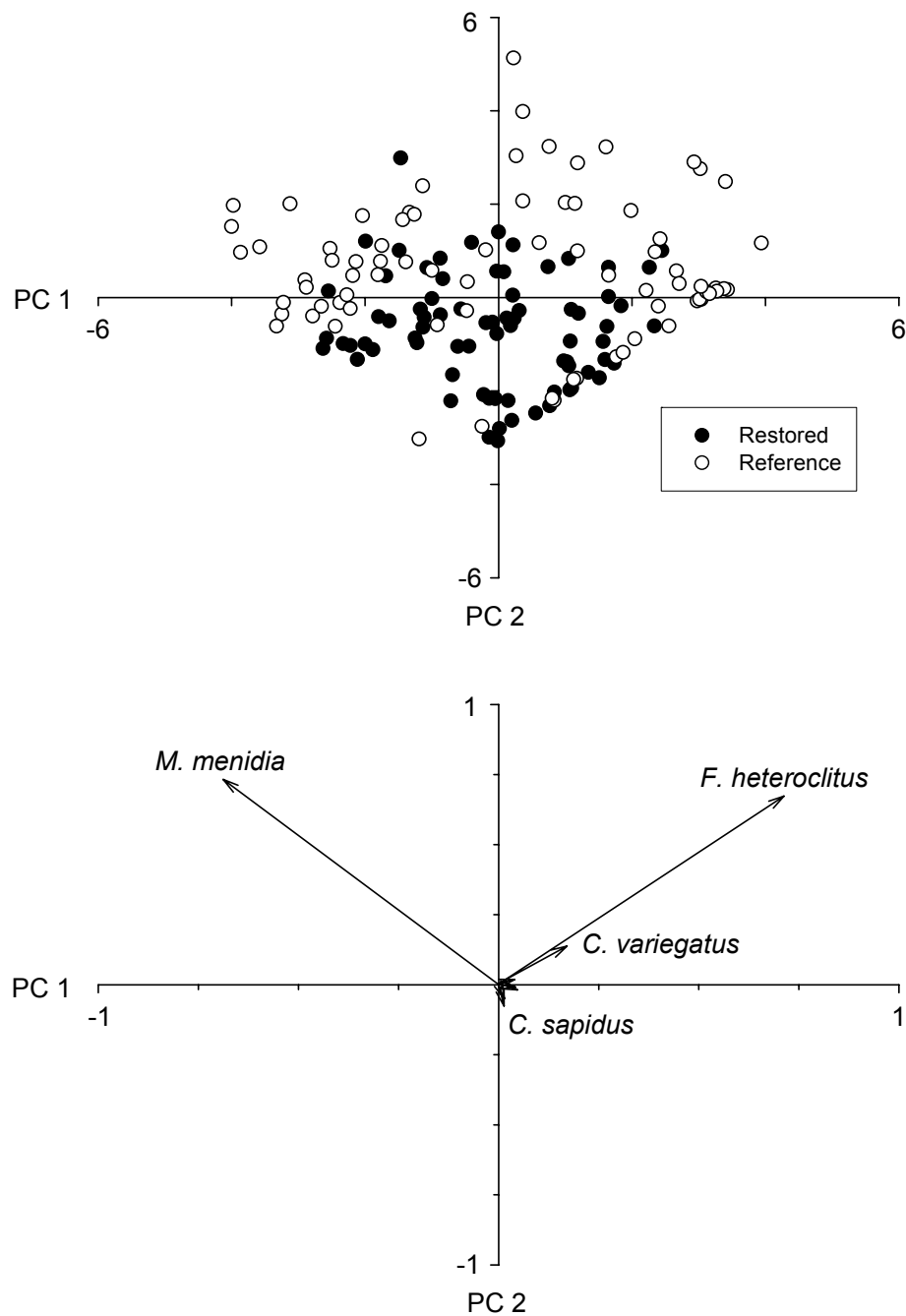
Figure 2-2. Principal component analysis of intertidal creek nekton assemblage. Principal component 1 (PC 1) explained 47% of the variation and principal component 2 (PC 2) explained 29%. Species eigenvector loadings are plotted on PC 1 and PC 2 (scores for *Alosa pseudoharengus*, *Brevoortia tyrannus*, and *Menidia beryllina* were close to the origin and are not shown).
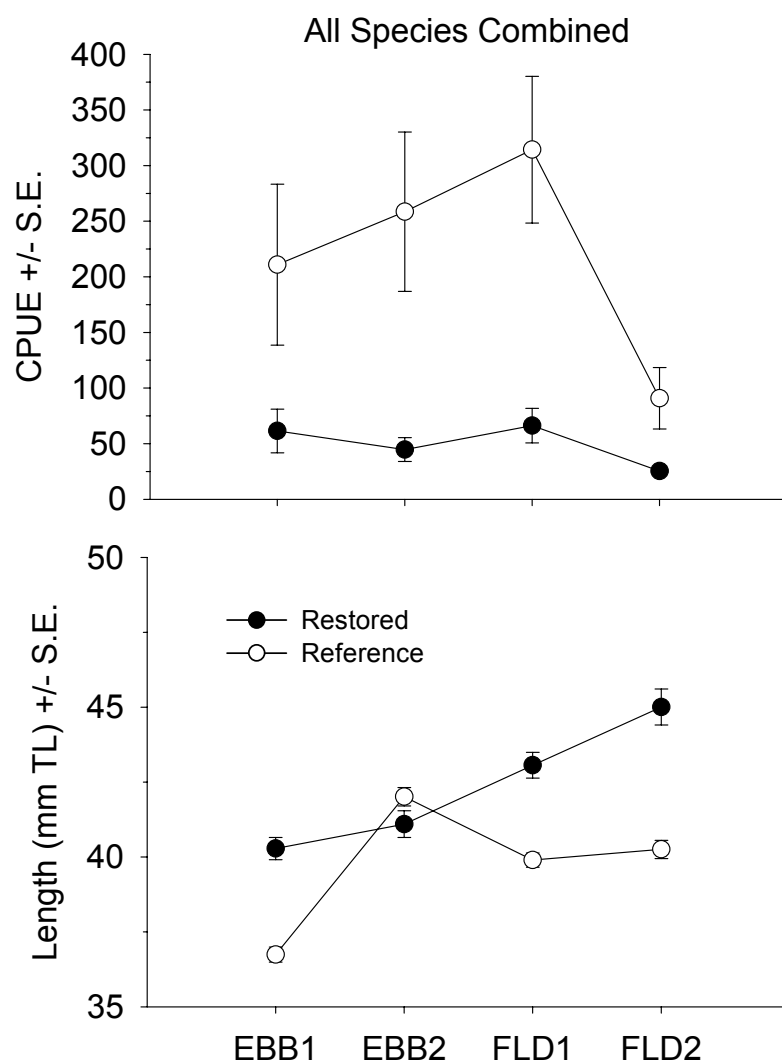
Figure 2-3. Catch-per-unit-effort (n = 61,450) and mean length (n = 18,270) by marsh type and tide stage for all species combined.
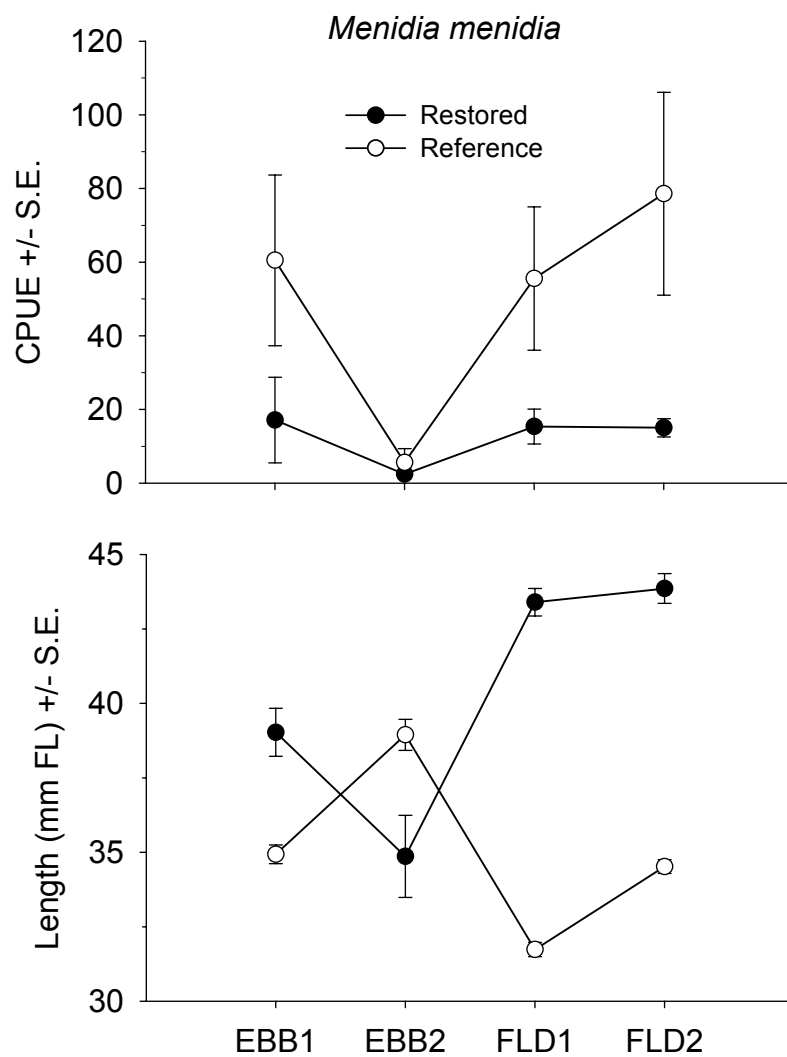
Figure 2-4. Catch-per-unit-effort (n = 14,603) and mean length (n = 6,671) by marsh type and tide stage for *Menidia menidia*.

Figure 2-5. Catch-per-unit-effort (n = 43,410) and mean length (n = 10,003) by marsh type and tide stage for *Fundulus heteroclitus*.

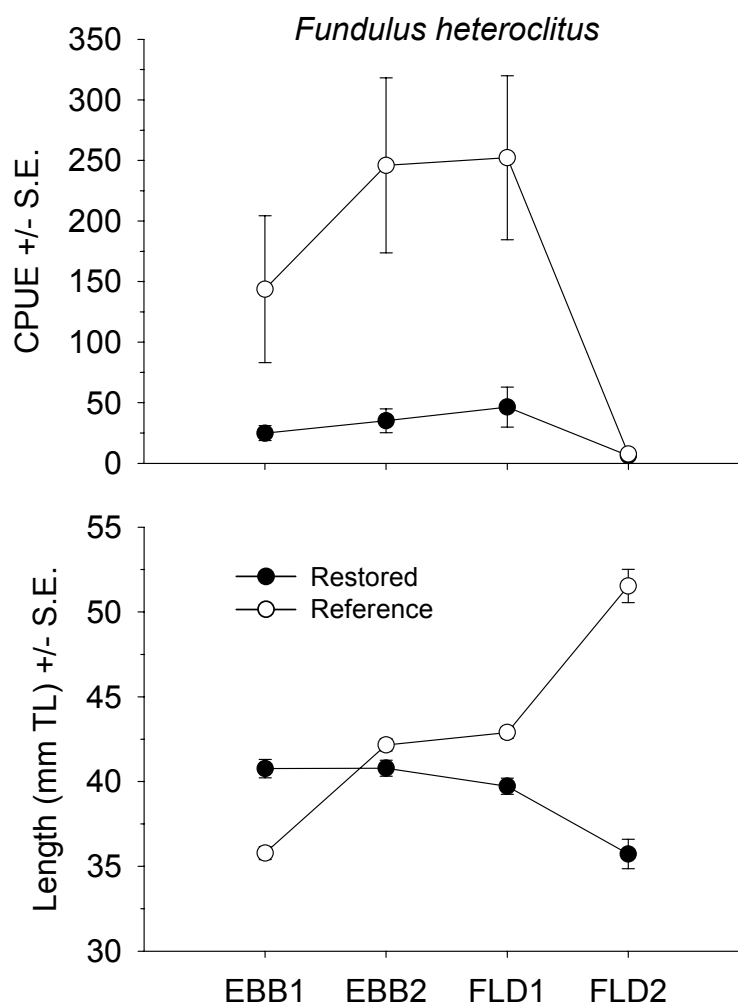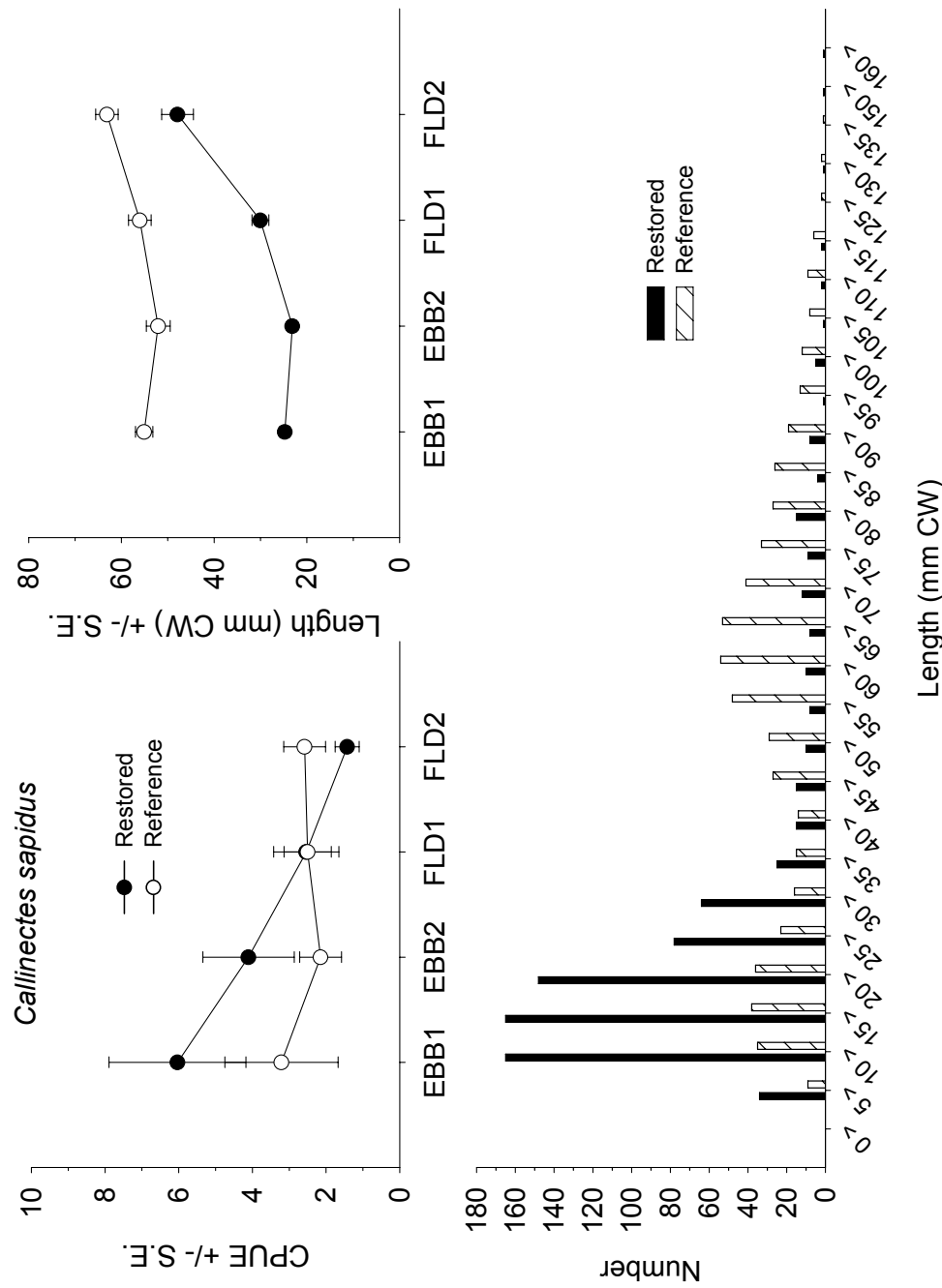Figure 2-6. Catch-per-unit-effort (n = 1,414) and mean length (n = 1,403) by marsh type and tide stage for *Callinectes sapidus*. Length-frequency distribution for *Callinectes sapidus* sorted into 5 mm groups (0 – 160 mm) for each marsh type.

CHAPTER 3

Evaluation of long-term response of intertidal creek nekton to *Phragmites* removal in

oligohaline Delaware Bay salt marshes

INTRODUCTION

Over the last several decades invasive *Phragmites australis* (hereafter

Phragmites) has become well established and now dominates many oligohaline and

mesohaline marshes along the Gulf (Peterson and Partyka, 2006) and Atlantic coasts

(Chambers et al., 1999; Rice et al., 2000; Philipp and Field, 2005; Lambert and

Casagrande, 2006). Intertidal creeks, an integral salt marsh habitat (Kneib, 1997b;

Cattrijsse and Hampel, 2006), are especially vulnerable to changes in the marsh

landscape that result from *Phragmites* invasions (Weinstein and Balletto, 1999; Able et

al., 2003; Teal and Peterson, 2005). Smaller intertidal creeks are susceptible to filling in

as stems and leaf litter accumulate, tidal flow is slowed, and sedimentation occurs,

eventually filling in creeks completely at late invasion stages, resulting in the loss of

habitat for nekton (Able et al., 2003; Osgood et al., 2003). Larger intertidal creeks in

Phragmites-dominated marshes generally have vertical or concave banks which can

increase flow rate, deepen channels, and further undercut creek banks. Such changes

may lead to greater predation and reduced access to the marsh surface for nekton using

intertidal creeks (McIvor and Odum, 1988; Teal and Weinstein, 2002). In the Delaware

Bay estuary, marsh restoration efforts were undertaken to recover lost nekton habitat and

restore salt marsh habitats to pre-invasion structure and function (Balletto et al., 2005).

The effects of *Phragmites* on nekton use of various salt marsh habitats have been examined (Weis and Weis, 2003), however, few studies have focused on intertidal creeks and none have examined the long term effects on nekton in intertidal creeks. In numerous prior studies *Phragmites* primarily had a negative effect on larval and juvenile marsh surface nekton (Able and Hagan, 2000, 2003; Able et al., 2003; Hunter et al., 2006; Osgood et al., 2003, 2006), although some studies found no effect (Fell et al., 1998, 2003). Studies examining the effects of *Phragmites* on larger nekton use of marsh fringe (Meyer et al., 2001), intertidal creek (Fell et al., 1998; Warren et al., 2001; Kimball and Able, 2007a) and subtidal creek (Able et al., 2001; Grothues and Able, 2003a, b) habitats observed little or no effect of vegetation on use patterns. Long-term studies of the effect of *Phragmites* on nekton have been conducted in some marsh habitats (e.g., subtidal creeks, 5 years: Grothues and Able, 2003a). However, the effect of *Phragmites* on nekton in many marsh habitats, including intertidal creeks, has only been examined for shorter time periods (e.g., intertidal creeks, 2 years or less: Fell et al., 1998; Warren et al., 2001; Kimball and Able, 2007a). Nekton responses to marsh restoration in the short-term may not necessarily equate to responses over the long-term, thus long-term studies may reveal patterns that would otherwise be overlooked (Weinstein et al., 1997; Williams and Zedler, 1999; Buchsbaum et al., 2006).

In this study nekton were examined in intertidal creeks over a 7 year period in three marsh types: natural *Spartina*, sites treated for *Phragmites* removal (hereafter referred to as Treated), and invasive *Phragmites* marshes. The primary objectives were to 1) compare nekton habitat use patterns among marsh types and determine the effects of *Phragmites* on nekton use of intertidal creeks, and 2) evaluate marsh restoration success.

All objectives were addressed based on nekton assemblage and individual species responses.

METHODS

Study area

The Alloway Creek watershed (Fig. 3-1), located in the oligohaline portion of the Delaware Bay estuary, has a long history of anthropogenic disturbance (Philipp, 2005; Lotze et al., 2006). This persistent disturbance regime degraded the salt marshes and facilitated the invasion and establishment of *Phragmites* in this watershed and elsewhere in Delaware Bay (Weinstein and Balletto, 1999; Philipp and Field, 2005). Large-scale treatment for *Phragmites* removal (via herbicide and burning; see Marks et al., 1994 for detailed description) in a 648 ha portion of the Alloway Creek watershed occurred in 1996-1998 and reduced, concentrated efforts continued on an as needed basis (Balletto et al., 2005; Hagan et al., 2007). Therefore, within the Alloway Creek watershed there are three distinct marsh habitat types: natural *Spartina*-dominated, Treated (and now dominated by *Spartina*), and invasive *Phragmites*-dominated marshes.

Field sampling

Two intertidal marsh creeks were sampled in each marsh type (*Spartina*, Treated, and *Phragmites* marshes, n = 6 creeks; Fig. 3-1). Intertidal creeks were approximately 1.5–3 m wide at the mouth, had a soft mud substrate bottom, and few residual pools of water at low tide. Nekton were collected using weirs (2.0 m x 1.5 m x 1.5 m bag, 5.0 m x 1.5 m wings, 3.2 mm mesh) set at high tide and removed at low tide approximately six hours later. At each intertidal creek sampled, the weir bag was stretched across the creek

channel with support poles embedded vertically in the sediment. Wings were extended

back onto the marsh surface from each end of the bag, and all net lead lines were buried

in the bottom sediment to eliminate gaps in the funnel-shaped weir. Sampling occurred

monthly between May and November from 1999 to 2005, with a combined total of 274

weir sets (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 = 294).

Sampling effort differed among individual marshes as follows: *Spartina*, n = 98; Treated,

n = 90; *Phragmites*, n = 86. Each marsh type was sampled completely (both creeks) in

one day during daylight hours each month.

All nekton captured were identified and enumerated. To obtain a relative estimate

of size, the first 20 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 10% formalin or 95% ethanol and processed

in the laboratory. Environmental parameters were measured for individual creeks at the

beginning of each weir sample by recording near surface temperature (Celsius), dissolved

oxygen concentration (mg / L), and salinity with a hand-held oxygen, conductivity,

salinity, and temperature system (YSI Model 85).

Data Analysis

Nekton assemblage variability was examined using principle response curves

(PRC) analysis, a method that analyzes assemblage change over time in treatments

relative to a control (Van den Brink and Ter Braak, 1998, 1999; Pardal et al., 2004). PRC

analysis allows a powerful statistical analysis of long-term data series along spatial

gradients (in this case, different marsh types) and facilitates a direct comparison of

treatment sites (i.e., Treated and *Phragmites*) with a control site (i.e., *Spartina*) (Pardal et

al., 2004). PRC analysis is a form of principal component analysis where eigenaxes are

constrained to qualitative control and treatment dummy variables so that principle

component factors are forced to center on the control assemblage (e.g., Grothues and

Able 2003b). Site scores (canonical coefficients, C_{dt}) of treatment samples are thus

calculated as deviating from zero (the control scores) and plotted against time.

Concomitant plotting of species scores (statistical species weight, b_k) represents the

degree and direction to which individual species drive the assemblage trendlines. Only

species with a total abundance greater than 50 individuals for all marsh types combined

were included in the PRC analysis (n = 8 species; this included 99.5% of all individuals

caught during the study period). Individual species abundances (catch-per-unit-effort,

CPUE) were log transformed (log (1 + CPUE)) prior to analysis. PRC analysis was

conducted with CANOCO software (Ter Braak and Smilauer, 1998).

Abundance (CPUE) was compared among marsh types for individual species and

all species combined. Species abundance was transformed (ln (1 + CPUE)) and analyzed

with a two factor analysis of variance (ANOVA) with marsh type and year as factors.

Differences in treatment means were examined using the Tukey-Kramer test for unequal

sample sizes (Dunnett, 1980; Day and Quinn, 1989; Sokal and Rohlf, 1997). In addition,

individual species were assigned to an estuarine category (i.e., resident, transient,

freshwater) to compare the relative abundance of different categories of estuarine nekton

(Able and Fahay, 1998; Arndt, 2004).

Environmental variables were examined for all marsh types. Temperature,

salinity, and dissolved oxygen were not recorded for some samples, thus sample sizes

vary. Temperature (n = 268), salinity (n = 264), and dissolved oxygen (n = 268) were

analyzed with a two factor ANOVA with marsh type and year as factors. Differences in

treatment means were examined using the Tukey-Kramer test.

RESULTS

Environmental Characteristics

Environmental parameters did not vary significantly among marsh types, and this

relationship did not vary with sampling year (Table 3-1). Temperature, salinity, and

dissolved oxygen levels fluctuated similarly in all marsh types throughout the sampling

season (May through November) (Fig. 3-2).

Nekton species composition and abundance

A total of 21 nekton species and 20,617 individuals were collected in intertidal

creeks (Table 3-2). Fish species (n = 20) overwhelmingly dominated the nekton catch

with 20,039 individuals, along with one frequently collected decapod crustacean, blue

crab (*Callinectes sapidus*). Resident species (n = 4) accounted for 92% of the total catch,

and *Fundulus heteroclitus* alone accounted for 91% of the total individuals. Transient

species (n = 11), primarily *C. sapidus* and *Menidia menidia*, made up 7% of the total

catch. Freshwater species (n = 6) were infrequently caught (except *Dorosoma

cepedianum*) and made up only 1% the total catch.

Overall species composition and abundance differed between marsh types (Tables

3-1 and 3-2). The fewest number of species (n = 11) were collected in the *Spartina*

marsh, the Treated marsh had a total of 15 species, and the *Phragmites* marsh had the

greatest number of species (n = 20). However, 11 of the 20 species collected at the

Phragmites marsh had five or less individuals total and were rarely caught in any marsh

type. Overall species abundance was an order of magnitude greater in the Treated marsh

(CPUE = 191.29, SE = 43.32) than in the *Spartina* (CPUE = 15.87, SE = 3.80) and

Phragmites (CPUE = 21.47, SE = 3.31) marshes (both $p < 0.0001$). This difference was

primarily due to an order of magnitude greater abundance of *F. heteroclitus* in the

Treated marsh (Table 3-2). Overall species abundance was not significantly different

between the *Spartina* and *Phragmites* marshes ($p = 0.4287$). Resident nekton dominated

the catch in *Spartina* (89%), Treated (93%), and *Phragmites* (81%) marshes. Transient

nekton made up a smaller percentage of the catch at the Treated marsh (6%) than at the

Spartina (10%) and *Phragmites* (13%) marshes. Freshwater nekton constituted a small

percentage of the catch at each marsh type (*Spartina* and Treated, 1%; *Phragmites*, 6%).

Size ranges of nekton (n = 5749 total measured) sampled in the *Spartina*, Treated, and

Phragmites marshes indicated that intertidal creeks were utilized by mostly juvenile and

some adult resident nekton and juvenile transient and freshwater nekton (Table 3-3).

The abundance of individual species also differed between marsh types (Tables 3-

1 and 3-2). *Anchoa mitchilli* were most abundant in the Treated marsh, but there was a

significant difference in abundances only between the Treated and *Spartina* marshes ($p = $

0.0074). *F. heteroclitus* abundance was significantly greater in the Treated marsh (Fig.

3-3) than in both the *Spartina* and *Phragmites* marshes (both $p < 0.0001$). *M. menidia*

were most abundant in the Treated marsh, but only abundances in *Spartina* and Treated

marshes were significantly different ($p = 0.0002$; Fig. 3-3). *M. menidia* abundance in

each marsh type also varied by year (Table 3-1), with much greater abundances in the

Treated marsh during 1999 and 2000 (Fig. 3-3). It is also important to note that for all three species with significant differences between marsh types (*A. mitchilli, F. heteroclitus*, and *M. menidia*), species abundances at the *Spartina* and *Phragmites* marshes were never significantly different.

Nekton Assemblages

Intertidal creek nekton assemblage response varied between the *Spartina*, Treated, and *Phragmites* marshes over the 7 year study period (Fig. 3-4). PRC analysis explained 50% of the total assemblage variation and the first principal response factor (PRF 1, eigenvalue = 0.288) accounted for 58% of this variation. The remaining principal response factors accounted for <9% of the variation each, and therefore were not examined further. Differences in nekton assemblages were greatest between the Treated and the other marsh types for 1999 through 2004. These differences were due to the greater abundance of most species observed at the Treated marsh than at the other marshes (Table 3-2). However, in 2005, the *Phragmites* marsh assemblage was more similar to the Treated marsh assemblage. Species scores (b_k) indicated that variation in *F. heteroclitus* abundance drove most of the assemblage variation observed in the PRC diagram of site scores (Fig. 3-4). *M. menidia*, *A. mitchilli*, and *C. sapidus* also contributed to overall assemblage differences between marsh types, while the remaining four species included in the analysis had little effect on overall assemblage patterns (Fig. 3-4).

DISCUSSION

Impacts of *Phragmites*

The response of intertidal creek nekton in this long-term marsh restoration study indicated that the *Spartina* and *Phragmites* marshes were both functioning similarly. This is in agreement with the results of a shorter term study focused on nekton use of other different intertidal creeks in the Alloway Creek watershed (Kimball and Able, 2007a). It appears that *Phragmites* marsh intertidal creeks serve as useful habitat for nekton until an invasion progresses to the point of total loss of intertidal creek habitat due to filling in and overgrowth (Able et al., 2003). From initial to mid invasion stages, stem density and above ground biomass of *Phragmites* increases, small intertidal creeks begin to fill in, and the marsh surface is less frequently flooded (Able et al., 2003; Hunter et al., 2006). Late invasion stage marshes are characterized by dense *Phragmites* monocultures and an elevated, infrequently flooded marsh surface with little or no standing water (Fig. 3-5) (Able et al., 2003; Hunter et al., 2006; Hagan et al., 2007). Intertidal creek nekton, particularly *F. heteroclitus*, may experience reduced foraging and reproduction opportunities because of reduced access to the marsh surface and loss of aquatic microhabitats in *Phragmites* marshes (Able et al., 2003). Thus the negative effects of *Phragmites* on larval and juvenile nekton on the marsh surface (Able and Hagan, 2000 2003; Able et al., 2003; Hunter et al., 2006; Osgood et al., 2003, 2006; Hagan et al., 2007), could conceivably affect nekton abundances in intertidal creeks (Fig. 3-5) and other marsh habitats. However, studies comparing use of intertidal creek, marsh fringe, and subtidal creek habitats in *Phragmites* and non-*Phragmites* vegetation marshes observed similar nekton use patterns in northeastern (Fell et al., 1998; Warren et al., 2001; Fell et al., 2003;) and Mid-Atlantic (Able et al., 2001; Meyer et al., 2001; Grothues and Able, 2003a, b) US salt marshes.

Response to Restoration

The Treated marsh intertidal creeks provided enhanced conditions for nekton as indicated by greater overall and individual nekton abundance levels than in the *Spartina* and *Phragmites* marsh creeks. Two of the most abundant intertidal creek nekton species, *F. heteroclitus* and *M. menidia*, and one less abundant species, *A. mitchilli*, were present in greater numbers in the Treated marsh intertidal creeks than those in other marsh types. Alone, the order of magnitude greater abundance of *F. heteroclitus* in the Treated marsh resulted in the overall species abundance being significantly greater in the Treated marsh relative to the *Spartina* and *Phragmites* marshes. Other species that were generally more abundant in the Treated marsh included *Alosa pseudoharengus*, *C. sapidus*, *D. cepedianum*, and *Morone americana*. Interestingly, *Morone saxatilis* and *Ameiurus nebulosus* have been observed in greater abundances in Treated marsh intertidal creeks over those in *Phragmites* marshes (Kimball and Able, 2007a). This was not the case in the present study, perhaps because of low overall abundances of both species. Similarly, *Gobiosoma bosc* and *Anguilla rostrata* were more abundant in *Phragmites* marsh intertidal creeks in a previous study (Kimball and Able, 2007a), but both species showed no significant marsh type abundance differences in this study. It should be noted that some metrics (i.e., species richness and composition, estuarine category percentage) were similar for all marsh types. Sizes were also similar for the dominant nekton in these *Spartina*, Treated, and *Phragmites* marsh intertidal creeks (Table 3-3). If infrequently caught and less abundant species were removed, the *Spartina*, Treated, and *Phragmites* marsh intertidal creeks were all comprised of the same relatively low number of highly abundant common intertidal species, primarily dominated by resident nekton, which is

characteristic of intertidal salt marsh creeks in North America (Kneib, 1997b), Europe (Cattrijsse and Hampel, 2006), and Asia (Jin et al., 2007).

Early treatment effects on the marsh surface may be responsible for greater nekton abundances in the Treated marsh intertidal creeks. *Phragmites* eradication results in a largely nonvegetated marsh surface, where *Spartina* and other mixed vegetation are slowly recolonizing the marsh (Weinstein et al., 1997; Grothues and Able, 2003a). The newly treated marsh surface is characterized by an increased amount of standing water (Fig. 3-5) (Able et al., 2003; Hagan et al., 2007), which may consist of aquatic microhabitats as well as large puddles and pannes. Several ephemeral salt pannes were observed on the marsh surface of the Treated marsh during the early years of this study. Resident and transient nekton that use the marsh surface during periods of tidal inundation may exploit such shallow water marsh surface habitats for foraging, refuge, or reproduction (Kneib, 1997b). The removal of the dense *Phragmites* canopy allows more light to penetrate to the marsh surface, which may facilitate microalgal growth (Currin et al., 2003) and increase food resources, especially for *F. heteroclitus*. More standing water on the marsh surface and increased food resources could result in marsh surface and intertidal creek habitats supporting greater nekton abundances in the early years after treatment (Fig. 3-5). Over time, as *Spartina* coverage increases on the marsh surface, the amount of standing water is reduced (i.e., large puddles and pannes no longer prevalent), the surface becomes more shaded, and the marsh becomes similar to an undisturbed *Spartina* marsh (Fig. 3-5) (Weinstein et al., 1997). As the amount of standing water on the marsh surface decreases, nekton abundances gradually decline to match the level of available habitat (Fig. 3-5). Therefore, the period along a restoration timeline (Fig. 3-5)

that is examined may influence comparisons among marsh types. Many of the dominant

intertidal species collected in this study, including *F. heteroclitus, C. sapidus,* and *M.*

menidia, were all more abundant in the Treated marsh during the early years (1999-2001)

after restoration. Abundance levels of these same species were more similar among

marsh types six or more years after restoration (2004-2005). Nekton comparisons among

Spartina, Treated, and *Phragmites* marshes focusing on a shorter duration, such as a

single year, may show different abundance patterns depending on the amount of time

passed since the initial restoration took place (e.g., Kimball and Able, 2007a). Other

types of marsh restorations that also involve clearing and natural recolonization of the

marsh surface, such as restoration of former salt hay farms (Able et al., 2008), may also

exhibit similar patterns in marsh surface and intertidal creek habitats. Dominant

intertidal species (e.g., *F. heteroclitus*, *M. menidia*, *A. mitchilli*) were also initially more

abundant in mesohaline Delaware Bay intertidal creeks after restoration (Able et al.,

2008). This early period of greater abundances was also subsequently followed by

gradually declining abundances until the completion of the 9 year long-term study (Able

et al., 2008).

The Treated marsh nekton assemblage was differentiated from those at the

Spartina and *Phragmites* marshes by greater abundances of most nekton, especially *F.*

heteroclitus, over most years during the 7 year study period. Throughout the study period

there was little assemblage variation observed for each marsh type independently, and

there was a lack of similarity between of the Treated marsh assemblage with that of the

Spartina marsh. Together, these observations suggest that assemblage differences were

likely not the result of stochastic processes. Examination of annual nekton assemblages

(Fig. 3-4) and annual abundances of *F. heteroclitus* (Fig. 3-3) for each marsh type demonstrates that *F. heteroclitus* was largely responsible for the observed assemblage differences. The *Phragmites* marsh nekton assemblage was similar to that of the *Spartina* marsh for 1999 through 2004, after which time the assemblage became more similar to that of the Treated marsh. This shift was likely due to slightly higher abundances of some dominant nekton species (i.e., *C. sapidus* and *M. menidia*) at the *Phragmites* marsh along with low nekton abundances at the *Spartina* marsh in 2005. Agreement between *F. heteroclitus* abundance and the Treated marsh assemblage pattern along with the assemblage shift observed in 2005 illustrates the close link between the assemblage response and the abundance of dominant and ubiquitous intertidal creek nekton species. Intertidal creeks in the *Spartina* and *Phragmites* marshes were generally used by a similar nekton assemblage for most years. The close similarity between nekton assemblages in the *Spartina* and *Phragmites* marshes implies that intertidal creek habitats in both marsh types may be equivalent, an idea already postulated for other marsh habitats (Weis and Weis; 2003).

Creek geomorphology likely did not contribute to nekton abundance differences. Intertidal creeks sampled with weirs in the Alloway Creek watershed were all similarly small and shallow (approximately 1 m deep or less at the mouth during typical high tides). Shallow creeks with sloped banks and slower flow are favorable for many intertidal nekton species, particularly *F. heteroclitus* (Allen et al., 2007). However, shallow creeks with slow flow are prone to filling in via sedimentation, and are also subject to altered hydroperiods caused by meteorological events. For example, some creeks in the Treated and *Phragmites* marshes could not be regularly sampled during

2001, 2002, and 2003 because of irregular tidal inundation periods (i.e., wind forcing that prevented flooding). During these years nekton were less abundant at the Treated marsh, but the assemblage at the *Phragmites* marsh appeared to be unaffected during this same period. Based on the nekton assemblage response and the limited geomorphological observations, the effects of creek geomorphology on nekton use of intertidal creeks were minor during the 7 year study. However, beyond the present study period, if creeks continue to fill in, intertidal creek habitats in the Treated and *Phragmites* marshes will be lost to nekton permanently.

Examination of long-term nekton assemblage and individual species utilization of intertidal creeks indicated that the Treated marsh supported greater nekton abundances throughout most of the 7 year study. Although habitat requirements for resident and transient nekton differ, abundance levels suggest that the Treated marsh intertidal creeks may have offered enhanced conditions for the dominant intertidal resident and transient species. Further, since nekton assemblages in all marsh types were largely reset annually (particularly for transient species, Grothues and Able, 2003a), it appears that these enhanced conditions were sustained throughout the early years after restoration, a result also observed in other long-term studies of mesohaline intertidal creek nekton (Able et al., 2008). The goal of many restorations is to return salt marsh habitats to pre-invasion structure and function (Hildebrand et al., 2005), which in this case would entail being similar to the natural *Spartina*-dominated marsh. Under this logic, it would be expected that Treated marshes occupy an intermediate position between natural *Spartina* and invasive *Phragmites* marshes, and gradually become more similar to *Spartina*-dominated marshes. However, while this predicted trajectory may be accurate for salt marsh

characteristics such as vegetation (Weinstein et al., 1997), the results of this and other long-term studies examining nekton in salt marsh restorations have not supported this thesis (see Able et al., 2008). Multiple salt marsh restoration studies have found that ecological attributes develop at varying rates on scales from one or two years to decades (Craft et al., 1999; Zedler and Callaway, 1999; Warren et al., 2002). The results of this long-term study suggest that nekton utilization of intertidal salt marsh habitats may follow a somewhat predictable pattern in the years after marsh restoration efforts occur.

Table 3-1. Analysis of variance results (F statistics) for effect of marsh type and year on temperature (°C), salinity, dissolved oxygen (mg/L), and overall and individual species abundance (catch-per-unit-effort, CPUE). Temperature, salinity, and dissolved oxygen were not recorded for some samples. Overall species CPUE included all species (n = 21) caught during this study. Individual species (n = 8) shown are those used in the principal response curves analysis. 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 = 2)	Marsh x Year (df = 12)
Temperature	247	ns	ns
Salinity	243	ns	ns
Dissolved Oxygen	247	ns	ns
Nekton			
Overall Species CPUE	253	37.16***	ns
Individual Species CPUE			
Alosa pseudoharengus	253	ns	ns
Anchoa mitchilli	253	4.33*	ns
Callinectes sapidus	253	ns	ns
Dorosoma cepedianum	253	ns	ns
Fundulus heteroclitus	253	38.25***	ns
Gobiosoma bosc	253	ns	ns
Menidia menidia	253	8.13***	2.29**
Morone americana	253	ns	ns

Table 3-2. Alloway Creek watershed intertidal creek species composition with catch-per-unit-effort (CPUE, with standard error), and total number collected for each marsh type (all creeks, months, and years combined). Final sample sizes: *Spartina*, n = 98; Treated, n = 90; *Phragmites*, n = 86. Each species was assigned to an estuarine category (EC): estuarine resident (R), estuarine transient (T), or freshwater (F). The relative abundance of estuarine resident, estuarine transient, and freshwater species is indicated as a percentage of the total abundance for each marsh type separately and combined.

Species	EC	*Spartina*			Treated			*Phragmites*			Combined
		CPUE	SE	Total	CPUE	SE	Total	CPUE	SE	Total	Total
Alosa mediocris	T	0	0	0	0.01	0.01	1	0	0	0	1
Alosa pseudoharengus	T	0	0	0	0.68	0.66	61	0.05	0.05	4	65
Ameiurus nebulosus	F	0.02	0.01	2	0.07	0.04	6	0.19	0.13	16	24
Anchoa mitchilli	T	0.03	0.02	3	1.43	0.86	129	0.26	0.11	22	154
Anguilla rostrata	T	0.04	0.02	4	0.03	0.02	3	0.06	0.03	5	12
Brevoortia tyrannus	T	0	0	0	0.33	0.28	30	0.10	0.09	9	39
Callinectes sapidus	T	1.33	0.23	130	3.82	1.61	344	1.21	0.29	104	578
Cyprinus carpio	F	0	0	0	0	0	0	0.05	0.03	4	4
Cyprinodon variegatus	R	0	0	0	0.04	0.02	4	0.01	0.01	1	5
Dorosoma cepedianum	F	0.05	0.04	5	1.83	1.81	165	1.07	0.97	92	262
Fundulus heteroclitus	R	13.42	3.75	1315	177.37	41.97	15963	16.85	2.93	1449	18727
Gobiosoma bosc	R	0.56	0.27	55	0.62	0.41	56	0.16	0.06	14	125
Hybognathus regius	F	0	0	0	0	0	0	0.01	0.01	1	1
Ictalurus punctatus	F	0	0	0	0	0	0	0.01	0.01	1	1
Leiostomus xanthurus	T	0.01	0.01	1	0.03	0.02	3	0.03	0.03	3	7
Lepomis macrochirus	F	0	0	0	0.00	0.00	0	0.02	0.02	2	2
Menidia menidia	T	0.20	0.08	20	4.16	1.49	374	1.01	0.33	87	481
Micropogonias undulatus	T	0.02	0.02	2	0	0	0	0.02	0.02	2	4
Morone americana	R	0.18	0.07	18	0.81	0.45	73	0.30	0.10	26	117
Morone saxatilis	T	0	0	0	0.04	0.03	4	0.03	0.02	3	7
Pogonias cromis	T	0	0	0	0	0	0	0.01	0.01	1	1
All Species Combined		15.87	3.80	1555	191.29	43.32	17216	21.47	3.31	1846	20617
Resident Species				89%			93%			81%	92%
Transient Species				10%			6%			13%	7%
Freshwater Species				1%			1%			6%	1%

Table 3-3. Mean length (mm) with standard error and total number measured for all species collected for each marsh type (all creeks, months, and years combined). Fishes and invertebrates were measured either in fork length (*), total length (†), or carapace width (‡).

| Species	*Spartina*			Treated			*Phragmites*			Combined
	Mean	SE	Total	Mean	SE	Total	Mean	SE	Total	Total
Alosa mediocris *	--	--	--	23	--	1	--	--	--	1
Alosa pseudoharengus *	--	--	--	31	0.43	52	31	0.75	4	56
Ameiurus nebulosus †	166	12.50	2	215	16.36	6	218	11.27	16	24
Anchoa mitchilli *	45	4.91	3	33	0.89	96	31	1.40	19	118
Anguilla rostrata †	150	48.15	4	104	25.34	3	196	52.80	5	12
Brevoortia tyrannus *	--	--	--	47	2.20	29	44	1.51	9	38
Callinectes sapidus ‡	43	3.14	129	31	1.74	247	43	2.96	102	478
Cyprinus carpio *	--	--	--	--	--	--	276	123.50	4	4
Cyprinodon variegatus †	--	--	--	34	5.74	4	42	--	1	5
Dorosoma cepedianum *	109	13.94	5	65	1.54	52	70	2.45	59	116
Fundulus heteroclitus †	46	0.64	750	49	0.37	2350	41	0.51	1124	4224
Gobiosoma bosc †	30	0.70	54	28	0.73	56	27	1.45	14	124
Hybognathus regius †	--	--	--	--	--	--	70	--	1	1
Ictalurus punctatus †	--	--	--	--	--	--	480	--	1	1
Leiostomus xanthurus †	120	--	1	79	20.43	3	120	10.33	3	7
Lepomis macrochirus *	--	--	--	--	--	--	47	13.00	2	2
Menidia menidia *	47	2.61	18	45	0.74	305	52	1.37	86	409
Micropogonias undulatus †	106	9.50	2	--	--	--	102	6.50	2	4
Morone americana *	95	9.35	18	75	3.79	74	87	10.86	25	117
Morone saxatilis *	--	--	--	62	5.72	4	56	7.62	3	7
Pogonias cromis *	--	--	--	--	--	--	173	--	1	1
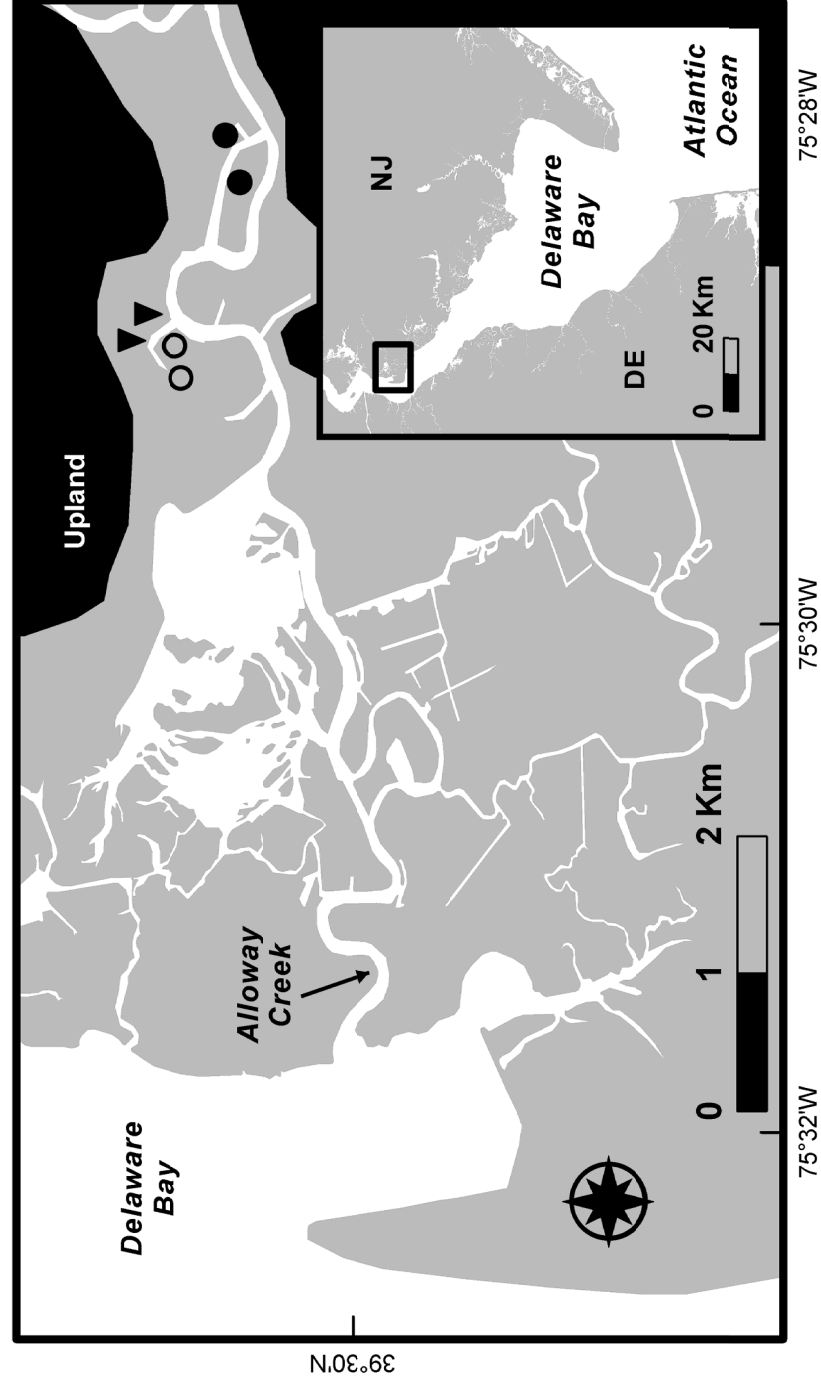
Figure 3-1. The Alloway Creek watershed in the oligohaline upper Delaware Bay estuary of New Jersey (NJ), USA. Intertidal creek weir sampling sites are shown for *Spartina* (closed circles), Treated (open circles), and *Phragmites* (closed triangles) marshes.
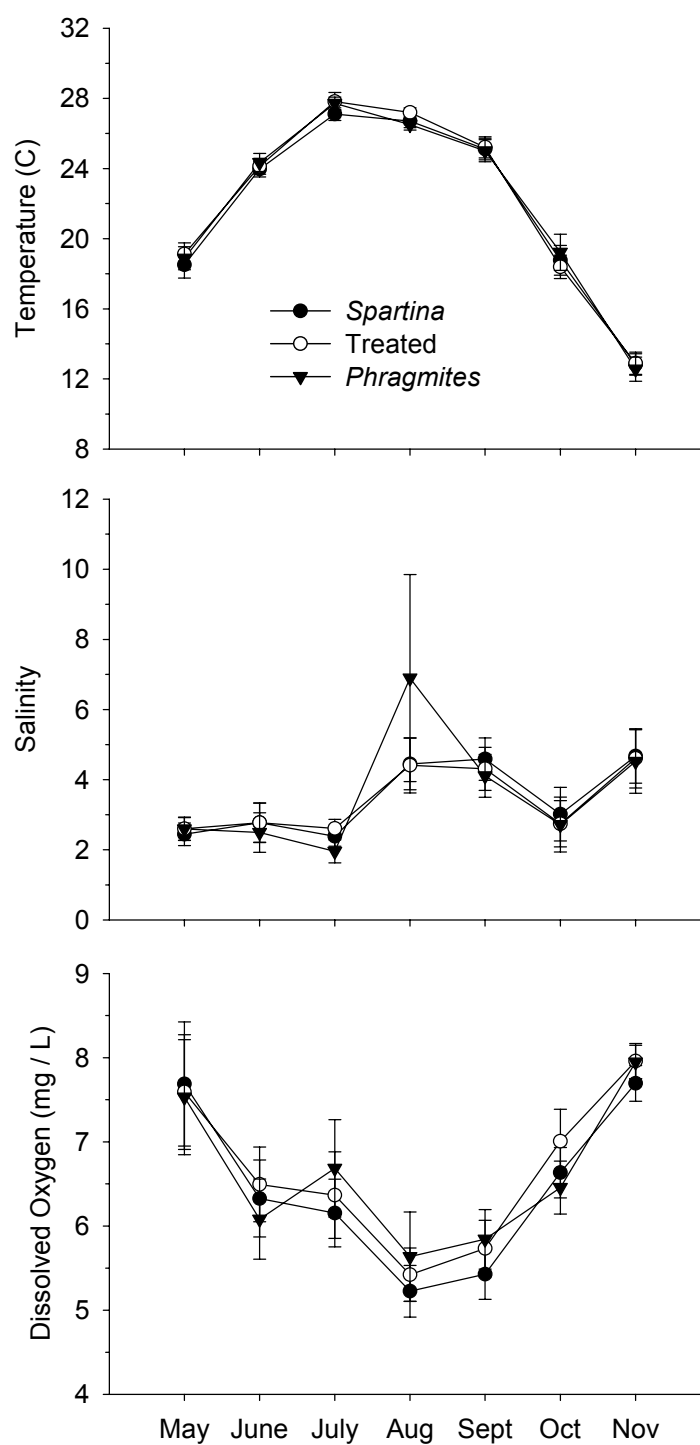
Figure 3-2. Mean temperature, salinity, and dissolved oxygen by marsh type and month in the Alloway Creek watershed study area.
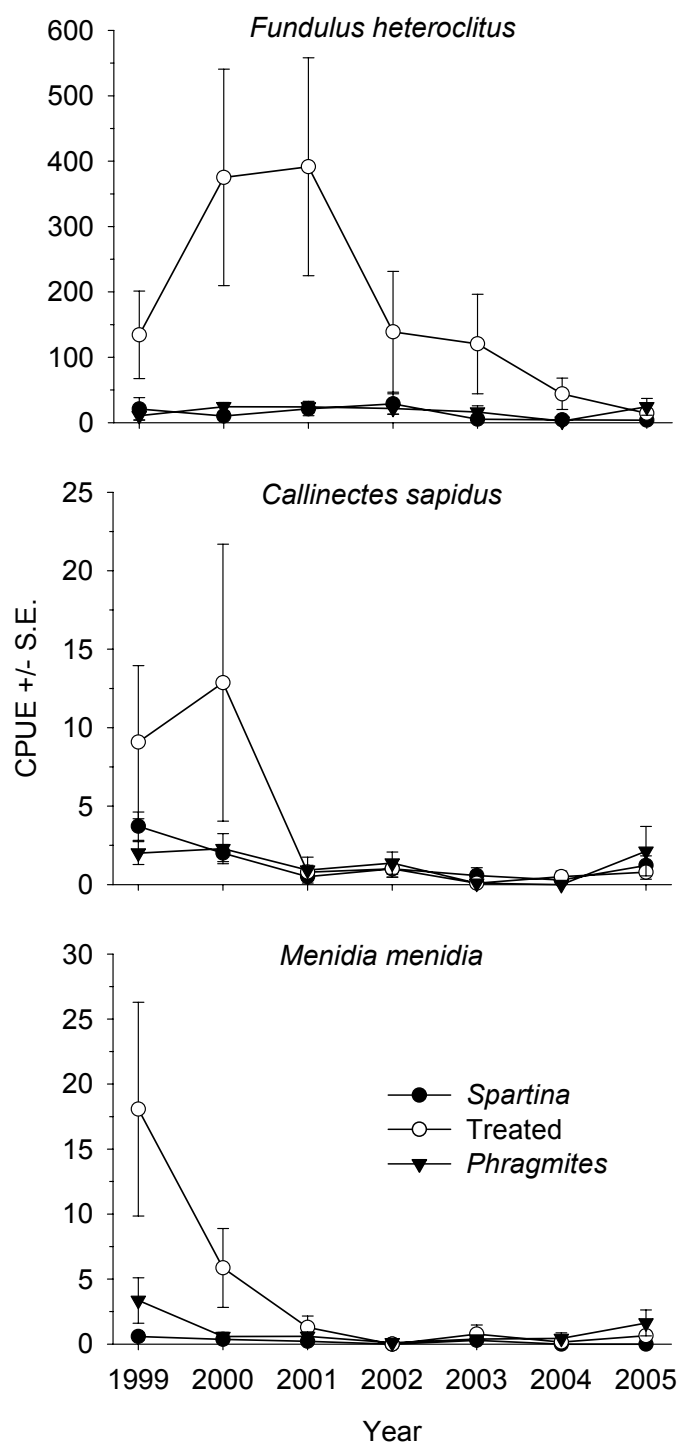
Figure 3-3. Catch-per-unit-effort (CPUE) by marsh type and year for *Fundulus heteroclitus* (n = 18,727), *Callinectes sapidus* (n = 578), and *Menidia menidia* (n = 481).
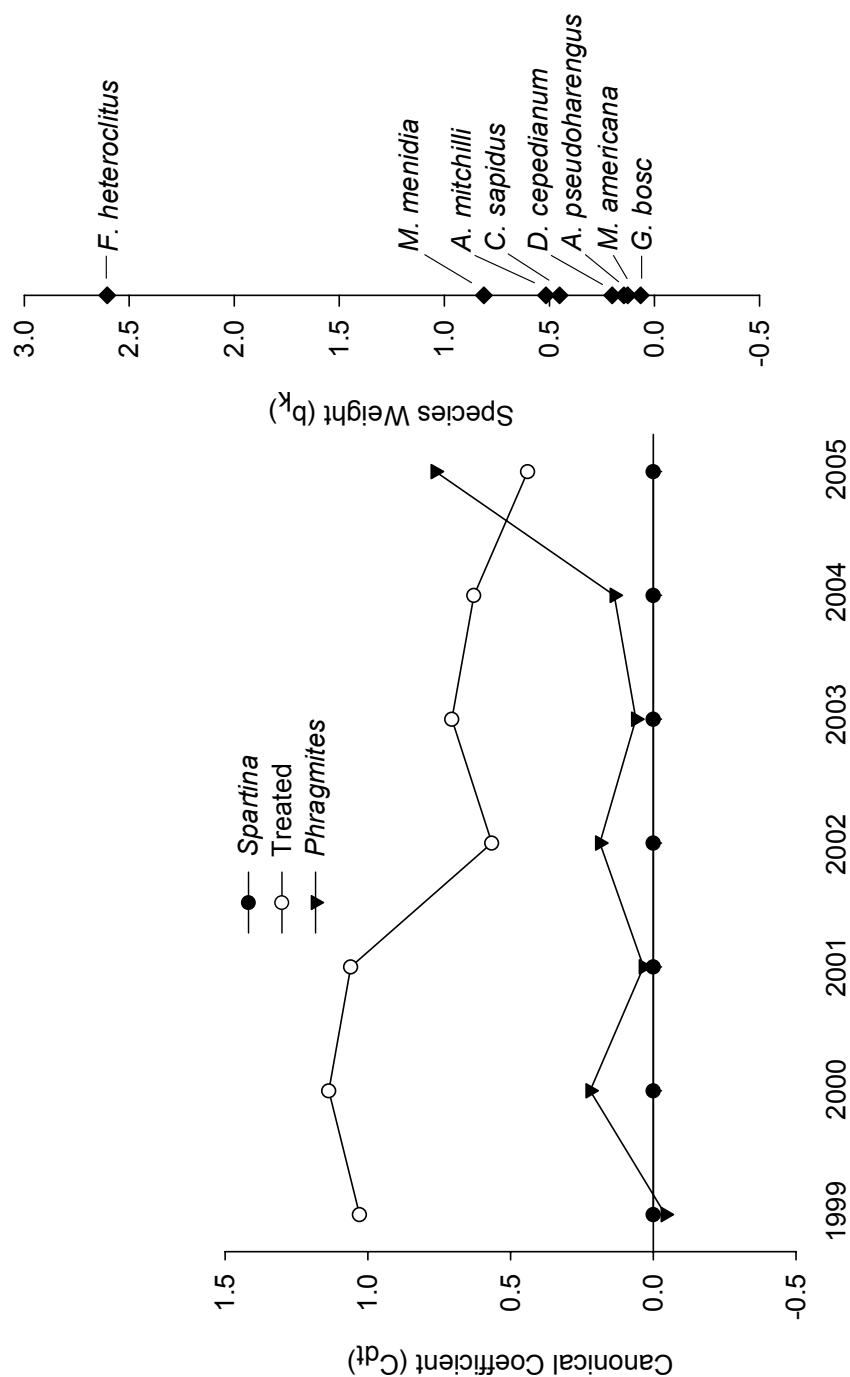
Figure 3-4. Principal response curves (PRC) diagram for the first canonical axis of variation for the intertidal nekton assemblage. Individual species (n = 8) with a total abundance greater than 50 individuals for all marsh types combined were included in the PRC. Plot points are the canonical coefficients of the first principal response factor (PRF 1) standardized by multiplying with the total standard deviation of the species data and then dividing by the standard deviation of the environmental variables. Species driving the assemblage change along PRF 1 and their relative contribution (b_k) to the change are plotted to the right.
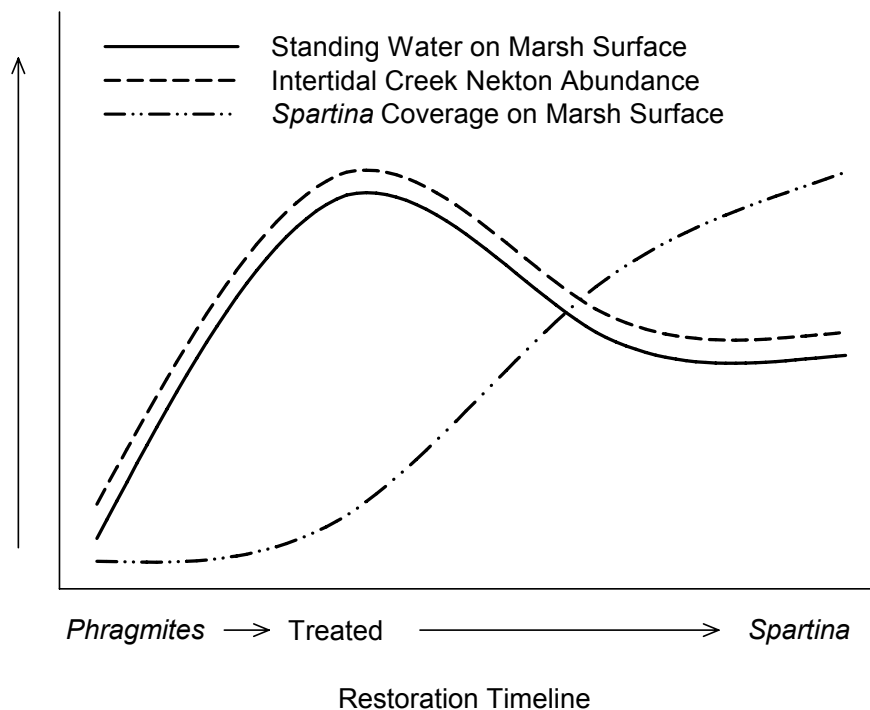
Figure 3-5. Conceptual relationship between the amount of standing water on the marsh surface, *Spartina* coverage, and intertidal creek nekton abundance for salt marsh restorations. The restoration timeline is depicted on the x-axis beginning with *Phragmites*-dominated marshes followed by the transition from initial treatment to *Spartina*-dominated marshes.

CHAPTER 4

Intertidal creek migrations of nekton in invasive *Phragmites* salt marshes and marshes

treated for *Phragmites* removal: small scale video observations

INTRODUCTION

Invasive *Phragmites australis* (hereafter *Phragmites*) has become established in

recent decades and now dominates many oligohaline and mesohaline tidal marshes in the

northeastern US (Chambers et al., 1999; Philip and Field, 2005; Lambert and Casagrande,

2006). *Phragmites* invasions result in changes to the marsh landscape (Windham and

Lathrop 1999; Hunter et al., 2006) and can alter the structure and function of intertidal

creeks (Weinstein and Balletto, 1999; Able et al., 2003; Teal and Peterson, 2005), which

serve as an important physical and biological corridor linking marsh surface and subtidal

habitats (McIvor and Odum, 1988; Rozas et al., 1988). Smaller intertidal creeks are

susceptible to filling in as detritus accumulates, tidal flow is slowed, and sedimentation

occurs, eventually filling in creeks completely in late invasion stages, thereby eliminating

nekton habitat (Able et al., 2003; Osgood et al., 2003). Larger intertidal creeks in

Phragmites-dominated marshes generally have vertical or concave banks and increased

flow rates, which may lead to greater predation and reduced access to the marsh surface

for nekton using intertidal creeks (McIvor and Odum, 1988; Teal and Weinstein, 2002).

Marsh restoration (i.e., treatment for *Phragmites* removal) may reverse habitat alterations

due to *Phragmites* and restore salt marsh habitats to pre-invasion structure and function

(Balletto et al., 2005).

Multiple studies have documented negative effects of *Phragmites* on larval and juvenile marsh surface nekton (Able and Hagan, 2000, 2003; Able et al., 2003; Osgood et al., 2003, 2006: Hunter et al., 2006), but research on nekton utilization of other salt marsh habitats has produced varying results. Nekton in marsh fringe, and intertidal and subtidal creek habitats were largely unaffected by invasive *Phragmites* (Able et al., 2001; Meyer et al., 2001; Grothues and Able, 2003a, b; Kimball and Able, 2007a; Kimball et al., in review). The majority of the above studies, however, focused on large spatial and temporal scales, and nekton were collected over single tide stages (e.g., ebb tide). To date, few studies have examined the effects of *Phragmites* on nekton use patterns in salt marsh habitats on small temporal and spatial scales, such as those within individual tidal cycles (but see Kimball and Able, 2007a). The difficulties associated with sampling nekton in salt marshes, along with the limitations of traditional nekton sampling techniques (e.g., seines, weirs, passive collectors), often limit the scale and scope of examination possible in various salt marsh habitats (Rozas and Minello, 1997; Connolly, 1999). However, the application of an established technology, such as underwater video (Barnes, 1952), to the novel setting of intertidal salt marsh creeks may elucidate nekton habitat use and tidal migration patterns that have heretofore been overlooked or unobservable. In this study, the nekton of intertidal creeks in invasive *Phragmites*-dominated and Treated (i.e., sites treated for *Phragmites* removal) marshes were examined with underwater video to 1) compare small scale temporal and spatial nekton habitat use patterns between marsh types and tide stages, and 2) evaluate marsh restoration success. This approach was complimented by also sampling nekton with more traditional techniques, weirs and wire mesh traps.

METHODS

Study Area

The *Phragmites* and Treated marshes were located in the oligo-mesohaline Hog Islands area of the Mullica River–Great Bay estuary (Fig. 4-1), which is part of the Jacques Cousteau National Estuarine Research Reserve located in southern New Jersey (Psuty et al., 1993). Over the last several decades, the invasion and subsequent dominance of *Phragmites* occurred on Hog Islands proper and in the surrounding marshes (Ferren et al., 1981; Windham and Lathrop, 1999). Treatment for *Phragmites* removal (via herbicide; for general procedure see Marks et al., 1994) in the marsh adjacent to Hog Islands was conducted in 2000 and again in 2002. After treatment, the marsh was left to recolonize naturally and was characterized during the study period by mixed native vegetation including (in order of relative abundance) *Pluchea purpurascens*, *Spartina alterniflora*, *Atriplex patula*, and *Scirpus maritimus*, with some small isolated patches of *Phragmites* remaining. Thus, restoration efforts resulted in two distinct marsh types in close proximity, the invasive *Phragmites*-dominated marsh on Hog Islands and the Treated marsh on the adjacent mainland (Fig. 4-1). Intertidal creeks in both marsh types had similar widths (mean width at mouth = 3.4 m, SE = 0.3) and lengths (mean length = 75.7 m, SE = 13.1), and all creeks had soft mud substrate bottoms with few remaining pools of water when drained at low tide. Creeks in the *Phragmites* marsh had steep banks (approximately vertical) and creeks in the Treated marsh had slightly sloping banks.

Field Sampling

Two intertidal creeks were sampled in each marsh type (*Phragmites* and Treated marshes, n = 4 creeks). Nekton were observed using an underwater video sampling system located upstream of the mouth of each creek (mean distance from creek mouth = 19.4 m, SE = 3.5), consisting of a flume (Fig. 4-2), low light camera (2.8 mm, f2.8 wide-angle lens, 0.27 Lux), self-contained video recorder, and battery. To guide intertidal creek nekton past the camera, the flume was constructed in an 'X' shape with a center channel (0.9 x 0.4 x 0.9 m) aligned with the creek channel. Four wings (1.2 x 0.9 m) extending onto the marsh surface at approximately 45° angles from each end of the channel funneled nekton through the flume and into camera view. The flume frame was constructed of PVC piping and cloth mesh (3.2 mm) was used for the walls of the wings and one side of the center channel (i.e., the camera side). The opposite wall of the center channel consisted of a solid sheet of white plastic to provide a contrasting background to enhance identification of nekton. The camera was placed 0.3 m above the creek bottom with the lens inserted through the mesh and positioned flush with the channel wall. In this configuration, the water column from approximately 0.15 – 0.5 m could be observed (field of view at distance of 0.4 m: 0.45 x 0.35 x 0.52 m), thus encompassing the depths of migration in intertidal creeks for both resident and transient nekton (Bretsch and Allen, 2006b). Once constructed, flumes were left in place in all creeks for the duration of the study, while video equipment was moved between sampling sites.

In order to determine nekton use throughout the tidal cycle, each intertidal creek was sampled during consecutive flood and ebb tides. On each sampling day, prior to tidal inundation, the camera, recorder, and battery were integrated with the flume. Video recording began when the camera was totally submerged on the flood tide and continued

uninterrupted until the camera emerged during ebb tide. Sampling occurred monthly

from August to September in 2005 (n = 8 days) and from July through September in 2006

(n = 10 days; two creeks, one of each marsh type, were not sampled in September). Each

creek was sampled completely, flood through ebb tide, in one day during daylight hours.

Surface temperature and salinity were measured in individual creeks once, at slack high

tide, on each sampling day with a handheld meter (YSI model 85). Temperature (n = 18)

was recorded on each sampling day, but salinity (n = 15) was not recorded on some days.

To ground-truth video observations and qualitatively assess the utility of

underwater video as a tool for sampling salt marsh nekton, intertidal creeks were also

sampled with weirs and wire mesh traps. Nekton were collected using weirs (2.0 x 1.5 x

1.5 m bag, 5.0 x 1.5 m wings, 3.2 mm mesh) set at high tide and removed at slack low

tide. At each intertidal creek sampled, the weir bag was stretched across the creek

channel with support poles embedded vertically in the sediment. Wings were extended

back onto the marsh surface from each end of the bag, and all net lead lines were buried

in the bottom sediment to eliminate gaps in the funnel-shaped weir. Nekton were also

collected using wire mesh traps (cylindrical, 0.4 x 0.2 m, 25 mm openings on each end,

3.2 mm mesh), placed approximately 3 m upstream and downstream (1 each) of the

flume, set at high tide and removed at slack low tide. Sampling occurred monthly from

July through September 2006 (final sample sizes: weirs, *Phragmites* n = 5, Treated n =

6; wire mesh traps, each marsh type n = 12). Individual creeks were sampled with weirs

and wire mesh traps on non-consecutive days, during daylight hours once each month.

All nekton collected were identified and enumerated. Individuals not identifiable to

species were preserved in 10% formalin or 95% ethanol and processed in the laboratory.

Data Analysis

Each video was viewed completely and all nekton were identified and enumerated for each one minute increment. To examine nekton tidal utilization patterns, video footage was broken down further within each tidal cycle. For each video, the complete flood (beginning of recording to slack high tide) and ebb (slack high tide to end of recording) tides were each divided into 8 tide stages of equal length (flood: tide stages 1-8, mean duration = 25 min, SE = 1; ebb: tide stages 9-16, mean duration = 20 min, SE = 1). For each tide stage, the counts (i.e., number of individuals of a given species) from each one minute increment were summed for each individual species observed. This removed the time component and provided species totals for each of the 16 tide stages. Each tide stage (1-16) was treated as a discrete sample (thus 18 sampling days, 16 tide stages: final sample size, n = 288).

Abundance (expressed as catch-per-unit-effort, CPUE) was compared among marsh types and tide stages for individual species and all species combined. Species abundance was transformed (ln (1 + CPUE)) and analyzed with a three factor analysis of variance (ANOVA) with marsh type, tide stage, and year as factors (SAS, Version 9.1). Differences in treatment means were examined using the Tukey-Kramer test, a test that is preferred when sample sizes are unequal (Sokal and Rohlf 1997). To compare nekton tidal migration patterns, the overall flood or ebb tide total abundance of a given species was used to calculate the percentage of that total abundance observed in each flood tide stage (1-8) or ebb tide stage (9-16). This was done for individual species and all species combined, and for each marsh type separately. 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). Environmental variables were analyzed with a two factor ANOVA with marsh type and year as factors. Differences in treatment means were examined using the Tukey-Kramer test.

For analysis of the weir and wire mesh trap data, ebb tide abundance (CPUE) for all species combined was transformed (ln (1 + CPUE)) and analyzed with a two factor ANOVA with marsh type and sampling gear as factors. Differences in treatment means were examined using the Tukey-Kramer test.

RESULTS

Environmental Characteristics

Environmental characteristics in the intertidal creeks did not differ between marsh types (Table 4-1). Temperature did not vary significantly between the *Phragmites* and Treated marshes or between years (Fig. 4-3). Salinity also did not vary significantly between marsh types, however, average salinities across marsh types were lower in 2006 (mean salinity = 5.6, SE = 1.3) than in 2005 (mean salinity = 11.9, SE = 0.6; p = 0.0035).

Sampling Effectiveness

The majority of species present in weir and wire mesh trap catches were observed with underwater video with the exception of three infrequently caught species: *Fundulus diaphanus*, *Lepomis gibbosus*, and *Cyprinodon variegatus* (Tables 4-2 and 4-3). Fishes (n = 8 species) and *Callinectes sapidus* dominated the intertidal creek nekton collected with weirs, and wire mesh traps almost exclusively collected *F. heteroclitus* (Table 4-3). Overall nekton abundance varied by marsh type and sampling gear (i.e., weirs, wire mesh

traps, underwater video), but the only significant difference in abundance was for underwater video ($p = 0.0198$), with much greater overall abundance in the Treated marsh than the *Phragmites* marsh (Fig. 4-4).

Nekton Species Composition, Abundance, and Tidal Migrations

Fishes dominated the intertidal creek nekton, with 9 species and 5,679 individuals out of a total of 11 species and 5,722 individuals observed with underwater video (Table 4-2). C. *sapidus* (n = 35) and *Malaclemys terrapin* (n = 8) were also observed during the study. Resident nekton species (n = 4) accounted for 88% of the total observed and were dominated by *F. heteroclitus*, which alone accounted for 87% of total individuals. Other resident nekton included *Morone americana*, *Gobiosoma bosc*, and *M. terrapin*. Transient nekton species (n = 5) made up 11% of the total individuals observed. These were primarily *Menidia menidia*, but also included *C. sapidus*, *Brevoortia tyrannus*, *Pomatomus saltatrix*, and *Anguilla rostrata*. Two freshwater species, *Ameiurus nebulosus* and *Notemigonus crysoleucas*, were infrequently observed and represented only 1% of the total.

Species composition differed slightly between marsh types (Table 4-2). The number of species observed in the *Phragmites* (n =9 species) and Treated (n = 10 species) marshes was similar, with several less abundant species only observed in one marsh type (i.e., *Ameiurus nebulosus*, *Gobiosoma bosc*, *Notemigonus crysoleucas*). Resident nekton, primarily *F. heteroclitus*, dominated the observations in the Treated marsh (91%), with transient (8%) and freshwater (1%) species combining for less than 10%. Resident (50%) and transient (46%) nekton were observed in similar percentages in the *Phragmites* marsh, and freshwater nekton accounted for the remaining 4% of the total.

Overall species abundance and the abundance of several individual species varied by marsh type and either tide stage or sampling year (Table 4-1). Overall nekton abundance was an order of magnitude greater in the Treated marsh than in the *Phragmites* marsh (Table 4-2), but this relationship varied according to tide stage (Table 4-1). *F. heteroclitus* abundance was two orders of magnitude greater in the Treated marsh than the *Phragmites* marsh (Table 4-2) but this relationship also varied according to tide stage (Table 4-1). *M. menidia* were much more abundant in the Treated marsh than the *Phragmites* marsh, and were observed only in the Treated marsh in 2006. Similarly, *Morone americana* were also more abundant in the Treated marsh, but were observed only in the *Phragmites* marsh in 2005. *A. nebulosus* and *N. crysoleucas* were observed only in one marsh type (*Phragmites* and Treated, respectively), and neither species was observed in 2005. *Pomatomus saltatrix* abundances were low for all marsh type and sampling year combinations.

Species composition and abundance also differed by tide stage (Table 4-4). The number of species collectively observed during flood (n = 10) and ebb (n = 11) tide stages was similar, however, resident nekton were dominant in early flood tide stages (1-3) and the majority of ebb tide stages (10-16) with relative abundances ≥ 75% (Table 4-4). Transient nekton were most abundant in the late flood tide stages (4-8) and the earliest ebb tide stage (9) when water depths were greatest, with a maximum of 82% just before slack high tide (Table 4-4). Although infrequently observed overall and absent from nearly half of all tide stages (Table 4-4), freshwater nekton abundance centered around middle flood tide stages (3-6) and early ebb tide stages (9-10). Overall nekton abundance differed with tide stage and was greatest in early flood (1-3) and late ebb (13-

16) tide stages, however, overall and individual species tide stage abundances varied with marsh type and tide stage (Tables 4-1 and 4-4). *F. heteroclitus* abundance was greatest in the early flood tide stages (1-2) and the latest ebb tide stages (13-16), but abundance also varied greatly with marsh type (Tables 4-1 and 4-4). *M. americana* abundance was greatest at ebb tide stage 10 (Table 4-4), with significant differences between abundances in early and late flood tide stages (1 and 7, both $p < 0.05$) and middle to late ebb tide stages (12-16, all $p < 0.05$).

Overall and individual nekton tidal migration patterns varied somewhat between *Phragmites* and Treated marsh intertidal creeks (Fig. 4-5). Overall nekton (all species combined, n = 11) displayed a somewhat symmetrical tidal migration pattern in the Treated marsh, with greater percentages in early flood and late ebb tides. In contrast, overall nekton migration patterns in the *Phragmites* marsh were characterized by greater percentages in both late flood and ebb tide stages. *F. heteroclitus* followed a symmetrical tidal migration pattern that was consistent in both marsh types, with the highest percentages in early flood and late ebb tide stages and few individuals present during the tide stages surrounding slack high tide. *M. menidia* migration patterns were opposite between marshes. *M. menidia* occurred almost exclusively during the late flood and early ebb tide stages in the *Phragmites* marsh, but were spread out among all flood and ebb tide stages in the Treated marsh. Flood and ebb tide migration patterns for *M. americana* were consistent between marsh types. *M. americana* occurred throughout the flood tide, but were only present in the early ebb tide stages, albeit in the highest proportions. Tidal migration patterns also varied for several less abundant species (Fig. 4-6), however, patterns were not always discernable in both marsh types due to limited observations for

some species. Greater percentages of *A. nebulosus* occurred in the middle flood and ebb

tide stages, but this species was only observed in the *Phragmites* marsh. *Brevoortia*

tyrannus displayed opposite migration patterns between marsh types, primarily occurring

in early flood and late ebb tide stages in the *Phragmites* marsh, and present during middle

flood and ebb tide stages in the Treated marsh. *C. sapidus* occurred throughout both the

flood and ebb tides and displayed no discernable migration pattern in either marsh type.

N. crysoleucas migration patterns varied, with individuals primarily found in the middle

flood tide stages and in the earliest ebb tide stages, however, this species was only

observed in the Treated marsh. *P. saltatrix* generally occurred during the early stages of

both the flood and ebb tides, but no individuals were observed in the Treated marsh

during flood tide stages.

DISCUSSION

Sampling Effectiveness

Underwater video was an effective method for sampling intertidal salt marsh

creek nekton (Fig. 4-7), and permitted the observation of small scale nekton utilization

patterns that are difficult (or impossible) to detect when sampling with other traditional

gears (i.e., weirs, wire mesh traps) over complete tide stages (e.g., ebb or flood tide).

Traditional sampling gears are typically inexpensive (to purchase) and widely used (and

therefore standardized), which facilitates data analyses and promotes multi-study

comparisons. However, deployment of traditional sampling gears is often labor intensive

and results in disturbance to the animals and habitat destruction. In contrast, underwater

video allows nekton sampling with minimal disturbance to the animals or habitat and

operation with much reduced labor intensity (e.g., 1 person) and minimal time constraints. However, initial equipment costs are often relatively high and the specific operating requirements (i.e., reduced turbidity) likely preclude the widespread use of underwater video in the shallow, turbid waters characteristic of many salt marshes.

The camera set-up underwater also influences data collection and may introduce sampling biases. In the present study, tidal migration patterns of nekton in intertidal creeks were observed for the same portion of the water column throughout the tidal cycle. Individuals migrating above or below the view of the camera would not be detected. Therefore species that migrate in surface waters at the highest tide stages, or those that migrate on or close to the creek bottom throughout all tide stages (e.g., *C. sapidus*) might be underrepresented. Further, because underwater video is not a widely used sampling technique in salt marsh habitats, the method is largely untested. In addition, analysis and interpretation of the copious amounts of data is difficult. For example, initial attempts to sub-sample video footage (at various rates less than analysis of all footage) were abandoned because several species that were present were not being detected. Conversely, there is a risk of individuals being counted multiple times, which is likely inherent to many underwater video field sampling protocols. Underwater video has been used successfully in multiple other aquatic habitats (Burrows et al., 1999; Jury et al., 2001; Mueller et al., 2006), and, despite the aforementioned disadvantages, is a promising tool for sampling salt marsh nekton. The small temporal and spatial scale data available with underwater video permits analyses beyond just presence/absence and allows researchers to examine previously elusive movement and behavioral patterns of

nekton. Underwater video will likely become more widely used as advances in camera

technology overcome application limitations and equipment becomes more affordable.

Nekton Species Composition, Abundance, and Tidal Migrations

The *Phragmites* and Treated marsh intertidal creeks were characterized by an

overall low number of species that were dominated by several abundant and ubiquitous

intertidal salt marsh resident and transient species. This is consistent with previous

studies of nekton in various marsh habitats in these same oligohaline salt marshes

(Hastings, 1984; Able and Hagan, 2000). *F. heteroclitus*, *M. menidia*, and *M. americana*

were the three most abundant species in each marsh type, but all three species were

observed in greater numbers in the Treated marsh than the *Phragmites* marsh. The

overwhelming abundance of *F. heteroclitus* in the Treated marsh translated into a high

relative abundance of resident nekton. In the *Phragmites* marsh, the similar relative

abundances of resident and transient species were due to almost equally high abundances

of *F. heteroclitus* and *M. menidia.* Early treatment effects on the marsh surface such as

an increased amount of standing water (e.g., microhabitats, large puddles and pannes) and

reduced canopy (due to *Phragmites* removal) may be responsible for greater nekton

abundances in the Treated marsh intertidal creeks (Kimball et al., in review). In

particular, newly treated marshes may provide especially favorable marsh surface

conditions for *F. heteroclitus* (Currin et al., 2003; Hagan et al., 2007), the most abundant

species in this study. *N. crysoleucas* and *A. nebulosus* were both only observed in 2006,

when intertidal creeks were characterized by lower salinity waters. The higher salinities

observed in 2005 likely precluded these two freshwater species from utilizing the more

saline intertidal creek habitats that year. This exemplifies the fluctuating environmental

conditions typical of tidal salt marsh habitats and also illustrates the influence of salinity on species distributions, as occurs for other species in the same estuary (Martino and Able, 2003).

Differences in creek geomorphology may explain some of the observed nekton abundance differences between the *Phragmites* and Treated marshes, especially for *F. heteroclitus*. The Treated marsh creeks had gradually sloping banks, which generally have slower flow (Allen et al., 2007), provide better refuges (McIvor and Odum, 1988; Hettler, 1989), and facilitate nekton movement onto the marsh surface (Rozas et al., 1988). Salt marsh creeks with sloped banks and slower flow have been documented to support greater abundances of many common salt marsh species (Williams and Zedler, 1999; Allen et al., 2007). In particular, *F. heteroclitus* has been found to favor creeks with sloped banks and low flow (Allen et al., 2007), which may explain the greater abundances observed in the Treated marsh creeks in the present study. Creeks in the *Phragmites* marsh had steep banks, which can concentrate water in the creeks and potentially increase flow rate. Further, steep banks can potentially keep water from spreading out onto the marsh surface until periods of maximum tidal inundation, thereby delaying nekton migration to marsh surface habitats and increasing the risk of predation (McIvor and Odum, 1988). Nekton abundance differences in the present study suggest that marsh restoration efforts to remove *Phragmites* may promote the development of creek geomorphologies more favorable to dominant salt marsh nekton.

In general, tidal use patterns of resident, transient, and freshwater nekton in intertidal creeks were similar to patterns observed for nekton in other intertidal salt marsh creeks in North America (Bretsch and Allen, 2006b; Kimball and Able, 2007a, b) and

Europe (Cattrijsse et al., 1994; Hampel et al., 2003). Resident species were most

abundant in early flood tide stages and were abundant in the majority of ebb tide stages.

Transient species abundance centered around slack high tide, with the greatest

abundances in late flood tide stages, which may be an optimal utilization period for many

common transient species (Bretsch and Allen, 2006b; Kimball and Able, 2007a, b). The

divergent tidal use patterns of resident and transient species in intertidal creeks may also

be due to a number of factors including refuge from predation and foraging (Salgado et

al., 2004a; Rypel et al., 2007). In the present study, freshwater species abundance was

greatest around slack high tide, which may indicate that freshwater and transient species

use intertidal creeks in a similar manner for similar purposes (e.g., foraging, access to the

marsh surface).

Individual species displayed distinct and often variable intertidal creek tidal

migration patterns. *F. heteroclitus* displayed a similar uniform tidal migration pattern

with peak abundance in both marsh types during the early flood and late ebb tide stages,

which is consistent with *F. heteroclitus* using marsh surface habitats during the period

around slack high tide in Georgia salt marshes (Kneib and Wagner, 1994). This same

tidal migration pattern was also observed for *F. heteroclitus* in South Carolina salt

marshes (Bretsch and Allen, 2006b). *F. heteroclitus* tidal migrations were also similar in

Phragmites and Treated intertidal creeks in oligohaline Delaware Bay marshes (Kimball

and Able, 2007a). This suggests that *F. heteroclitus* tidal use of intertidal creeks does not

differ according to the dominant vegetation. Thus, the factors that may negatively affect

F. heteroclitus abundance in *Phragmites* marshes such as loss of marsh surface habitats

(Able and Hagan, 2000, 2003; Able et al., 2003; Hagan et al., 2007) and unfavorable

creek geomorphologies (Allen et al., 2007), appear not to affect the timing of migration

for those individuals using intertidal creeks in *Phragmites*-dominated marshes. *M.*

menidia, however, appear to be migrating in *Phragmites* and Treated creeks in different

patterns. Similar to the migration pattern observed in *Phragmites* creeks, studies in

mesohaline Delaware Bay salt marshes found *M. menidia* tidal migrations centered

around slack high tide with a peak occurrence during late flood tide (Kimball and Able,

2007b). An additional different tidal migration pattern was observed in South Carolina

intertidal creeks, where *M. menidia* peak occurrence was during mid-ebb tide (Bretsch

and Allen, 2006b). The tidal migration pattern of *M. americana* was consistent between

marsh types, with peak occurrence in early ebb tide stages. *M. americana* exhibited this

same tidal migration pattern, also in both Treated and *Phragmites* creeks, in Delaware

Bay salt marshes (Kimball and Able, 2007a). This suggests that *M. americana* tidal use

of intertidal creeks may also be unaffected by dominant marsh vegetation or restoration

activities. Tidal migration patterns varied for several less abundant species (e.g., *A.*

nebulosus, B. tyrannus, *C. sapidus*, *N, crysoleucas, P. saltatrix*), however, patterns were

not always discernable in both marsh types due to limited observations (Fig. 4-6). Biotic

factors, such as species co-occurrence, have been shown to influence the water depth

preferences of common salt marsh nekton in shallow waters (Bretsch and Allen, 2006a),

and may have influenced tidal migration patterns. Predation risk has been shown to

differ with depth for smaller prey fishes in tidal creeks and intertidal habitats (Ellis and

Bell, 2004; Rypel et al., 2007), and therefore may dictate the timing of migration for

common prey species, such as *F. heteroclitus* (Kneib, 1997; Tupper and Able, 2000;

Nemerson and Able, 2003). While the variable tidal migration patterns observed for

some species in this study may be due to low abundances, even at greater abundances, some salt marsh nekton exhibit migrations that extend over much of the tide with no distinct pattern (Bretsch and Allen, 2006b).

Implications for Marsh Restorations

The impact of marsh restoration efforts in the Hog Islands area marshes of the Mullica River- Great Bay estuary on nekton use of intertidal creek habitats varied with the response metric examined over the two year study period. Nekton generally used *Phragmites* and Treated intertidal creeks in a similar manner, as evidenced by species composition and tidal migration patterns, indicating that *Phragmites* marsh intertidal creeks serve as useful habitat for nekton until they fill in completely during late invasion stages (Able et al., 2003; Kimball et al., in review). The *Phragmites* and Treated marshes supported similar species compositions, and three ubiquitous oligohaline intertidal salt marsh species, *F. heteroclitus*, *M. menidia*, and *M. americana*, were the most abundant species (in that order) in each marsh type. An important exception is that for *F. heteroclitus*; differences in overall nekton abundance between marsh types were primarily due to greater abundances of *F. heteroclitus* in the Treated marsh. Favorable creek geomorphologies and marsh surface habitats at the Treated marsh likely contributed to greater *F. heteroclitus* abundances during this study, which took place in the early years following restoration efforts. Over time, as the marsh becomes more similar to an undisturbed, *Spartina alterniflora*-dominated marsh (i.e., increased vegetation coverage, reduced amounts of standing water on the marsh surface), the abundance of intertidal creek nekton, particularly *F. heteroclitus*, will likely gradually decline to match the level of habitat available (Kimball et al., in review).

Despite differences in abundances, however, tidal migration patterns indicated that *F. heteroclitus* and *M. americana* used the *Phragmites* and Treated creeks in a similar manner throughout the tidal cycle. This was reflected in the overall nekton tidal migration patterns, which differed primarily because of a peak in *M. menidia* abundance during late ebb tide in the *Phragmites* marsh. In combination, the results herein are in agreement with multiple other studies that also observed similar nekton utilization patterns in intertidal creek, marsh fringe, and subtidal creek habitats in *Phragmites* and non-*Phragmites* vegetation marshes (Fell et al., 1998; Able et al., 2001; Meyer et al., 2001; Warren et al., 2001; Fell et al., 2003; Grothues and Able, 2003a, b; Kimball and Able, 2007a). Thus, the negative effects of *Phragmites* are largely limited to larval and juvenile nekton using the marsh surface, such as *F. heteroclitus* and *F. luciae* (Able and Hagan, 2003; Able et al., 2003; Osgood et al., 2003, 2006; Hagan et al., 2007). However, as a result, marsh restoration efforts may diminish (or reverse) the negative impacts of *Phragmites* on marsh surface nekton, which may increase marsh production and therefore trophic transfer through the multiple interconnected marsh habitats (Hagan et al., 2007), especially intertidal creeks, as reflected in this and a related study (Kimball et al., in review).

Table 4-1. Analysis of variance results (F statistics) for effect of marsh type, tide stage, and year on overall and individual species abundance (catch-per-unit-effort, CPUE). Temperature (°C) and salinity were only tested for the effect of marsh type and year. Salinity was not recorded for some samples. Overall species CPUE included all species (n = 11) observed with underwater video during this study. The Tide Stage*Year and Marsh*Tide Stage*Year interactions were never significant and therefore dropped from the model. 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 Stage (df = 15)	Marsh x Tide Stage (df = 15)	Marsh x Year (df = 1)
Temperature	14	ns	--	--	ns
Salinity	11	ns	--	--	ns
Nekton					
Overall Species CPUE	254	152.86***	6.16***	4.38***	ns
Individual Species CPUE					
Ameiurus nebulosus	254	4.51*	ns	ns	4.51*
Anguilla rostrata	254	ns	ns	ns	ns
Brevoortia tyrannus	254	ns	ns	ns	ns
Callinectes sapidus	254	ns	ns	ns	ns
Fundulus heteroclitus	254	136.69***	12.02***	6.65**	ns
Gobiosoma bosc	254	ns	ns	ns	ns
Malaclemys terrapin	254	ns	ns	ns	ns
Menidia menidia	254	34.01***	ns	ns	26.66***
Morone americana	254	ns	2.67**	ns	8.83**
Notemigonus crysoleucas	254	6.55*	ns	ns	6.55*
Pomatomus saltatrix	254	ns	ns	ns	3.91*

Table 4–2. Intertidal creek nekton species composition and abundance (catch-per-unit-effort, CPUE, with standard error and total number observed with underwater video for each marsh type (all creeks, tide stages, months, and years combined). Final sample sizes: *Phragmites* n = 144; Treated n = 144. Each species was assigned to an estuarine category (EC): estuarine resident (R), estuarine transient (T), or freshwater (F). The relative abundance of estuarine resident, estuarine transient, and freshwater species is indicated as a percentage of the total abundance.

Species	EC	*Phragmites*			Treated			Combined
		CPUE	SE	Total	CPUE	SE	Total	Total
Ameiurus nebulosus	F	0.10	0.04	14	0	0	0	14
Anguilla rostrata	T	0.01	0.01	1	0.01	0.01	2	3
Brevoortia tyrannus	T	0.08	0.04	11	0.13	0.05	19	30
Callinectes sapidus	T	0.07	0.02	10	0.17	0.05	25	35
Fundulus heteroclitus	R	0.94	0.45	136	33.69	7.70	4852	4988
Gobiosoma bosc	R	0	0	0	0.01	0.01	1	1
Malaclemys terrapin	R	0.03	0.02	4	0.03	0.01	4	8
Menidia menidia	T	0.82	0.65	118	2.79	0.62	402	520
Morone americana	R	0.16	0.04	23	0.36	0.10	52	75
Notemigonus crysoleucas	F	0	0	0	0.20	0.08	29	29
Pomatomus saltatrix	T	0.08	0.05	12	0.05	0.02	7	19
All Species Combined		2.28	0.79	329	37.45	7.68	5393	5722
Resident Species				50%			91%	88%
Transient Species				46%			8%	11%
Freshwater Species				4%			1%	1%

Table 4-3. Intertidal creek nekton species composition and abundance (catch-per-unit-effort, CPUE, with standard error) and total number collected with weirs and wire mesh traps for each marsh type (all months and creeks combined for weirs; all months, creeks, and creek locations combined for wire mesh traps). Final sample sizes: Weirs, *Phragmites* n = 5, Treated n = 6; Wire Mesh Traps, *Phragmites* n = 12, Treated n = 12.

Species	*Phragmites*			Treated			Combined
	CPUE	SE	Total	CPUE	SE	Total	Total
Weir							
Brevoortia tyrannus	0	0	0	0.33	0.33	2	2
Callinectes sapidus	8.00	2.30	40	21.50	9.88	129	169
Fundulus diaphanus	0	0	0	0.50	0.50	3	3
Fundulus heteroclitus	6.00	6.00	30	38.50	35.31	231	261
Gobiosoma bosc	0	0	0	0.17	0.17	1	1
Lepomis gibbosus	0	0	0	0.17	0.17	1	1
Menidia menidia	0	0	0	1.17	0.75	7	7
Morone americana	5.20	2.40	26	3.83	2.40	23	49
Notemigonus crysoleucas	0	0	0	0.17	0.17	1	1
All Species Combined	19.20	3.99	96	66.33	36.36	398	494
Wire Mesh Trap							
Callinectes sapidus	0	0	0	0.08	0.08	1	1
Cyprinodon variegatus	0	0	0	1.17	0.99	14	14
Fundulus heteroclitus	171.42	40.55	2057	147.67	49.17	1772	3829
All Species Combined	171.42	40.55	2057	148.92	49.76	1787	3844

Table 4-4. Intertidal creek nekton abundances (total numbers) observed with underwater video for each tide stage (all marsh types, creeks, years, and months combined). Final sample size for each tide stage (1-16): n = 18. The relative abundance of estuarine resident, estuarine transient, and freshwater species is indicated as a percentage of the total abundance.

| Species	Flood Tide Stages								Ebb Tide Stages							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Ameiurus nebulosus	0	0	0	3	0	0	0	1	0	3	1	0	2	0	0	0
Anguilla rostrata	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
Brevoortia tyrannus	7	0	1	2	1	5	5	0	0	2	3	0	3	0	0	1
Callinectes sapidus	3	3	2	1	0	4	2	0	0	1	0	4	1	5	5	4
Fundulus heteroclitus	1027	371	164	13	9	1	4	10	4	75	128	191	476	917	921	677
Gobiosoma bosc	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Malaclemys terrapin	0	0	2	0	1	0	0	2	0	0	0	0	3	0	0	0
Menidia menidia	46	98	7	31	28	14	11	98	21	17	7	23	34	17	43	25
Morone americana	1	4	8	6	5	7	1	7	13	20	2	1	0	0	0	0
Notemigonus crysoleucas	0	0	4	6	2	3	0	1	8	4	0	1	0	0	0	0
Pomatomus saltatrix	1	0	0	0	0	0	0	0	8	4	3	0	2	1	0	0
All Species Combined	1085	476	192	63	46	34	23	119	54	126	144	220	522	941	969	708
Resident Species	95%	79%	91%	30%	33%	24%	22%	16%	31%	75%	90%	87%	92%	98%	95%	96%
Transient Species	5%	21%	5%	56%	63%	68%	78%	82%	54%	19%	9%	12%	8%	2%	5%	4%
Freshwater Species	--	--	4%	14%	4%	8%	--	2%	15%	6%	1%	1%	--	--	--	--
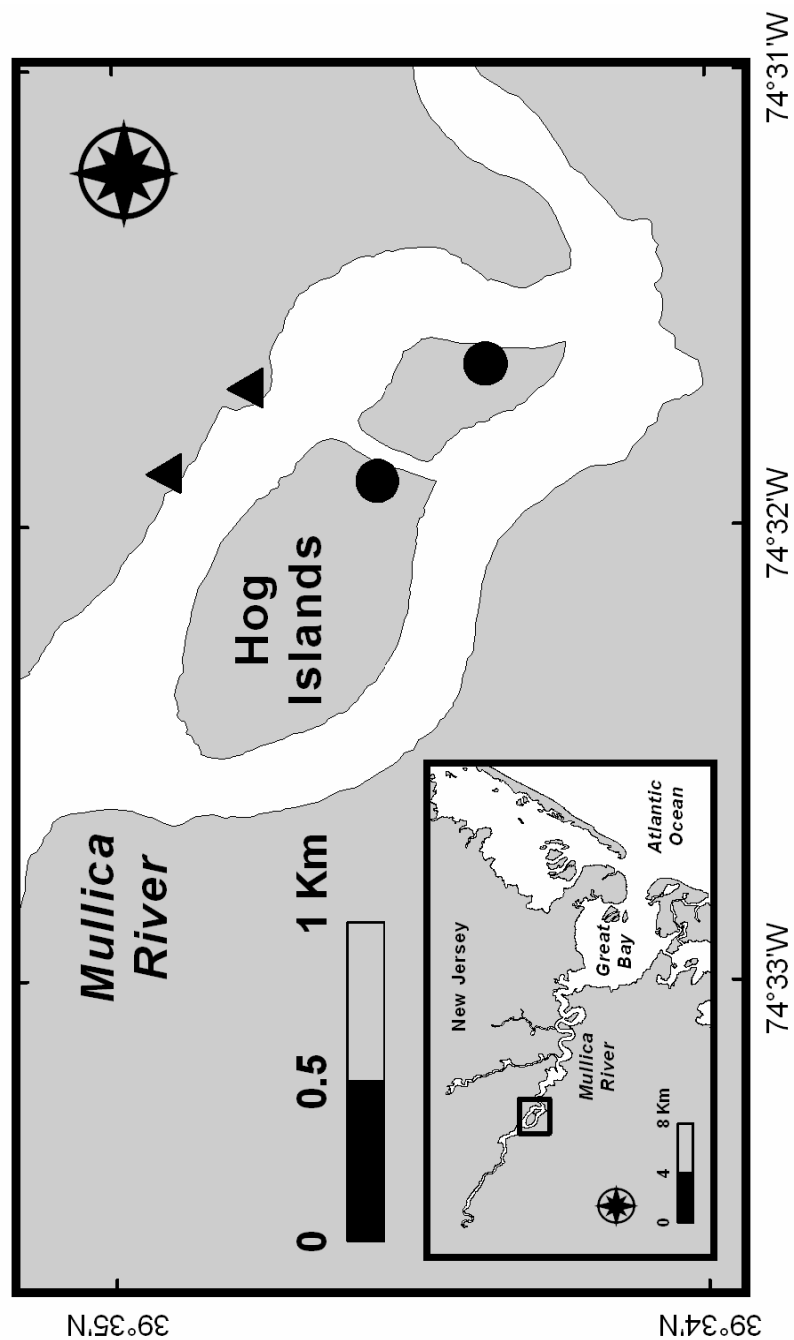
Figure 4-1. The Hog Islands area of the Mullica River-Great Bay estuary in southern New Jersey, USA. Intertidal creek sampling sites are shown for *Phragmites* (circles) and Treated (triangles) marshes.
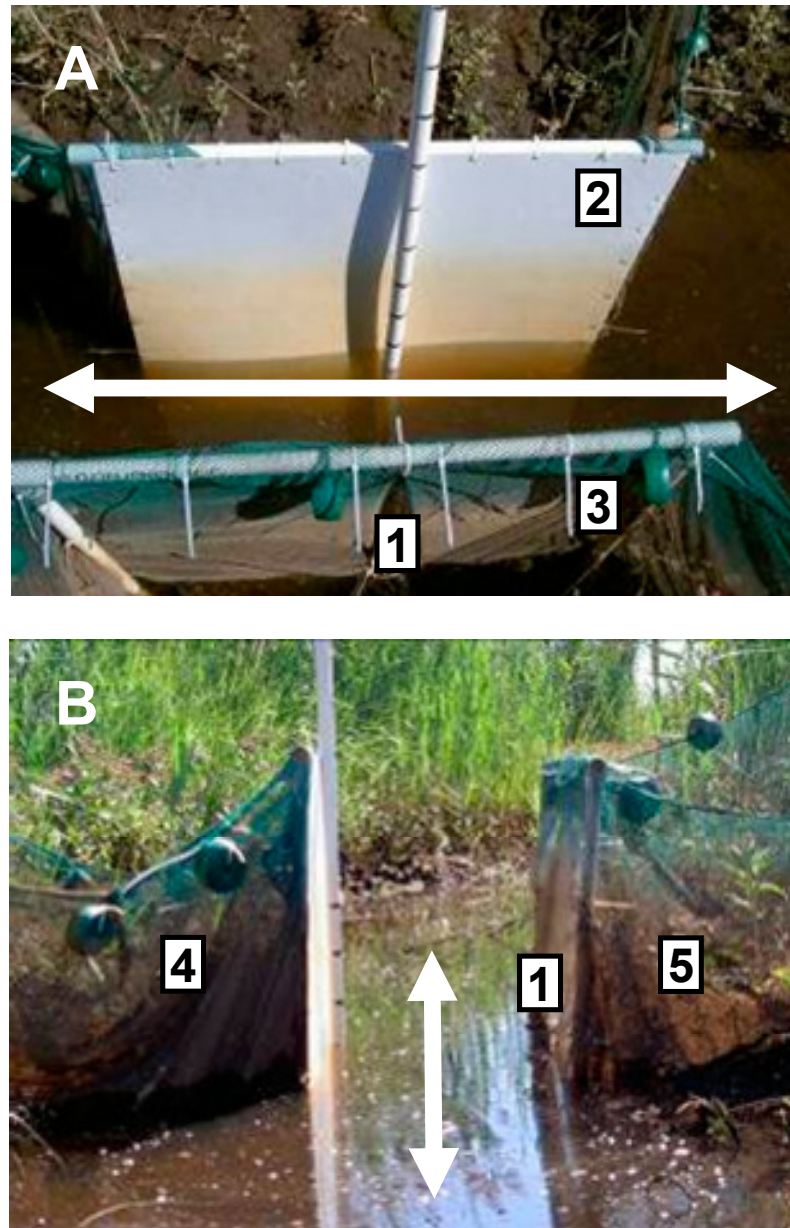
Figure 4-2. Creek side (A) and cross sectional view (B) of underwater video sampling system flume in intertidal creek (camera, video recorder and battery are not pictured). Numbers indicate: 1 – camera location; 2 – camera backdrop; 3 – mesh channel wall; 4, 5 – mesh wings. Arrows indicate the creek channel and flow directions.
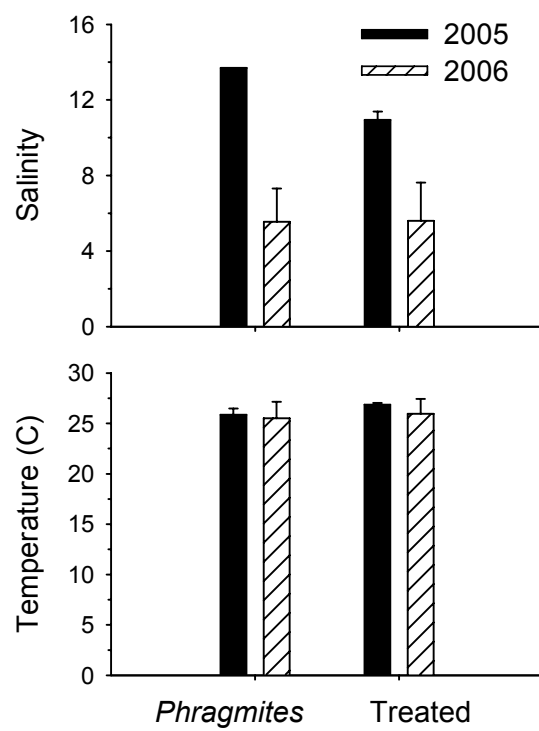
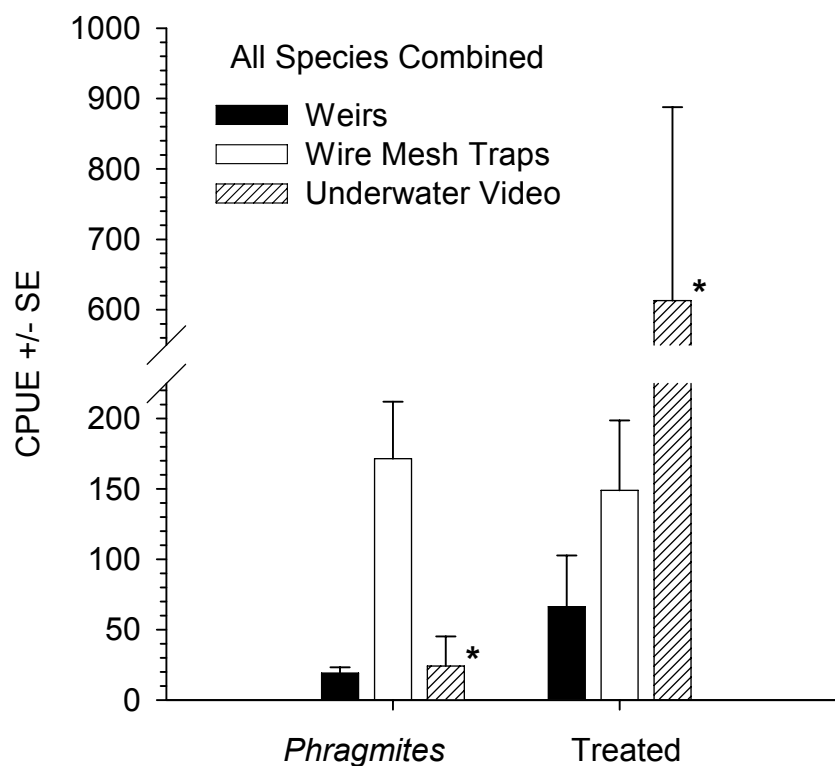Figure 4-3. Mean salinity and temperature by marsh type and year.

Figure 4-4. Abundance (catch-per-unit-effort, CPUE, and standard error) for all nekton species combined by marsh type and gear. Underwater video 2006 ebb tide stage nekton observations pooled for each marsh type (ebb tide sample sizes used for comparison: *Phragmites* n = 5; Treated n = 5). Significant differences in abundances between marsh type and gear combinations are indicated with an asterisk (*).
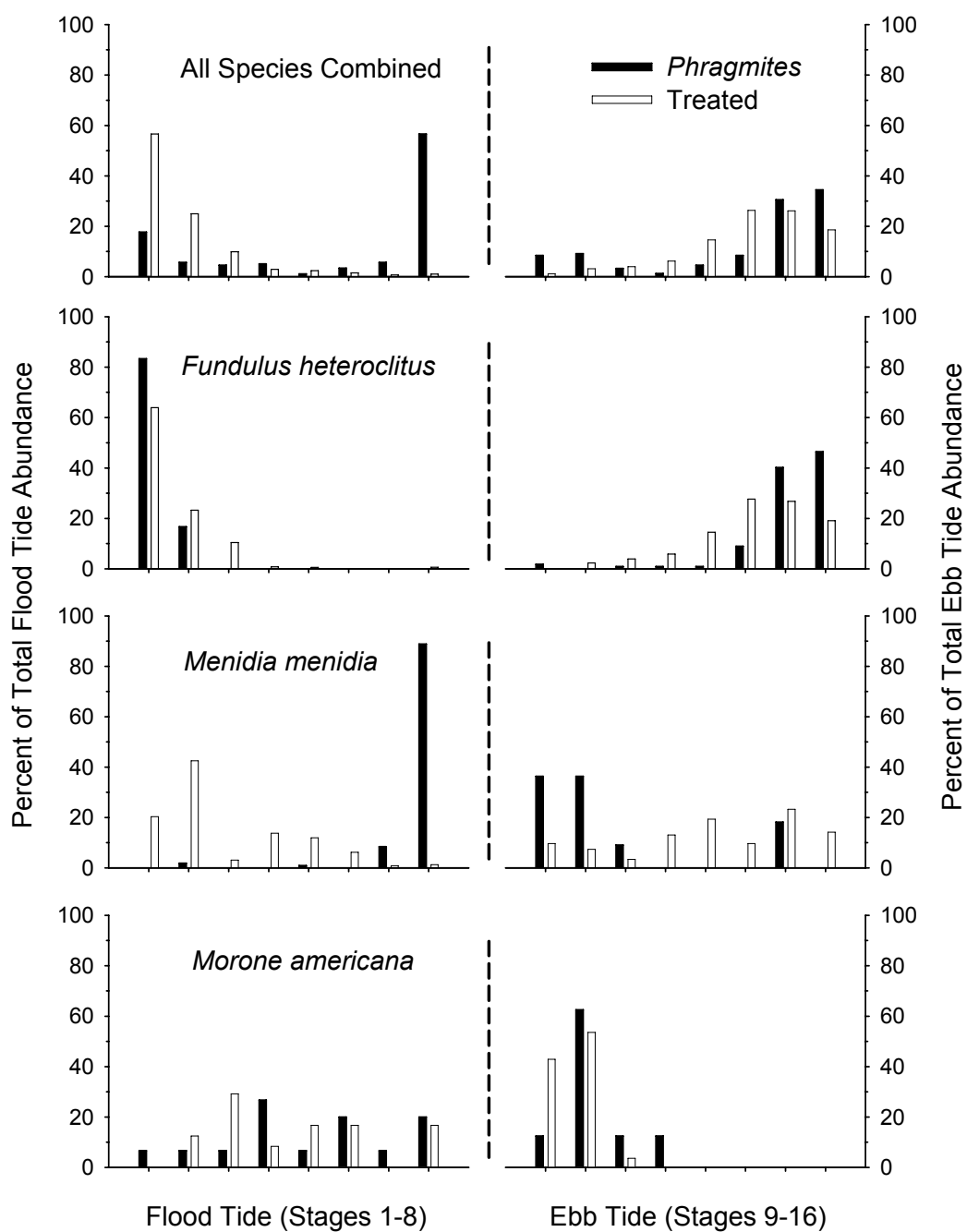
Figure 4-5. Tidal migration patterns for all species combined and the three most abundant species observed with underwater video. Dashed lines indicate slack high tide.
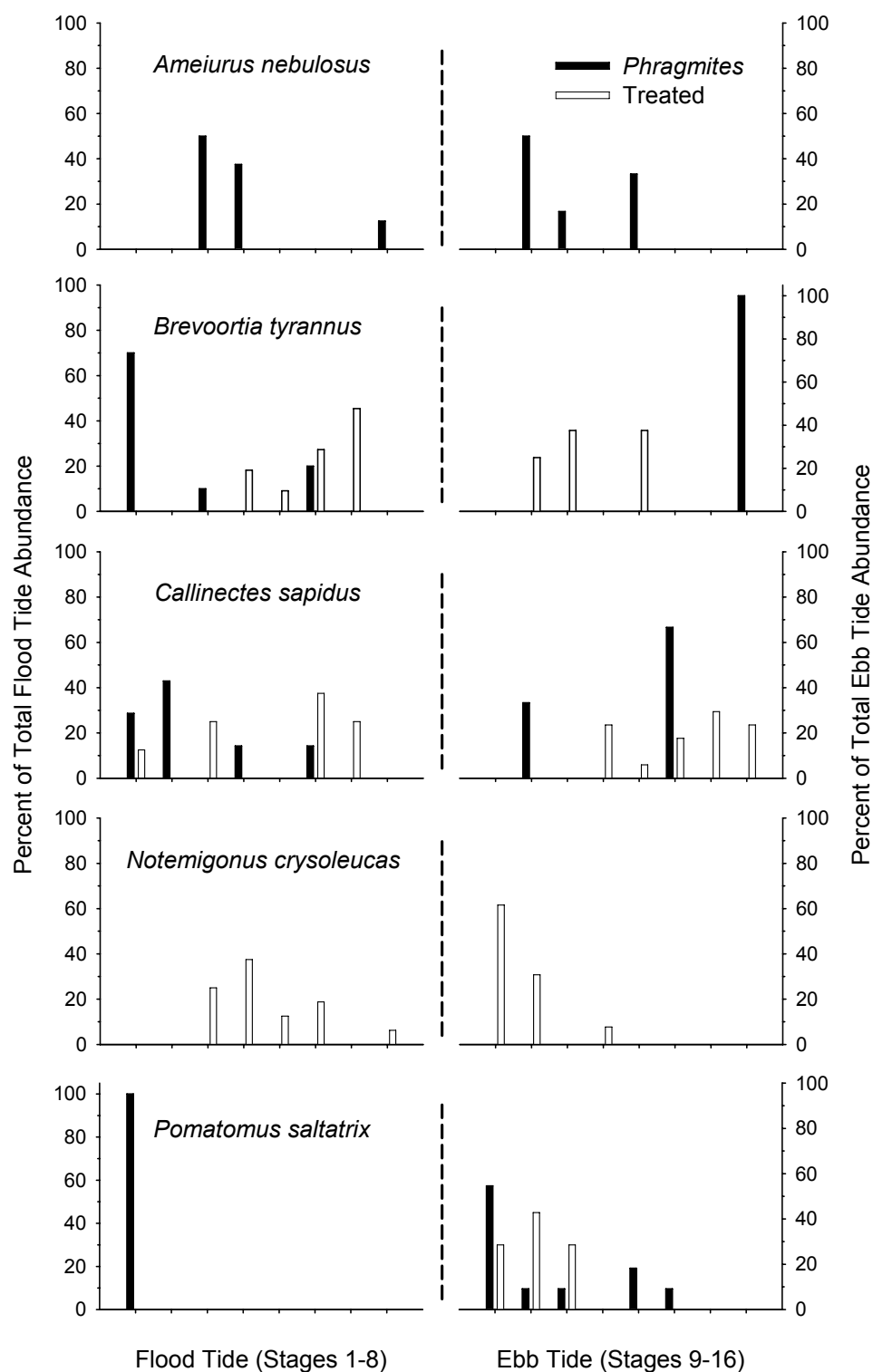
Figure 4-6. Tidal migration patterns for less abundant species observed with underwater video. Dashed lines indicate slack high tide.
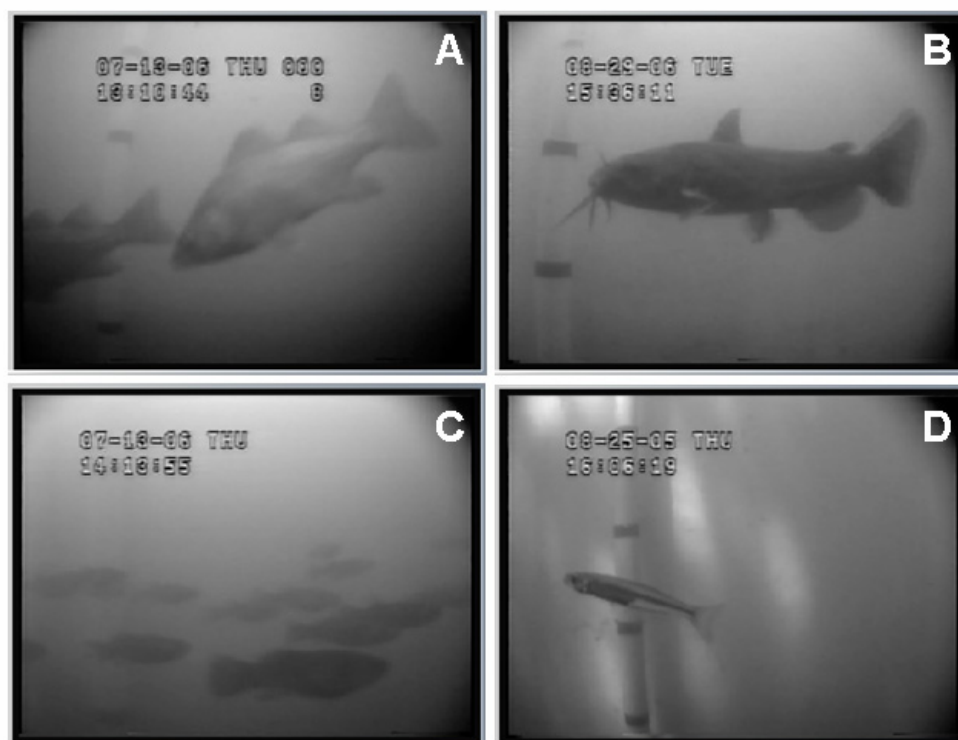
Figure 4-7. Underwater video images of *Morone americana* (A), *Ameiurus nebulosus* (B), *Fundulus heteroclitus* (C), and *Menidia menidia* (D) in intertidal creeks.

GENERAL CONCLUSIONS

Numerous studies have examined the effect of marsh restoration efforts on nekton utilization of marsh surface habitats (Able and Hagan, 2000, 2003; Able et al., 2003; Fell et al., 2003; Teo and Able, 2003a, b; Hunter et al., 2006; Hagan et al., 2007) and subtidal creeks (Tupper and Able, 2000; Miller and Able, 2002; Grothues and Able, 2003a, b; Jivoff and Able, 2003; Nemerson and Able, 2003, 2005). However, relatively few studies have focused on intertidal creeks when evaluating marsh restoration efforts (Williams and Zedler, 1999; Able et al., 2000, 2004), and no studies examined nekton utilization at small temporal and spatial scales within tide stages. This dissertation research was undertaken to gain a better understanding of nekton habitat utilization and movement patterns within tidal cycles in intertidal salt marsh creeks. Tidal utilization of nekton was examined in the context of several different marsh restorations in an effort to determine if nekton utilized intertidal creeks in natural, treated, and invasive-dominated marshes in a similar manner.

Chapter 1 focused on the Alloway Creek watershed located in the oligohaline upper Delaware Bay, where marsh restoration was conducted to ameliorate the deleterious effects of *Phragmites* invasion and restore marshes to pre-invasion form and function. Intertidal creeks in three marsh types (natural *Spartina*-dominated, sites treated for *Phragmites* removal and now dominated by *Spartina*, and invasive *Phragmites*-dominated) were sampled during summer 2004 with seines multiple times during flood and ebb tides to determine juvenile nekton habitat and tidal utilization patterns and identify possible effects of marsh restoration efforts on intertidal nekton. Total nekton abundance was greater at *Spartina* and Treated marshes than *Phragmites* marshes. The

overall nekton assemblage did not vary between marsh types, but the nekton assemblage did vary between tide stages, with low tide stages dominated by resident nekton (primarily *Fundulus heteroclitus*) and high tide stages consisting of a mix of transient and resident species (e.g., *A. mitchilli, M. americana, A. rostrata, M. saxatilis*). The effect of marsh restoration efforts on intertidal creek nekton was inconsistent, but most metrics examined indicated that restoration efforts had little effect in intertidal creek habitats, likely because the intertidal assemblage in all creek types was greatly influenced by many species moving from subtidal habitats and primarily a single (but abundant) species, *F. heteroclitus*, moving from the marsh surface.

Chapter 2 focused on degraded marshes (i.e., former salt hay farms) in the mesohaline lower Delaware Bay where ecological engineering principles were applied to reconstruct inlets and a tidal creek system in marshes formerly blocked off from tidal flow and used for agriculture (Philip, 2005; Weishar et al., 2005). Nekton response in intertidal creeks was evaluated by sampling with seines multiple times during flood and ebb tides 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 *F. heteroclitus* and *M. 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, therefore 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 (Able et al., 2008).

Chapter 3 also focused on intertidal creeks in *Spartina*, Treated, and *Phragmites* marshes within the Alloway Creek watershed, but sampling took place in different intertidal creeks than those used in Chapter 1. Intertidal creek nekton were sampled with weirs from May to November for 7 years (1999-2005) in three marsh types: natural *Spartina*, sites treated for *Phragmites* removal (hereafter referred to as Treated), and invasive *Phragmites* marshes. Intertidal creek collections in all three marsh types consisted primarily of resident nekton and were dominated by a relatively low number of ubiquitous intertidal species. The Treated marsh nekton assemblage was distinguished by greater abundances of most nekton, especially *Fundulus heteroclitus*, during the 7 year study period. *Phragmites* had little impact on nekton use of intertidal creeks over this period as evidenced by similar nekton assemblages in the *Spartina* and *Phragmites* marshes for most years. Long-term assemblage level analyses and nekton abundances indicate that the Treated marsh provided enhanced conditions for intertidal creek nekton. The response of intertidal creek nekton suggests that the stage of the restoration may influence the results of comparisons between marsh types and should be considered when evaluating marsh restorations.

Chapter 4 focused on the oligohaline marshes of the Great Bay-Mullica River estuary on the Atlantic coast of southern New Jersey where marsh restoration efforts were conducted to remove invasive *Phragmites*. The nekton of intertidal creeks in *Phragmites* and Treated marshes were sampled with underwater video during summer 2005 and 2006 to determine small scale temporal and spatial nekton use patterns throughout the tidal cycle. Because *Phragmites* has largely displaced *Spartina* from the many oligohaline marshes in this estuary (Windham and Lathrop, 1999), suitable *Spartina* marshes were not available for comparison. *Phragmites* and Treated marshes supported similar species compositions, and three ubiquitous intertidal salt marsh species, *Fundulus heteroclitus*, *Menidia menidia*, and *Morone americana*, were the most abundant species (in that order) in each marsh type. Overall nekton abundance was greater in the Treated marsh, but this varied with tide stage, and was largely due to greater abundances of *F. heteroclitus*. Tidal use generally varied according to estuarine classification, with resident nekton most abundant in early flood and late ebb tide stages, and transient nekton most abundant around slack high tide. *F. heteroclitus* and *M. americana* each exhibited uniform tidal migration patterns in both marsh types that were in agreement with previous observations from multiple salt marshes elsewhere (Kimball and Able, 2007a,b). In general, species composition and tidal migration patterns indicated that nekton generally used *Phragmites* and Treated intertidal creeks in a similar manner. The greater abundances of the resident species *F. heteroclitus* accounted for most differences observed and the enhanced use of the Treated marsh relative to *Phragmites*.

Together, these studies provide unique insights into the tidal utilization patterns of intertidal creek nekton at multiple spatial and temporal scales within the tidal cycle. The

combination of short-term and long-term studies (sometimes in the same salt marshes) illustrate that the period along a restoration timeline that is examined may influence comparisons among marsh types (e.g., Fig. 3-5). By examining nekton in multiple types of marsh restorations that involve clearing and natural recolonization of the marsh surface (e.g., *Phragmites* eradication and restoration of former salt hay farms), general patterns of nekton habitat use were discernable in marsh surface and intertidal creek habitats. The observed nekton habitat use patterns may aid future researchers when evaluating other salt marsh restoration projects of this type. These studies provide much needed information on nekton utilization of intertidal creeks in marsh restorations which can be integrated with studies from other salt marsh habitats for a more comprehensive evaluation of the effects of restoration on nekton (see Able et al., 2007, 2008).

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