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## *A Meta-analysis of Nekton Responses to Restoration of Tide-Restricted New England Salt Marshes*

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Salt marsh landscapes provide a mosaic of valuable habitats for a diverse array of estuarine nekton (defined here as free-swimming fish, shrimp, and crabs). Different species and life-history stages of nekton use salt marshes for foraging (Allen et al. 1994; James-Pirri et al. 2001; McMahan et al. 2005; Nemerson and Able 2005; Shervette and Gelwick 2007), overwintering (Smith and Able 1994; Raposa 2003), spawning (Taylor et al. 1977; Kneib 1997), as nurseries (Talbot and Able 1984; Rountree and Able 1992; Able and Fahay 1998; Minello et al. 2003), and as a refuge from predation (Kneib 1987; Minello 1993; Kneib 1997). Nektonic marsh species in turn play an important ecological role in adjacent estuaries by physically transporting energy from salt marshes into deeper estuarine habitats (Cicchetti and Diaz 2000; Deegan et al. 2000). Marsh nekton are also the primary prey items of economically valuable fishery species (e.g., Grant 1962; Nelson et al. 2003; Gartland et al. 2006) and charismatic estuarine birds such as herons and egrets (e.g., Parsons and Master 2000; McCrimmon et al. 2001). The importance of salt marshes to nekton is well documented, and the link that nekton forges between marshes and estuaries is clear. Unfortunately, human activities have long compromised the direct, physical connections between salt marshes and estuaries that are essential for nekton transport.

In the northeastern United States, humans have altered salt marshes for a variety of purposes dating back to at least colonial times (Rozsa 1995; Philipp 2005). A common type of alteration was the construction of a tide-restricting barrier across a marsh. These barriers led to changes in marsh hydrology and sediments (Portnoy 1991; Portnoy and Giblin 1997), vegetation (Roman et al. 1984), and marsh elevation (Portnoy and Giblin 1997), all of which can act in concert to change and often negatively impact nekton. Further, these effects on nekton seem to be

related to the degree or severity of tidal restrictions (Raposa and Roman 2003; Wozniak et al. 2006).

In an effort to remediate the negative ecological impacts of tidal restrictions, projects to restore natural tidal regimes to tide-restricted marshes are under way in New England and elsewhere (e.g., Warren et al. 2002; Teal and Peterson 2005; Konisky et al. 2006). Successful tidal restoration projects should lead to more natural marsh conditions and improve nekton habitat function and assemblage structure. The only way to validate this is to compare nekton monitoring data before and after restoration from restoration and reference/control sites. This is occurring throughout coastal New England, and a number of case studies have been published (Burdick et al. 1997; Dionne et al. 1999; Raposa 2002; Roman et al. 2002; Buchsbaum et al. 2006; Raposa 2008).

This chapter presents a meta-analysis of tidal restriction impacts on nekton communities in New England and explores how these communities in turn respond to tidal restoration efforts. The chapter's focus includes the five New England coastal states of Maine, New Hampshire, Massachusetts, Rhode Island, and Connecticut. Datasets reviewed in this chapter were obtained from the peer-reviewed scientific literature and by soliciting unpublished reports, posters, and complete and summary datasets from restoration practitioners and scientists throughout New England. This chapter also includes a broader discussion of nekton's role in marsh–estuarine connectivity with an emphasis on how connectivity is affected when humans alter tidal flow.

### Assessing Nekton in New England Marshes

Nekton data for this review were primarily obtained from monitoring programs in Rhode Island and Massachusetts. All of these data were collected with 1-square-meter (11-square-foot) throw traps following the same standardized protocol (Raposa and Roman 2001), which requires that samples be taken from shallow unvegetated habitats such as creeks and pools during the lower stages of the tide when water is not on the vegetated marsh surface. The use of the same sampling gear and monitoring protocol ensures that all of these data are directly comparable.

We used throw trap data collected from a total of twenty sites in this review (table 6.1; fig. 6.1). In some cases, a site contained two marshes (e.g., the upstream tide-restricted marsh and downstream reference marsh at Galilee, RI). We considered each marsh (total equal to twenty-five), including pairs of marshes within the same site, independent for statistical purposes. In most cases data were collected from an individual marsh for more than one year. Because variability was often high among years within the same marsh, and because data were some-

times collected by different personnel, annualized means of structural nekton variables (e.g., density and richness) were calculated and considered as independent datasets. Thus from the twenty sites/twenty-five marshes, sixty-nine total annualized throw trap datasets were used in this analysis. Of these sixty-nine datasets, thirty-three were from reference marshes, twenty-five from tide-restricted marshes, and eleven from restoring marshes (table 6.1).

Throw trap datasets were augmented with data from seven additional sites throughout New England, including one each from Connecticut, Massachusetts, and Maine, and four from New Hampshire (table 6.1; fig. 6.1). These data were only available in summary form and were collected with seines, lift nets, fyke nets, and minnow traps. These data therefore were not directly compatible with the throw trap datasets. Instead they were used to examine relative changes in nekton between pre- and postrestoration conditions and to place the findings from Rhode Island and Massachusetts into a broader perspective. While this is surely not an exhaustive collection of nekton data associated with tidal restrictions and restoration in New England, these datasets provide a quantitative aggregate dataset from which general patterns and trends can be examined. In total, this review of nekton in tide-restricted, restoring, and reference marshes in New England is based on datasets from twenty-seven sites throughout the entire region (fig. 6.1).

### *Data Analyses*

The throw trap datasets were used for examining trends in nekton density, richness, and community composition. Datasets were placed into three groups (reference, tide-restricted, and restoring marshes), and statistical comparisons were made among these three groups of marshes. For each individual dataset, mean densities of each species or species group were calculated and the number of species was totaled (and considered an indicator of species richness). Densities of individual species, all fishes combined, all decapods combined, and all nekton combined were analyzed among reference, tide-restricted, and restoring marshes using one-way analysis of variance (ANOVA). To address the assumptions of normality and equal variance, all data were  $\log(x + 1)$  transformed prior to analysis. If significant differences in density were detected, pairwise comparisons among treatment groups were then conducted using Tukey's Honestly-Significant-Difference (HSD) Test. The same technique was used to compare richness of total decapods, total fish, and total nekton among the three groups of marshes. All density and richness statistical analyses were conducted using SYSTAT version 12 (SYSTAT Software, Inc.).

Comparisons of overall nekton community structure were made among marsh groups (reference, tide-restricted, and restoring) using analysis of similarity

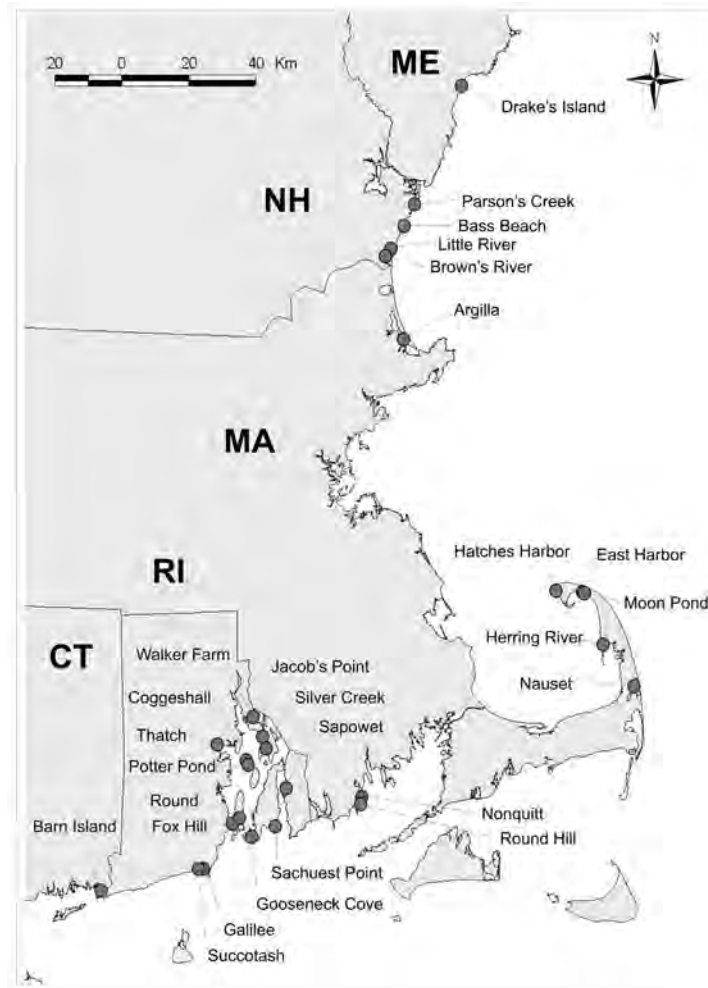
**TABLE 6.1.**  
*Nekton data set characteristics from reference, tide-restricted, and restoring salt marshes in New England*

Marsh name	Marsh type	Sampling gear	Years sampled	Months sampled	Sample size per year and (total)	Data set type
Barn Island, CT (upstream)	Restoring	Minnow trap	1999	Feb–Nov	Unspecified	Summary
Barn Island, CT (downstream) <sup>1</sup>	Reference	Minnow trap	1999	Feb–Nov	Unspecified	Summary
Argilla, MA (downstream)	Reference	Seine	1997; 1999	Jul–Oct	8, 8 (16)	Summary
Argilla, MA (upstream)	Restoring	Seine	1999	Jul–Oct	8 (8)	Summary
Argilla, MA (upstream)	Tide-restricted	Seine	1997	Jul–Oct	8 (8)	Summary
East Harbor, MA	Tide-restricted	Throw trap	2003–2006	Jul–Oct	20, 30, 53, 56 (159)	Full
Hatches Harbor, MA (downstream)	Reference	Throw trap	1997; 1999; 2003; 2005	Jun–Sep	120, 120, 21, 31, (292)	Full
Hatches Harbor, MA (upstream)	Restoring	Throw trap	1999; 2003; 2005	Jun–Sep	90, 13, 74 (177)	Full
Hatches Harbor, MA (upstream)	Tide-restricted	Throw trap	1997	Jun–Sep	90 (90)	Full
Herring River, MA (downstream)	Reference	Throw trap	1998; 2005	Jul–Oct	40, 40 (80)	Full
Herring River, MA (upstream)	Tide-restricted	Throw trap	1998; 2005	Jul–Oct	80, 34 (114)	Full
Moon Pond, MA	Tide-restricted	Throw trap	2003–2006	Jul–Oct	25, 31, 45, 24 (125)	Full
Nauset, MA	Reference	Throw trap	1998; 2004–2006	Jun–Oct	200, 68, 42, 27 (337)	Full
Nonquitt, MA	Tide-restricted	Throw trap	2005–2006	Aug–Sep	20, 22 (42)	Full
Round Hill, MA	Reference	Throw trap	2005–2006	Aug–Sep	15, 14 (29)	Full
Drake's Island, ME	Restoring	Fyke net	1 year (unspecified)	unspecified	2 (2)	Summary
Drake's Island, ME	Tide-restricted	Fyke net	1 year (unspecified)	unspecified	2 (2)	Summary
Bass Beach, NH	Restoring	Lift net	1 year (unspecified)	unspecified	21 (21)	Summary
Brown's River, NH	Restoring	Fyke net	1 year (unspecified)	unspecified	2 (2)	Summary
Brown's River, NH	Tide-restricted	Fyke net	1 year (unspecified)	unspecified	2 (2)	Summary

Little River, NH	Restoring	Lift net	3 years (unspecified)	unspecified	18, 24, 20 (62)	Summary
Parson's Creek, NH	Restoring	Fyke net	1 year (unspecified)	unspecified	2 (2)	Summary
Parson's Creek, NH	Tide-restricted	Fyke net	1 year (unspecified)	unspecified	2 (2)	Summary
Coggeshall, RI	Reference	Throw trap	2000; 2003–2005	Jul–Sep	50, 50, 50, 20 (170)	Full
Fox Hill, RI	Reference	Throw trap	2005	Aug	20 (20)	Full
Galilee, RI (downstream)	Reference	Throw trap	1997–1999	Jun–Sep	40, 40, 40 (120)	Full
Galilee, RI (upstream)	Restoring	Throw trap	1998–1999	Jun–Sep	64, 64 (128)	Full
Galilee, RI (upstream)	Tide-restricted	Throw trap	1997	Jun–Sep	64 (64)	Full
Gooseneck Cove, RI	Tide-restricted	Throw trap	2006; 2008	Jul, Aug	30, 31 (61)	Full
Jacob's Point (downstream)	Reference	Throw trap	2005; 2007–2008	Jul, Sep	10, 10, 10 (30)	Full
Jacob's Point, RI (upstream)	Tide-restricted	Throw trap	2005; 2007–2008	Jul, Sep	12, 12, 12 (36)	Full
Potter Pond, RI	Restoring	Throw trap	2003–2004	Jul, Sep	50, 50 (100)	Full
Potter Pond, RI	Tide-restricted	Throw trap	2000	Jul, Sep	50 (50)	Full
Round Marsh, RI	Reference	Throw trap	2005; 2008	Jul–Aug	20, 34 (54)	Full
Sachuest Point, RI (downstream)	Reference	Throw trap	1997–1999; 2004	Jul–Oct	30, 60, 60, 66 (216)	Full
Sachuest Point, RI (upstream)	Restoring	Throw trap	1998–1999	Aug–Oct	60, 60 (120)	Full
Sachuest Point, RI (upstream)	Tide-restricted	Throw trap	1997	Aug–Oct	30 (30)	Full
Sapowet, RI	Reference	Throw trap	2005	Aug	20 (20)	Full
Silver Creek, RI	Tide-restricted	Throw trap	2005; 2007–2008	Jul, Sep	30, 30, 29 (89)	Full
Succotash, RI	Reference	Throw trap	2008	Jul, Aug	39 (39)	Full
Thatch, RI	Reference	Throw trap	2006–2007	Aug	15, 12 (27)	Full
Walker Farm, RI	Restoring	Throw trap	2006–2007	Jul, Sep	22, 22 (44)	Full
Walker Farm, RI	Tide-restricted	Throw trap	2002	Sep	15 (15)	Full

Note: Full data set types are those with structural nekton data from each individual sample; summary data sets contained only a summary of a few basic parameters indicative of nekton structure. Refer to figure 6.1 for locations of each marsh.

<sup>1</sup>The Barn Island (downstream) marsh is referred to as Headquarters Marsh in Warren et al. (2002).



**FIGURE 6.1.** New England salt marshes where structural nekton data have been collected and are included in this review. These twenty-seven sites include tide-restricted, restoring, and reference salt marshes.

(ANOSIM). All data were square-root transformed prior to analysis to lessen the overall effects of the most abundant species on community structure. To create the resemblance matrix prior to analysis, Bray-Curtis similarity was calculated among samples. To identify the relative contributions of individual species to any significant differences in community structure between paired marsh groups, one-way similarity percentages (SIMPER) was used. ANOSIM and SIMPER analyses were conducted using PRIMER (Clarke and Warwick 2001; Clarke and Gorley 2006).

To assess nekton responses to restoration over time, the relative change (expressed as a percentage) in density and richness was compared between pre- and postrestoration conditions within each marsh where data were available (e.g., between tide-restricted and restoring conditions within the upstream Sachuest Point marsh), and then averaged across all marshes. The relative changes were broken into the first year postrestoration and then into an aggregate group of two or more years after restoration. This is the same approach used by Konisky et al. (2006) and was necessary because replication was limited beyond the second year following restoration.

### Results

Forty-two nektonic taxa were collected in the three marsh groups (table 6.2). As is typical of salt marshes in general, the southern New England nekton community was dominated by a small number of highly abundant species, and the majority of species were relatively rare. Based on density, over 90 percent of the nekton assemblage consisted of *Palaemonetes* spp. (grass shrimp; 69 percent), *Fundulus heteroclitus* (mummichog; 18 percent), *Cyprinodon variegatus* (sheepshead minnow; 2 percent), and *Crangon septemspinosa* (sand shrimp; 2 percent). In contrast, thirty-three of the forty-two species each made up less than 1 percent of the overall community, and fourteen species were found in only one or two of the datasets. When considering only fishes, the families Fundulidae (killifish; 77 percent of all fish based on density) and Atherinopsidae (silversides; 10 percent) were overwhelmingly dominant; the family Palaemonidae (grass shrimp) represented 95 percent of all decapods.

Based on ANOSIM, nekton community composition did not differ between reference and restoring marshes (ANOSIM,  $R = -0.04$ ,  $p = 0.77$ ), nor did it differ between restoring and tide-restricted marshes (ANOSIM,  $R = -0.04$ ,  $p = 0.72$ ). A significant difference was detected, however, between reference and tide-restricted marshes (ANOSIM,  $R = 0.18$ ,  $p = 0.001$ ). The species that were most responsible for the significant difference in community structure between reference and tide-restricted marshes include *Palaemonetes* spp. (responsible for 29 percent of the dissimilarity), *F. heteroclitus* (10 percent), *Fundulus majalis* (striped killifish; 7 percent), and *C. septemspinosa*, *C. variegatus*, and *Menidia menidia* (Atlantic silverside; 6 percent each).

The mean number of species per marsh was relatively low in each marsh group, with reference marshes supporting an average of 10.5 nekton species and tide-restricted and restoring marshes supporting 9.2 and 10.0 nekton species, respectively. Neither the total number of fish species nor all nekton species combined differed among the three groups (ANOVA,  $p = 0.97$  and 0.35, respectively;

**TABLE 6.2.**  
*Mean nekton density (number m<sup>-2</sup> ± SE) in reference, tide-restricted, and restoring salt marshes in Rhode Island and Massachusetts*

Species	Common name	Reference (n = 33)	Restricted (n = 25)	Restoring (n = 11)	Overall (n = 69)
<i>Palaemonetes</i> spp. <sup>1</sup>	Grass shrimp	69.57 (22.30)	29.79 (9.48)	50.82 (35.32)	52.17 (12.55)
<i>Fundulus heteroclitus</i>	Mummichog	13.83 (1.46) <sup>ab</sup>	10.96 (1.82) <sup>b</sup>	20.09 (3.41) <sup>a</sup>	13.79 (1.15)
<i>Cyprinodon variegatus</i>	Sheepshead minnow	1.13 (0.33)	1.85 (0.74)	1.99 (0.72)	1.53 (0.33)
<i>Crangon septemspinosa</i>	Sand shrimp	1.85 (0.60)	0.75 (0.39)	0.60 (0.49)	1.25 (0.33)
<i>Lucania parva</i>	Rainwater killifish	0.31 (0.16)	2.96 (2.06)	0.13 (0.11)	1.24 (0.76)
<i>Menidia menidia</i>	Atlantic silverside	1.64 (0.81)	0.96 (0.26)	0.68 (0.34)	1.24 (0.40)
<i>Fundulus majalis</i>	Striped killifish	1.74 (0.44) <sup>a</sup>	0.06 (0.02) <sup>b</sup>	0.97 (0.34) <sup>a</sup>	1.01 (0.23)
<i>Pagurus longicarpus</i>	Long-armed hermit crab	1.95 (0.69) <sup>a</sup>	0.01 (0.00) <sup>b</sup>	0.01 (0.01) <sup>b</sup>	0.94 (0.35)
<i>Menidia beryllina</i>	Inland silverside	0.12 (0.05) <sup>b</sup>	1.04 (0.43) <sup>a</sup>	0.34 (0.10) <sup>ab</sup>	0.49 (0.16)
<i>Apeltes quadracus</i>	Fourspine stickleback	0.21 (0.10) <sup>b</sup>	0.91 (0.26) <sup>a</sup>	0.01 (0.01) <sup>b</sup>	0.43 (0.12)
<i>Brevoortia tyrannus</i>	Atlantic menhaden	0.70 (0.44)	0.23 (0.22)	0.03 (0.02)	0.42 (0.23)
<i>Garcinus maenas</i>	Green crab	0.64 (0.14) <sup>a</sup>	0.17 (0.06) <sup>b</sup>	0.29 (0.14) <sup>ab</sup>	0.41 (0.08)
<i>Menidia</i> spp.	Silversides	0.16 (0.10)	0.51 (0.51)	0.00	0.26 (0.19)
<i>Pungitius pungitius</i>	Ninespine stickleback	0.06 (0.04)	0.28 (0.20)	<0.01	0.13 (0.07)
<i>Anguilla rostrata</i>	American eel	0.05 (0.02) <sup>b</sup>	0.18 (0.05) <sup>a</sup>	0.05 (0.02) <sup>ab</sup>	0.10 (0.02)
<i>Callinectes sapidus</i>	Blue crab	0.10 (0.05)	0.03 (0.02)	0.15 (0.07)	0.08 (0.03)
<i>Gasterosteus aculeatus</i>	Threespine stickleback	0.16 (0.15)	<0.01	0.01 (0.01)	0.08 (0.07)
Panopeidae <sup>2</sup>	Mud crabs	0.12 (0.06)	0.02 (0.02)	<0.01	0.07 (0.03)
<i>Morone americana</i>	White perch	0.00	0.10 (0.06)	<0.01	0.04 (0.02)
<i>Mugil curema</i>	White mullet	0.07 (0.05)	<0.01	<0.01	0.03 (0.02)
<i>Gobiosoma</i> spp. <sup>3</sup>	Gobies	0.05 (0.04)	<0.01	0.02 (0.02)	0.03 (0.02)
<i>Syngnathus fuscus</i>	Northern pipefish	0.03 (0.01)	0.04 (0.02)	<0.01	0.03 (0.01)
<i>Limulus polyphemus</i>	Atlantic horseshoe crab	0.02 (0.02)	<0.01	0.09 (0.09)	0.03 (0.02)



<i>Pseudopleuronectes americanus</i>	Winter flounder	0.01 (0.01)	0.02 (0.01)	<0.01	0.02 (0.01)
<i>Lepomis macrochirus</i>	Bluegill	0.00	0.00	0.00	0.01 (0.01)
<i>Centropristis striata</i>	Black sea bass	<0.01	0.00	0.03 (0.03)	<0.01
<i>Ovalipes ocellatus</i>	Lady crab	<0.01	0.00	<0.01	<0.01
<i>Tautoglabrus adspersus</i>	Cunner	<0.01	0.00	0.00	<0.01
Unknown crab	Unknown crab	<0.01	<0.01	0.00	<0.01
<i>Alosa pseudoharengus</i>	Alewife	<0.01	<0.01	0.00	<0.01
<i>Tautoga onitis</i>	Tautog	<0.01	0.00	0.00	<0.01
<i>Notropis</i> spp.	Shiners	0.00	<0.01	<0.01	<0.01
<i>Trinectes maculatus</i>	Hogchoker	0.00	<0.01	0.00	<0.01
<i>Opsanus tau</i>	Oyster toadfish	<0.01	0.00	0.00	<0.01
<i>Libinia</i> spp. <sup>4</sup>	Spider crabs	0.00	<0.01	0.00	<0.01
Unknown crayfish	Unknown crayfish	0.00	<0.01	0.00	<0.01
<i>Ammodytes americanus</i>	American sand lance	<0.01	0.00	0.00	<0.01
<i>Uca pugnax</i>	Atlantic marsh fiddler	<0.01	0.00	0.00	<0.01
<i>Clupea harengus</i>	Atlantic herring	<0.01	0.00	0.00	<0.01
<i>Alosa aestivalis</i>	Blueback herring	0.00	0.00	<0.01	<0.01
<i>Hemigrapsus sanguineus</i>	Asian shore crab	0.00	0.00	<0.01	<0.01

Note: For each marsh group, all data were averaged across available annualized datasets. For each species, significant differences in density among the three groups of marshes are indicated by different superscripts (ANOVA, Tukey,  $p < 0.05$ ).

<sup>1</sup>Predominantly *Palaeomonetes pugio*, but all individuals were not identified to species.

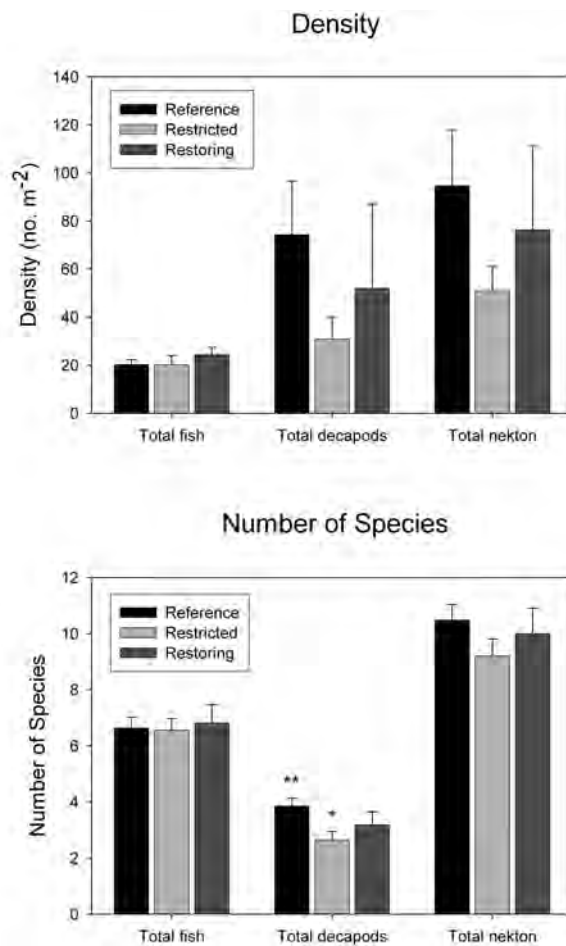
<sup>2</sup>Identified species include *Dyspanopeus sayi*, *Panopeus herbstii*, and unidentified mud crab species.

<sup>3</sup>Includes *Gobiosoma ginsburgi* and *Gobiosoma bosc*.

<sup>4</sup>Includes *Libinia dubia* and unidentified *Libinia* species.

fig. 6.2). Tide-restricted marshes, however, supported a significantly smaller number of decapod species than did reference marshes (ANOVA/Tukey's HSD,  $p < 0.001$ ; fig. 6.2).

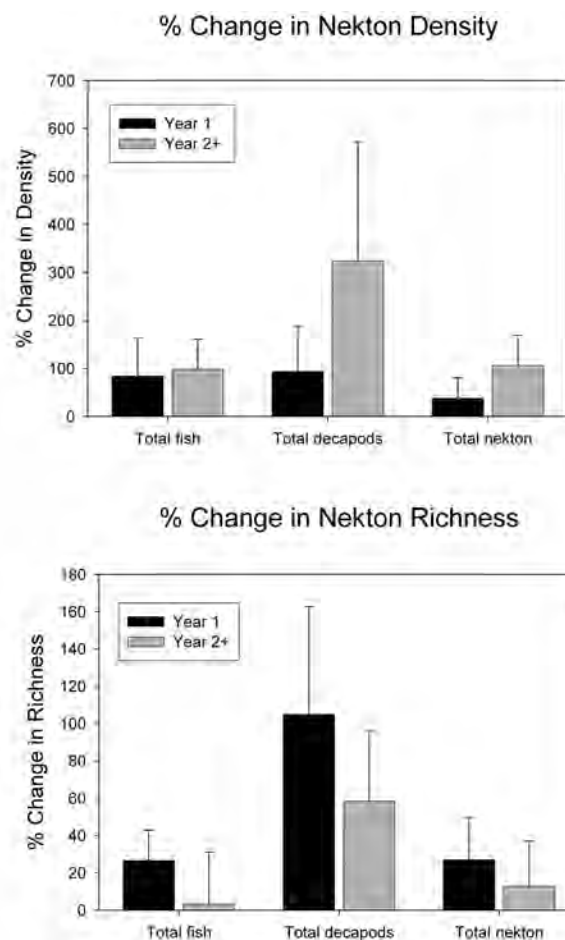
Of the forty-two species or species groups collected with throw traps, the densities of only seven were found to differ among the three marsh groups (table 6.2). Reference marshes supported significantly higher densities of *F. majalis* and *Carcinus maenas* (green crab) than tide-restricted marshes, and more *Pagurus longicarpus* (long-armed hermit crab) than either tide-restricted or restoring marshes. Tide-restricted marshes supported higher densities of *Menidia beryllina*



**FIGURE 6.2.** Mean nekton density and richness in reference, tide-restricted, and restoring salt marshes in Rhode Island and Massachusetts. All data were collected with 1 m<sup>2</sup> throw traps.  $N = 33$  nekton datasets for reference marshes, 25 for tide-restricted marshes, and 11 for restoring marshes. The asterisks denote a significant difference in decapod richness between reference and restricted marshes (ANOVA, Tukey,  $p < 0.05$ ). Error bars are  $\pm 1$  SE.

(inland silverside) and *Anguilla rostrata* (American eel) relative to reference marshes and more *Apeltes quadracus* (fourspine stickleback) than did either reference or restoring marshes. Finally, restoring marshes supported higher densities of *F. heteroclitus* and *F. majalis* than tide-restricted marshes. Densities of all other species, all fish combined, all decapods combined, and all nekton combined did not differ among marsh groups (ANOVA,  $p > 0.05$  in all cases; table 6.2; fig. 6.2).

When compared directly to tide-restricted conditions on a site-specific basis, densities of total fish, total decapods, and total nekton all increased during the first year postrestoration and continued to increase in subsequent years (fig. 6.3). Rich-



**FIGURE 6.3.** Changes in nekton density and richness between pre- and postrestoration conditions. The relative changes, expressed as a percentage of the level before restoration, are given for the first year postrestoration and then combined for years 2 and beyond. For density of each nekton group and richness of total nekton,  $n = 8$  marshes for year 1 and  $n = 6$  for year 2. For fish and decapod richness,  $n = 6$  marshes for year 1 and  $n = 5$  for year 2. Error bars are +1 SE.

ness of each of the three groups of nekton also increased on a percentage basis during the first year of restoration, though this increase was lower in subsequent postrestoration years (fig. 6.3).

### *Overall Trends and Patterns*

Based on the foregoing results, few significant differences in nekton community structure were detected among reference, tide-restricted, and restoring salt marshes in New England at the regional scale. When considering nekton density and richness, differences between any two groups of marshes were found for only 17 percent of all species and for decapod richness (on average, one fewer decapod species was found in tide-restricted marshes compared to reference marshes). The most notable finding is that nekton community composition differed significantly between reference and tide-restricted salt marshes. On a regionwide scale, these findings suggest that tide-restricted, restoring, and reference salt marshes may differ less than previously thought in nekton structure (or nekton habitat value); instead they may simply tend to support different assemblages of marsh nekton species.

At the scale of an individual marsh, however, nekton tends to respond favorably to tidal restoration efforts. For example, when averaged across eight marshes where data were available, total nekton density and richness both increased on a percentage basis over tide-restricted conditions during the first year after restoration. However, even this is a simplification since nekton density was decreased at four of the eight sites where data were available. In fact, the percent change in nekton density during the first year of restoration ranged from negative 68 percent to 225 percent.

Based on the findings presented here, it is difficult to generalize nekton responses to tidal restoration, which appear to depend on environmental and hydrologic conditions inherent to each site and on the scale at which analyses are conducted. At the regional scale, variability in nekton structure among marshes within the same group (i.e., reference, tide-restricted, restoring) can be introduced by factors that include latitudinal species shifts, estuarine geomorphology, and levels of anthropogenic impacts. This large-scale variability may mask patterns of nekton responses to restoration that would be apparent if examined on a smaller scale or within more homogeneous groupings of marsh types.

Although the effects of restoration can be quantified at any one site (if the proper experimental design is used), these results may not broadly apply to many other sites, thus limiting the ability to generalize based on data from a small number of studies. In light of this, the best ways to better understand the effects of restoration on nekton at multiple scales are to (1) continue to compile case studies that include before and after monitoring data at restoring and control/reference

marshes, and (2) ensure that it is possible to classify and group each marsh prior to analysis by better defining the specific ecological, geomorphic, and hydrologic conditions at each restoration site.

### *Diked/Drained versus Diked/Impounded*

One way to better understand nekton responses to restoration is to group tide-restricted marshes into subgroups of diked/drained or diked/impounded marshes as described by Warren et al. (2002). Raposa and Roman (2003) showed an inverse relationship between nekton density and the degree of tidal restriction among three diked/drained marshes in southern New England. At each of these sites, nekton density increased immediately after restoration. Conversely, nekton density decreased after restoration at Potter Pond in Narragansett Bay, Rhode Island (Raposa 2008) and Argilla Marsh in Massachusetts (Buchsbaum et al. 2006), both of which were diked/impounded marshes prior to restoration.

Opposite responses of nekton to restoration of these two different types of tidal restrictions make ecological sense. By definition, diked/drained marshes hold little water over the tidal cycle and therefore cannot support large nekton populations. Drained conditions also dampen high tides, thereby limiting nekton access to foraging, spawning, and refuge areas on the vegetated marsh surface. These factors can worsen already physiologically demanding conditions of tidal marshes and eliminate less tolerant species (i.e., a reduction in richness) and reduce densities of those species that remain.

In contrast, diked/impounded marshes provide marsh nekton with a relatively stable and deep body of water. In some cases, storm and spring tides can lead to extended periods when the marsh surface is flooded and is therefore accessible to nekton. Along the Gulf Coast of the United States, extended periods of marsh surface flooding from meteorological forcing can be beneficial for nekton (Rozas 1995), and it is possible that the same benefit is conveyed to nekton in impounded marshes in New England. Impounded conditions can also lead to the proliferation of subtidal macroalgal mats. At a site in Narragansett Bay, Rhode Island, these mats provided some benefit to nekton by providing a vegetated refuge from wading bird predation (Raposa 2008). These and other factors may help explain why nekton abundance is artificially high at some diked/impounded marshes in New England and why decreases in abundance can be observed after tidal restoration (e.g., Buchsbaum et al. 2006; Raposa 2008).

### *Species-Specific Assessments*

A shift in upstream nekton community composition appears to be a fundamental effect of tidal restrictions in New England. The statistical difference in

composition between tide-restricted and reference marshes, but not between restoring and reference or between restoring and restricted marshes, suggests that compositional shifts generally take longer than two years to develop, and most monitoring programs have not been in place long enough to detect such changes.

Species that are indicative of areas upstream of tidal restrictions are generally tolerant of variable salinity, temperature, and dissolved oxygen levels and are often associated with macroalgae. In southern New England, these species include *F. heteroclitus*, *C. variegatus*, *Lucania parva* (rainwater killifish), and *M. beryllina*. These species are less abundant in reference and restoring marshes than in tide-restricted marshes. In contrast, tidal restoration generally improves conditions for species less tolerant of extreme environmental conditions and those species that favor sandy, high-energy environments, including *F. majalis*, *M. menidia*, *P. longicarpus*, and *C. septemspinosa*. Except under moderate to severe diked/drained conditions, when density and richness both decline, the difference between tide-restricted and restoring conditions is a shift between these two groups of marsh species.

#### *Restoration Trajectories and Reference Conditions*

Postrestoration changes in nekton occur rapidly and reflect the high mobility and reproductive capacity of many species. Although the trajectory of structural variables may differ depending on prerestoration hydrology, the response of nekton to restoration is generally toward a community that is more similar to unrestricted or reference marshes. The lack of a significant difference in nekton community structure between reference and restoring and between tide-restricted and restoring marshes suggests that marshes in the early stages of restoration represent an intermediate phase between these two end points (restricted and reference/restored). Whether or not nekton structure in restoring marshes continues to trend toward reference marshes is generally unknown due to a lack of long-term monitoring data. In Connecticut, the nekton community from a restoring marsh was similar to that in a nearby reference marsh twenty-one years after restoration (Swamy et al. 2002), but this is only one example. In addition, this site was not continuously monitored following restoration, making it impossible to know how nekton changed over time. Monitoring nekton by collecting quantitative data at intervals over the long term is critically needed for salt marsh restoration projects in New England.

The selection of a reference marsh is an important consideration when designing monitoring plans for restoration projects (White and Walker 1997). Often, the area downstream of a tidal restriction is chosen as the reference marsh, which helps control for differences in geographic location, setting within the estuary,

and other factors. However, downstream marshes are not entirely independent of upstream tide-restricted marshes since free-swimming nekton can move between them after tidal restoration. For example, if a decrease in nekton density is observed after restoring an impounded marsh, a concurrent density increase could theoretically occur in the downstream reference marsh as nekton travel downstream with ebbing tides. When possible, it may be more appropriate to choose a nearby, though separate, marsh to ensure independence, and since nekton populations vary greatly among marshes, it may be best to choose multiple reference marshes as suggested by Underwood (1992). Alternatively, if an ecologically similar marsh cannot be found to establish reference conditions, other marshes should be monitored anyway to serve as an experimental control for the restoration marsh. Using a reference allows one to distinguish changes in nekton actually due to restoration from large-scale changes occurring throughout the estuary.

#### *Confounding Factors to Consider when Monitoring Nekton*

Actual nekton responses to restoration could be superimposed and obscured by the chronic effects of eutrophication on marsh nekton. For example, true reference conditions are difficult to obtain in Narragansett Bay, Rhode Island, because many marshes in this urbanized estuary are impacted by eutrophication, and they support altered nekton communities (specifically, high densities of *Palaemonetes* spp., James-Pirri unpublished data; Raposa unpublished data). In this case, it is difficult to define the structure of a natural nekton community and, subsequently, to define restoration targets based on nekton. Thus the degree of eutrophication of a prospective restoration site (or a proposed reference site) should be considered when one is setting reasonable targets for postrestoration nekton assemblage structure.

Choice of sampling gear can also influence the interpretation of nekton responses to restoration. For example, two separate nekton monitoring programs at the Galilee salt marsh in Rhode Island, one using throw traps (Raposa 2002) and the other using minnow traps (Golet et al., chap. 20, this volume), yielded different results; these differences can be solely attributed to the use of these two sampling gears that differ drastically in terms of capture efficiencies, biases, and the sizes and species of captured nekton (Rozas and Minello 1997; Kneib and Craig 2001; Steele et al. 2006). In some cases it is possible to carefully combine datasets collected with different sampling gear. For example, Konisky et al. (2006) were able to combine data obtained from a variety of methods to examine patterns across the Gulf of Maine. In the analysis presented here, data collected with seines, lift nets, and throw traps were all normalized to look for relative changes in nekton over time expressed as a percentage. Density data from each gear type

were available but were not directly comparable on an absolute basis due to substantial differences in capture efficiencies among the gear (Rozas and Minello 1997; Steele et al. 2006). Because of data compatibility issues, the most powerful analyses are derived from programs that consistently use the same gear and protocol. It is also important to compute the statistical power of each gear and sampling program. Without knowing the statistical power (and therefore the number of samples necessary for statistical analysis) a finding of no significant difference between treatments may simply be due to too few samples being collected. For throw traps, approximately twenty to twenty-five samples should be collected to accurately assess nekton within a marsh (Raposa et al. 2003), but there is a need to determine statistical power for other sampling gear as well.

### *Moving Beyond Structural Assessments*

Most nekton monitoring of salt marsh restoration projects in New England has focused on collecting structural data (e.g., density and community composition). This focus is likely a reflection of the relative ease with which these kinds of data can be collected. Enough structural data have been collected to support the regional analysis presented here, and our understanding should improve as more data from additional case studies emerge. There is a pressing need, however, to move beyond examining structure only and into investigations of the effects of marsh restoration on the functional roles of estuarine nekton.

A few studies of nekton function from New England salt marsh restoration projects already exist. Notable examples include studies on nekton foraging (Allen et al. 1994; James-Pirri et al. 2001) and a carbon stable isotope food web analysis (Wozniak et al. 2006). While these studies are illustrative and provide a solid starting point, the difficulties encountered when trying to identify trends in simple structural metrics across the region despite a relatively large number of datasets indicate that much more functional research is needed. An excellent precedent has been set in Delaware Bay, where an impressive number of publications on the effects of salt marsh restoration on both nekton structure and function are emerging (see brief review in Teal and Peterson 2005).

### **Tidal Restrictions in the Context of Habitat Connectivity**

Recently, ecologists have begun to recognize a multitude of connections between seemingly distinct and independent habitat types (e.g., Polis and Strong 1996). These connections take many forms, including trophic, demographic, and physical, with powerful ecological effects that can ramify through entire ecosystems (see Talley et al. 2006 and references therein). Wetlands form a nexus between the



aquatic and terrestrial realms, and often between freshwater and saltwater habitats; thus habitat connectivity is a prominent feature of this zone. These functional linkages are not restricted to the interface itself. Habitat linkages have effects that extend beyond the habitats of the coastal zone, ranging from the continental shelf and seaward to hundreds of kilometers inland (e.g., Willson et al. 2004; Talley et al. 2006).

Tidal restrictions can impact these connections, both directly and indirectly. Access to the intertidal and secondary production in estuarine nekton are strongly linked (e.g., Weisberg and Lotrich 1982; Irlandi and Crawford 1997; Kneib 1997), but the potential effects of altering flow can extend over a much broader spatial and taxonomic scale. Altering the exchange of oceanic water may not only interrupt the movement of adult or larval forms of nekton (e.g., Nordby and Zedler 1991; Roman et al. 2002; Ritter et al. 2008) but also may affect species interactions. For example, limiting their movement not only directly affects anadromous fish populations (e.g., Nehlsen et al. 1991) but also may reduce the input of marine nutrients to terrestrial plants (Nagasaka et al. 2006) and animals (Gende et al. 2002; Willson et al. 2004) far upstream. This terrestrial reliance on wetland input is not an isolated phenomenon restricted to anadromous fishes. More than eighty fish and brachyuran species are prey for maritime mammals (Carlton and Hodder 2003), and that number is undoubtedly an underestimate when indirect transfer of nutrients as described by Gende et al. (2002) is included. Thus water control structures can affect taxa and ecosystems hundreds of kilometers from a project site.

Similarly, hydrologic changes that degrade nursery habitat or alter the rate of movement of organisms or materials from a marsh can have profound effects on distant marine habitats. In addition to the potential alteration of populations of migratory species that facultatively (e.g., *Paralichthys californicus* [California halibut]; Fodrie and Mendoza 2006) or obligately (e.g., *Brevoortia tyrannus* [Atlantic menhaden]; Kroger and Guthrie 1973) use wetlands, these effects can ramify through offshore ecosystems. For example, the English sole, *Pleuronectes vetulus*, disproportionately uses wetlands as nursery habitat (Gillanders et al. 2003) and yet can potentially affect offshore ecosystems, where it plays a role both as an abundant predator (down to 250 meters [820 feet] deep) and as prey for marine mammals (Lassuy 1989). Similarly, marsh resident species, such as killifish (*Fundulus* spp.), are prey for many taxa and thus can act as net exporters of energy from impounded areas (Kneib 1997; Talley 2008).

Changes to flow in wetland systems have extensive, nonlinear, and site- and taxa-specific effects, most of which are poorly understood at present. Teasing apart these linkages will require a sustained research effort across a variety of hydrologic conditions, wetland types, and regions to better understand the consequences of these modifications and the best methods of mitigating them.

## Summary of Responses and Research Opportunities

Nekton responds rapidly to hydrologic restoration of tide-restricted salt marshes in New England, but trends in nekton responses across the region are not clear. Although nekton density and richness both tend to increase after tidal restoration, the response by nekton depends on prerestoration hydrologic conditions upstream of the restriction. Limited evidence suggests that moderate to severe diked/drained marshes support degraded nekton communities, which then respond favorably to salt marsh restoration. In contrast, tide-restricted marshes that are diked/impounded can support viable nekton assemblages, and nekton density may decrease at these sites after restoration. Based on the available structural data, the only clear trend across the region is that restoration of tide-restricted salt marshes in New England elicits a change in overall nekton density and a shift in upstream nekton community composition.

Numerous opportunities and gaps remain with regard to understanding the effects of tidal restrictions and restorations on estuarine nekton. Specific needs include (1) long-term monitoring of nekton responses to restoration from multiple sites, (2) additional published case studies on restorations of different types of tidal restrictions to improve the ability to identify large-scale patterns in nekton responses, and (3) more emphasis on examining functional responses of nekton to tidal restrictions and hydrologic restorations.

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