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NEW ENGLAND SALT MARSH POOLS:
ANALYSIS OF GEOMORPHIC AND GEOGRAPHIC PARAMETERS,
MACROPHYTE DISTRIBUTION, AND NEKTON USE

BY

SUSAN C. ADAMOWICZ

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN
OCEANOGRAPHY

UNIVERSITY OF RHODE ISLAND

2002

DOCTOR OF PHILOSOPHY DISSERTATION

OF

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2002

ABSTRACT

Salt marsh pools are shallow, steep-sided depressions that remain flooded throughout a tidal cycle and provide important habitat for nekton (fish and decapod crustaceans). Although New England pools are relatively unstudied, efforts are underway to expand pool habitat through an open marsh water management technique known as ditch plugging. The purpose of this study was to quantify pool geomorphic and geographic characteristics, to determine distribution of vegetative cover types and nekton species, and to evaluate effects of ditch plugging on nekton use of pools.

Over 30 ditched and unditched marshes were surveyed from the Connecticut shore of Long Island Sound to southern Maine, USA for pool physical traits. Pools from ditched and unditched marshes had similar sizes, depths, and distances to tidal flow, but pool density (#/ha marsh) and coverage (m^2 pool/ha marsh) were over twice as great at unditched versus ditched marshes. Ditch intensity (m ditch/ ha marsh) was negatively correlated to pool density and coverage.

Pool vegetative cover was surveyed at 12 New England marshes using 0.25 m^2 quadrats and the Braun-Blanquet scale for coverage estimation. Eight cover types were identified with the most common being "bare" (pool bottom visible), filamentous green algae, algal flocculation, and *Ruppia maritima*. Pool cover types varied by region, with bare more prevalent at northern sites. Canonical correlation analysis indicated that environmental conditions supporting *R. maritima* and algal floc coverage were distinguished by water depth, soft sediment depth, and water column nitrogen concentrations.

Pool nekton sampling using 1m² throw traps in 1999 and 2000 documented 12 fish and 4 decapod species with *Fundulus heteroclitus* comprising 80% of the fish catch. Species richness and density were greater in southern than in northern New England sites. In contrast to results from other studies, fish densities were not affected by the presence of submerged aquatic vegetation (*R. maritima*). Data suggested that *F. heteroclitus* use pools as nursery habitat and as refuges from predation, selecting among pools with different environmental conditions as the season progressed and juvenile size increased. Restoration efforts, therefore, should maintain a range of pool conditions to support a diverse nekton community and its changing needs.

The effects of ditch plugging at 3 salt marshes in the Rachel Carson National Wildlife Refuge, Maine, USA, were evaluated using a BACI (Before-After-Control-Impact) study design. Throw-trap sampling produced a total of 7 fish and 3 decapod species in salt marsh pools with *F. heteroclitus* accounting for 89% of the fish catch. After controlling for natural variation using the BACI design, nekton community and total fish density remained unaltered at Moody and Granite Point. Decreased species richness at Granite Point marsh was thought due to physical barriers created by ditch plugs and a 51% reduction in tidal interface. At Marshall Point, ditch plugging resulted in increased pool habitat and nekton use at the experimental versus control area pools. Both fish and decapods occupied newly created pools within weeks and within months new pools were not different from old pools in terms of nekton use. This study documents only initial nekton response to ditch plugging; longer term monitoring is necessary to ensure achieving management goals.

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This work is dedicated to Mom and Dad -- Ann Bernadette (Renquin) Adamowicz and Walter Adamowicz. Thank you for believing in me and for the thousands of big and little things you have done to make this endeavor possible.

PREFACE

This dissertation was prepared according to manuscript format. It contains four chapters (manuscripts) that evaluate physical attributes, macrophyte occurrence, and nekton use of salt marsh pools throughout New England. Chapter 1 quantifies salt marsh pools throughout New England in terms of their geomorphic and geographic attributes. In this chapter, pool characteristics from ditched and unditched marshes are compared. Chapter 2 gives the first regional and quantitative inventory of pool vegetative cover types and evaluates their association with physical and water quality parameters. Chapter 3 examines the distribution of nekton in pools, comparing southern New England to northern New England and discerning patterns in nekton use of pools with regard to environmental measures and changes over time. Chapter 4 assesses the effect of ditch plugging, an experimental habitat enhancement measure, on pool quality and nekton use of pools.

This work provides the first regional evaluation of salt marsh pools as landscape features and nekton habitat. It also serves as a benchmark for future evaluations of the effects of ditch plugging on nekton use of pools. Resource managers will be able to use this report for establishing salt marsh restoration goals for different regions within New England. Future studies should determine the means by which salt marsh pools are formed and senesce, since this would provide significant insight to their role in salt marsh ecology and the suitability of particular restoration methods.

Each chapter in this dissertation is intended for publication in a peer-reviewed scientific journal. These journals include *Wetlands* (Chapters 1,3) and the *Bulletin of the Torrey Botanical Society* (Chapter 2), and *Estuaries* (Chapter 4).

TABLE OF CONTENTS

Section	Page
Abstract.....	ii
Acknowledgements.....	iv
Preface.....	vi
List of Tables.....	ix
List of Figures.....	xiii
Chapter 1. New England Salt Marsh Pools: A Quantitative Analysis of Their Geomorphic and Geographic Features.....	1
Appendix A. Metadata.....	40
Chapter 2. Factors Controlling Macrophyte Distribution among New England Salt Marsh Pools.....	41
Appendix I. List of scientific and common names.....	70
Appendix II. Additional salt marsh pool water column and sediment characteristics from intensive pool survey.....	71
Chapter 3. An Analysis of Factors Controlling Nekton Distribution among New England Salt Marsh Pools.....	72
Appendix 1. List of scientific and common names.....	131
Appendix 2. Average nekton length by species, site, and sample date....	132

Chapter 4. Initial Effects of Ditch-plugging on Nekton Use of Salt Marsh	138
Pools.....	
Appendix 1. List of scientific and common names.....	189
Appendix 2. Average nekton densities (#/m ²) for 1999 and 2000.....	190
Appendix 3. Average fish lengths (mm) and crab widths (mm) for 1999 and 2000.....	193
Appendix 4. Average pool characteristics for 1999 and 2000.....	196
Bibliography.....	199

LIST OF TABLES

Section	Page
Chapter 1:	
New England Salt Marsh Pools: A Quantitative Analysis of Their	
Geomorphic and Geographic Features	
Table 1. List of salt marshes and assessment techniques.....	27
Table 2. Survey of salt marsh pool density in New England.....	29
Table 3. Average values for geographic measures of pools in ditched and unditched New England salt marshes.....	31
Table 4. Salt marsh pool measures from around the world.....	32
Chapter 2:	
Factors Controlling Macrophyte Distribution among New England Salt	
Marsh Pools	
Table 1. Locations used for pool macrophyte surveys.....	62
Table 2. Braun-Blanquet cover values averaged by site.....	63
Table 3. Percent similarity (SIMPER) results for northern versus southern salt marsh pools.....	64
Table 4. Average values for physical traits of salt marsh corresponding to Figure 3.....	65
Table 5. Salt marsh pool water column nutrient data corresponding to Figure 4.....	66

Chapter 3:
 An Analysis of Factors Controlling Nekton Distribution Among New England Salt
 Marsh Pools

Table 1 A-B. Nekton trapping locations and numbers of pools sampled for nekton in 1999 and 2000.....	110
Table 2 A-B. Nekton species trapped at sampling locations in 1999 and 2000.....	111
Table 3. Percent <i>F. heteroclitus</i> juveniles, adult males, and adult females sampled at each site and date.....	112
Table 4. Average nekton length by site and sample date for cases with significant differences among months sampled.....	113
Table 5. Comparison of nekton in natural and created pools.....	115
Table 6. Coefficients used in "best fit" equations for <i>F. heteroclitus</i> density versus environmental conditions including elevation data.....	116
Table 7. Coefficients used in "best fit" equations for <i>F. heteroclitus</i> density versus environmental conditions without elevation data..	117
Table 8. Coefficients used in "best fit" equations for <i>F. heteroclitus</i> length versus environmental conditions including elevation data	119
Table 9. Coefficients used in "best fit" equations for <i>F. heteroclitus</i> length versus environmental conditions without elevation data...	120
Table 10. Comparison of salt marsh pools from different regions.....	121

Chapter 4:
Initial Effects of Ditch-plugging on Nekton Use of Salt Marsh Pools

Table 1. Number of salt marsh pools sampled at each location and study area 1999 – 2000.....	172
Table 2. Species collected from throw-trap samples 1999, 2000.....	173
Table 3. Comparison of nekton variables before and after ditch plugging at Granite Point and Moody marsh, Maine.....	174
Table 4. Percent similarity (SIMPER) results for significant ANOSIM comparisons at Marshall Point.....	175
Table 5. Comparison of Marshall Point control and experimental areas in 1999 and 2000.....	176
Table 6. Comparison of pool water quality and physical variables before and after ditch plugging at Granite Point and Moody marsh, ME	177
Table 7. Comparison of pool water quality and physical variables at Marshall Point control and experimental areas in 1999 and 2000	178
Table 8. Estimates of species richness using the jack-knife estimate in different pool types at two sites in Maine.....	179
Table 9. Comparison of nekton densities (#/m ²) among different pool types.....	180
Table 10. Comparison of average nekton sizes (mm) among different pool types at Granite Point and Moody marsh, ME.....	181

Table 11. Comparison of water quality and physical variables measured three different pool types at Granite Point and Moody marsh, ME	182
Table 12. Area of surface water at control and experimental sites before and after ditch plugging.....	183
Table 13. Categories of surface water identified in the "Experimental- After" study areas in Table 12.....	184

LIST OF FIGURES

Section	Page
Chapter 1:	
New England Salt Marsh Pools: A Quantitative Analysis of Their Geomorphic and Geographic Features	
Figure 1. Salt marsh study locations.....	33
Figure 2. Diagram showing total pool depth and water depth	34
Figure 3. Pool density and total pool surface area versus ditch length per hectare.....	35
Figure 4. Pool number and total pool surface area versus total creek length per hectare.....	36
Figure 5. Creek versus ditch length per hectare salt marsh.....	37
Figure 6. Paired marshes for effects of ditching on pools.....	38
Figure 7 A-B. Installation of marine plywood and packing salt marsh peat into plug area, Moody marsh, Wells, Maine.....	39
Chapter 2:	
Factors Controlling Macrophyte Distribution among New England Salt Marsh Pools	
Figure 1. Locus map for macrophyte survey sampling sites.....	67
Figure 2. Biplot of pool cover types and pool physical variables.....	68
Figure 3. Biplot of pool cover types and water column inorganic nutrient concentrations.....	69

Chapter 3:
 An Analysis of Factors Controlling Nekton Distribution among New England Salt
 Marsh Pools

Figure 1. Locus map for nekton sampling sites.....	122
Figure 2. Average fish densities in 1999 and 2000.....	123
Figure 3. Average decapod densities in 1999 and 2000.....	124
Figure 4. Biplot of nekton from southern sites, September 1999.....	125
Figure 5. Biplot of nekton from northern sites, September 1999.....	126
Figure 6. Biplot of nekton from northern sites, summer 2000.....	127
Figure 7. Mean values for salt marsh pool environmental variables corresponding to Figure 4.....	128
Figure 8. Mean values for salt marsh pool environmental variables corresponding to Figure 5.....	129
Figure 9. Mean values for salt marsh pool environmental variables corresponding to Figure 6.....	130

Chapter 4:
 Initial Effects of Ditch-plugging on Nekton Use of Salt Marsh Pools

Figure 1. Salt marsh study sites.....	185
Figure 2. Granite Point showing surface waters before and after ditch plugging.....	186

Figure 3. Moody marsh showing surface waters before and after ditch plugging.....	187
Figure 4. Marshall Point showing surface waters before and after ditch plugging.....	188

Chapter 1:

New England Salt Marsh Pools: A Quantitative Analysis of Their Geomorphic and Geographic Features

ABSTRACT

New England salt marsh pools provide important wildlife habitat and are the object of on-going salt marsh restoration projects. These pools, however, have not been quantified in terms of their basic geomorphic and geographic traits. An examination of over 30 ditched and unditched salt marshes from the Connecticut shore of Long Island Sound to southern Maine, USA revealed that pools from ditched and unditched marshes had similar average size ($\sim 215\text{m}^2$), depth ($\sim 29\text{ cm}$), distance to tidal flow ($\sim 11\text{ m}$), and dispersion index (a measure of spatial arrangement). Unditched marshes had 3 times the density (18 pools/ha, $p < 0.001$), 2.5 times the pool coverage (83 m pool/km transect, $p < 0.005$), and 4 times the total pool surface area per hectare (913 m^2 pool/ha salt marsh, $p < 0.001$) of ditched sites. Linear regression analysis demonstrated that an increasing density of ditches (m ditch/ha salt marsh) was negatively correlated with pool density and total pool surface area per hectare ($R^2 = 0.47$, $p < 0.0001$; $R^2 = 0.44$, $p < 0.0002$, respectively). Creek density was positively correlated with these variables ($R^2 = 0.46$, $p < 0.0005$; $R^2 = 0.56$, $p < 0.00005$, respectively). Tidal range was not correlated at all to pool density or total pool surface area ($p > 0.46$), while marsh latitude had only a weak correlation to total pool surface area per hectare ($R^2 = 0.16$, $p < 0.05$). Because of their use by wildlife, pools should be incorporated into salt marsh restoration planning and the parameters quantified here could be used as initial design targets.

INTRODUCTION

Salt marsh pools are soft-bottomed depressions within salt marshes that hold water throughout a tidal cycle and do not dry as shallower pannes often do (Chapman 1960). Despite the extensive literature on salt marshes, research specific to marsh pools is quite limited. Harshberger (1916), Miller and Egler (1950), and Redfield (1972) have provided the most extensive descriptions of pools but no quantitative analyses. While several authors (Daiber 1982, Clarke et al. 1984, Smith and Able 1994, Erwin 1996, Wolfe 1996) have concluded that pools provide important fish and wildlife habitat, no research has been conducted in New England that quantifies basic geomorphic and geographic pool features.

Salt marsh pools are significant because they provide habitat for numerous bird species. In Massachusetts, for example, Clarke et al. (1984) noted that shorebirds, wading species, terns, swallows, and crows were strongly attracted to salt marsh pools. In southern New Jersey, Master (1992) documented that various shore and wading birds actually aggregated at pools to feed on dense fish populations. Erwin's (1996) review paper on Mid-Atlantic coastal habitat supported the conclusion that salt marsh pools are vital year-round habitat for dabbling ducks, shorebirds, and wading birds. Pools are valuable to birds because they provide food items including fish and macrophytes, specifically *Ruppia maritima* L. (Daiber 1982).

New England salt marshes have been extensively ditched for mosquito control and salt hay farming, resulting in lowered watertable levels and drainage of the marsh surface often including salt marsh pools. Salt hay farming has been a fairly common practice since colonial times (Rozsa 1995), but the most extensive and widespread

ditching occurred in the early-to-mid 1900's for mosquito control (Daiber 1986). Bourn and Cottam (1950) stated that by 1938, approximately 90% of Atlantic coastal marshes from Maine to Virginia had been ditched in an effort to reduce breeding habitat for the salt marsh mosquito (*Aedes sollicitans* (Walker)). Many natural pools, therefore, were eliminated before the middle of the century. Clarke et al. (1984) determined that the effect of ditching on bird habitat was negative -- while prey items were still abundant in marshes, they were located in ditches and were harder to capture due to the ditches' steep sides and fluctuating water levels.

Given their ecological benefits, restoring pool habitat should be an important salt marsh restoration objective. To enhance the success of such work, well-documented targets for pool creation are necessary. The objective of this paper is to address this need by providing a quantitative baseline analysis of geomorphic (e.g. pool depth, size (m^2)) and geographic (e.g. density, spatial arrangement, and coverage) attributes of salt marsh pools for a number of ditched and unditched salt marshes throughout New England (Figure 1).

Not all marshes, however, have the same density of ditches. Therefore, it should be possible to determine whether ditch density correlates with pool density and pool surface area per hectare of marsh. While expected trends might seem intuitively obvious, Miller and Egler (1950) suggested that ditch levees caused large pools to form, whereas Redfield (1972) concluded that ditching resulted in decreased pool size and number.

METHODS

Salt marsh pools were assayed using both field investigations and aerial photographic surveys coupled with geographic information system (GIS) analysis. The complete effort extended from the Long Island Sound shoreline of Connecticut to mid-coast Maine. A total of 27 sites were surveyed by either or both methods.

Field Survey

Field surveys were conducted at 17 salt marshes throughout New England during the 1999 and 2000 growing seasons (Table 1). Impounded, filled, tidally flow-restricted, and privately owned marshes were not sampled. Unditched marshes were very uncommon; in Rhode Island, the few unditched sites were substantially smaller than other surveyed marshes and were not included in this study. After much investigation, one unditched site was located in Connecticut but it was included only in the aerial photographic analysis described below.

At each salt marsh, a study area was identified as a discrete region bounded by major creeks, roads, upland, etc. Line transects were used to select sample pools for a number of measures described below. The initial transect was randomly located along the main tidal channel or shoreline with subsequent transects set at 100m intervals. Transects extended from the edge of the marsh to the upland border and were measured using a metric survey tape. Only pools in direct contact with transect lines were included in the study. The number of pools located on the transects was used to calculate a measure of pool density (# pools/km transect). Adapting the standard line-

intercept method used in vegetation ecology (Mueller-Dombois and Ellenberg 1974), pool coverage was defined as the total portion of the transects in contact with pools (m of pool/km transect).

For each individual pool encountered along the transects, pool surface area was estimated by measuring the major and minor axes of regularly shaped pools (Ingolfsson 1994) and applying the formula for the surface area of an ellipse. Irregular pools were subdivided into simple geometric shapes, with appropriate data taken to calculate surface area. For each pool, geographic parameters such as distance to nearest neighboring pool and distance to tidal flow (either a ditch or creek) were also measured. Total pool depth was measured as the distance from the surface of the marsh to the pool bottom. Water depth was recorded for use in comparison with other studies, but it is less consistent than total pool depth since the depth of water alone depends on tides, rainfall, etc. (Figure 2).

In order to determine if pools were restricted to certain locations within a marsh, study areas were divided into three zones based on vegetation. The low marsh zone was dominated by *Spartina alterniflora* Loisel (tall form), the high marsh was dominated by *S. patens*, while a third zone was dominated by *S. alterniflora* (intermediate height). Location was determined by a visual inspection of vegetation adjacent to a pool's perimeter.

Aerial Photography and Geographic Information System Analysis

Digital orthophotographic quadrangle (DOQ) images were used to increase the number of marshes studied. Black and white DOQ images (MrSID compression) were

downloaded from World Wide Web sites for Connecticut (0.5 m per pixel resolution) and Massachusetts (1.0 m per pixel resolution) marshes. DOQs at the same resolution were obtained from the University of Rhode Island Environmental Data Center and the United States Fish and Wildlife Service Gulf of Maine Program, for Rhode Island and Maine, respectively. It should be noted that DOQs were not yet complete for southern Maine and are not expected to become available until late in 2001 (R. Houston, pers. comm.). In addition, color infrared (CIR) images were available for a limited number of sites in Connecticut and Maine. A summary of data sources is provided in Table 1; additional metadata are provided in Appendix A. A total of 21 ditched and 6 unditched marshes were surveyed with ArcView 3.2 geographic information system (GIS) software applied to the DOQs and CIR photographs.

Study sites were selected based on availability of high quality digital images and minimal degree of anthropogenic alteration. Site boundaries were delineated in the same manner as in the field surveys. Tidal channels greater than 10m wide were excluded from the salt marsh study area while natural channels less than 10 m wide ("creeks") and all ditches were included. Large channels were excluded as representative of open water or aquatic habitat (Dame et al. 1992, Heck et al. 1995, Bertness 1999).

Within the study boundary for each site, all pools, creeks, and ditches were delineated with ArcView shape files to calculate pool density and total pool surface area per hectare of salt marsh. Transects were established following methods used in the field survey. Pool data (individual pool surface area, density, distance measures,

coverage) were calculated from the transects to compare with the field survey methods and to permit some combining of the GIS and field survey data.

Comparison of Survey Methods

The two methods (field survey transects and DOQ transects) used to survey salt marsh pools were compared. Paired t-tests were run for each variable (pool density, pool coverage, nearest neighbor distance, distance to tidal flow, and average individual pool size) obtained from both methods. Pool size data were log-transformed prior to analysis; no other transformations were necessary.

Statistical Analyses

Pool densities for field and digital orthophotographic quadrangle (DOQ) transect studies were combined to test for differences attributable to marsh type (ditch vs. unditched) using a two-sample t-test. Relying on field data alone, ANOVA was used to determine whether the proportion of pools differed among the three marsh zones (*S. alterniflora* (tall), *S. patens*, *S. alterniflora* (intermediate)) or between marsh types. Logistic regression was applied to determine which environmental variable(s) best predicted pool location (SAS 1985). The effect of marsh type on a series of pool variables measured from DOQs was determined by two-sample t-test.

An index of dispersion was calculated for each marsh surveyed with the DOQ/GIS method. The index (I) is based on nearest neighbor distances (NND) from a minimum of 10 to a maximum of 20 randomly selected pools (Skellam 1952, Moore

1954). The resulting values were then averaged by marsh type (ditched or unditched) and subjected to a two-sample t-test.

While it is instructive to examine ditched versus unditched marshes, it is also clear that some marshes have been ditched more intensively than others. Similarly, ditched and unditched marshes also varied in the amount of natural creek length each possessed. Because ditches and creeks both convey water to and from the marsh, these parameters may be correlated with pool density and the amount of pool surface area per hectare of marsh. Tide range and latitude were also suggested as possibly affecting these parameters. Therefore, simple linear regressions were used to determine the relationship between these factors and pool density and pool surface area per hectare obtained from DOQ sources. Mean tidal range data for each site was obtained from Tides and Currents for Windows (Nautical Software, Inc.). Latitude was obtained from DeLorme TopoUSA Regional Series topographic maps, a commercially available compact disc product.

In order to more closely examine the effect of ditching on salt marsh pools and to control for potential effects of tidal range and latitude, ten areas (five paired sites) were selected from the DOQ data set that were large marshes where a ditched section adjoined or immediately adjacent to an unditched portion of marsh. These pairings ranged from Long Island Sound (Connecticut shore) to southern Maine. The same procedures were followed for delineating study areas, ditches, creeks, and pools as previously noted. Linear regressions and paired t-tests were used to determine the effect of ditching on pool density (# pools/ha salt marsh) and total pool surface area per hectare salt marsh (m^2 pool/ha salt marsh).

RESULTS

Pool Density, Size, Spatial Pattern, and Other Geographic Measures

Transect data from field and DOQ evaluations showed that unditched marshes had a significantly greater density of pools than ditched marshes (Table 2, t-test, $p < 0.0001$). Pool density ranged from 0 to 19.8 pools/km transect in ditched sites, while the range in unditched locations was 4.8 to 31.3 pools/km transect.

It should be noted that while 100 Acre Cove, RI was included in the density calculations of Table 2, it was not included in further analysis because it possessed several exceptionally large pools (the largest was approximately 35 ha in size.) Since none of the other marshes in this study had similarly large pools, it was decided that 100 Acre Cove represented an outlier. The next largest pool encountered was only 0.56 ha for the field survey (Scarborough Marsh, ME) or 0.38 ha for the DOQ analysis (Nauset Marsh, MA).

When calculated on an area basis, pool density (# pools/ha of salt marsh) was three times greater in unditched marshes compared to ditched marshes (Table 3). Other parameters with significant differences between marsh types included total pool surface area per hectare (m^2 pool/ha salt marsh), pool coverage (m pool/ km transect), ditch length (m ditch/ ha salt marsh), and creek length (m creek/ha salt marsh). While there was no significant difference in the Index of Dispersion (I), a measure of spatial arrangement, between the two marsh types, fully one-third of the ditched marshes had an index value greater than 1.0 (indicating a uniform pattern), whereas the I-values for unditched marshes were all less than 1.0 (indicating an aggregated pattern; Moore 1954,

Skellam 1952). These results suggest a non-significant tendency for pools to be more spread out in ditched marshes compared to unditched sites.

Somewhat unexpectedly, several pool measures were the same between ditched and unditched marshes. Pool size averaged nearly 200 m² and the distribution of pool size (log-transformed data, t-tests) was the same in both marsh types. Pools in ditched marshes were no further from nearest neighboring pools or tidal flow than pools in unditched marshes.

Influence of Ditching, Creeks, Tidal Range, and Latitude

Along a gradient from unditched to highly ditched marshes, both pool density (# pools/ha salt marsh) and total pool surface area per hectare (m² pool/ha salt marsh) declined significantly (Figure 2). The correlation coefficient reflects variability in the data, especially among marshes with little or no ditching; not all unditched marshes have abundant pool habitat. When pool parameters were regressed against creek length per hectare (Figure 3) there was a positive relationship in each case; as creek density increased, so too did pool density and total pool surface area (m² pool/ha salt marsh) also increased. The opposing relationship between surface creeks and ditches is most evident in Figure 4; the regression equation indicates that 314 m of ditching per hectare of salt marsh was sufficient to eliminate the creeks.

Mean tidal range and latitude were not correlated to pool density ($p=0.08$, $p=0.52$, respectively). Alternatively, both mean tidal range and latitude were correlated to total pool surface area per hectare ($p=0.02$, $p=0.04$, respectively) but their coefficients of determination values ($R^2=0.20$ for tidal range, $R^2=0.16$ for latitude) were

low. When subjected to multiple linear regression, creek length per hectare and tidal range were the most significant variables ($p < 0.05$, both), but the coefficient of determination also was very low ($R^2 = 0.17$).

Five paired salt marsh study areas (1 pair = 1 ditched site adjacent to an unditched site) were selected from among the DOQs throughout the study region in order to control for the influence of tidal range and latitude. Among these pairs, average site size was 5.4 ha. The ditched area for an unnamed island in Old Lyme, CT was only 0.7 ha and ditches penetrated only partially into the island. A nearby island (Great Island, 132.8 ha) was added to provide a better representation of ditching in that location, increasing average site area to 17.0 ha. Linear regressions confirmed the decrease in pool density and total pool surface area per hectare of salt marsh with increasing total ditch length per hectare of salt marsh ($n = 11$, $R^2 = 0.40$, $p < 0.05$; $R^2 = 0.63$, $p < 0.005$; respectively, Figure 5). Even when subjected to paired t-test analysis (removing Great Island to provide a conservative estimate of ditch effects), unditched marshes had greater pool density and total pool surface area than ditched sites ($n = 5$ pairs, $p < 0.05$, $p < 0.05$, respectively). Creek length per hectare of salt marsh was not correlated to pool density or to total pool surface area per hectare salt marsh ($p = 0.37$, $p = 0.15$, respectively).

Pool Location within Marshes

Pools were unequally distributed in the three marsh zones (MANOVA, arcsine square-root transformation of proportion data, $p < 0.0001$) and were most common in the high marsh (least squares means post hoc test, $p < 0.0005$) compared to low marsh or

intermediate *S. alterniflora* zones. Marsh type (ditched vs. unditched) was not a significant factor (ANOVA, $p>0.79$) and there was no significant interaction between marsh type and pool location.

Distance to tidal flow (DTF) was the best predictor for determining pool location (logistic regression, $p=0.0008$) when given the three marsh zones. DTF was greater for high marsh pools (31.4 m) compared to low marsh (6.9 m) or the intermediate *S. alterniflora* regions (13.9 m) (least squares means post-hoc test; $p=0.003$, $p=0.001$, respectively). When discriminating between just low and high marsh locations, distance to tidal flow and pool size were both significant variables (logistic regression; $p=0.01$, $p=0.03$, respectively). Pool size was greater in the high marsh (52 m²) and intermediate *S. alterniflora* zones (53 m²) compared to low marsh sites (13 m²) (least squares means post-hoc test, $p<0.05$ for both comparisons).

Pool Depth and Water Depth

Total pool depth was the same regardless of marsh type (ANOVA; ditched = 26.8 cm, unditched = 30.7 cm, $p>0.05$) or pool location (high marsh = 27.9 cm, intermediate *S. alterniflora* = 27.8 cm, low marsh = 30.4 cm, $p>0.05$). Water depth similarly did not differ between marsh types ($p>0.05$) or marsh zone ($p>0.05$). Water depth averaged 19.1 to 18.1 cm for ditched and unditched marshes, respectively; water depths ranged from 1 to 71 cm for unditched marshes and 1 to 65 cm for ditched marshes. The shallowest depths were from pools that were breached and drained almost completely at low tide. The maximum water depth (71cm) and maximum total pool depth (92 cm) were both from pools in Nauset Marsh, MA (an unditched marsh).

Methodology Comparison

Nine sites (6 ditched, 3 unditched), where both DOQ and field surveys had been conducted, were used to compare transect results obtained from the two methodologies. Because some surveys (variously among the field and DOQ methods) did not encounter pools, sample size was either 7 or 9 sites for the 5 parameters of concern. Paired t-test results indicated no significant difference between the methods for pool density (# pools/km transect), pool coverage (m pool/km), nearest neighbor distance, or distance to tidal flow. However, there was a significant difference ($p < 0.02$) in average individual pool size (m^2) (log transformed data, paired t-test). In general, average individual pool size for those pools encountered in the transect method was larger in the DOQ data set. This may have been due to the limited resolution of DOQs (the smallest pools would have been difficult to detect on any aerial image compared to a field survey) or merely due to the fact that the DOQ transects were located in slightly different positions compared to those in the field, resulting in a different set of pools actually being sampled.

DISCUSSION

New England salt marsh pools are remarkably similar between ditched and unditched sites. Average values for pool size, depth, nearest neighbor distance, distance to tidal flow, and spatial patterns are consistent between marsh types. Additionally, most pools are located in the high marsh zone of all salt marshes.

While pools are similar between marsh types, ditched marshes have less pool habitat than unditched marshes. This relationship holds for both pool density and pool coverage (m pool/km transect). In fact, whether based on the number of pools per kilometer transect or the number of pools per hectare of salt marsh, ditched marshes have 70% fewer pools than unditched marshes. This now quantitatively supports Redfield's (1972) hypothesis that increased ditching resulted in decreased pool density and size.

The opposing relationship of ditch and creek density to pools (increased ditch density corresponded to a decrease in pool density and total area whereas increased creek density corresponded to high pool values) may be due to the way these channels drain a marsh. It is suggested that ditches are generally deeper than the first and second order tidal creeks (as defined by Bayliss-Smith 1979) delineated in this study, and thus are capable of more dramatic drainage. Shallow creeks would be capable of draining surface water, but it would require more substantial sub-surface drainage to affect a pool. Nuttle (1988) found that a 2 m deep channel affected horizontal porewater drainage up to 15 m away. While not all ditches are 2 m deep, the fact remains that intensively ditched marshes have neither pools nor creeks common to unditched marshes. The finding that pools in ditched and unditched marshes exhibited the same distance to tidal flow, though ditched marshes had significantly fewer pools, supports this hypothesis further.

Effect of Marsh Ditching on Wildlife and Open Marsh Water Management as a Remediation Technique

The extensive ditching found throughout New England salt marshes is largely due to public works programs of the Depression Era that enabled mosquito ditching to proceed on a large-scale, rapid basis. By the late 1930s, many East Coast states were reporting near complete drainage of designated salt marshes. Deleterious effects of ditching on wildlife habitat were reported early on (Urner 1935) with the discussion continuing throughout the 1930s (Harris 1937, Corkran 1938) and the remainder of the century (Reinert et al. 1981, Clarke et al. 1984, Wolfe 1996).

The numerous alterations to salt marshes, from ditching, draining, and filling, to diking and restricting tidal flow (Miller and Egler 1950, Chapman 1960, Roman et al. 1984, Rozsa 1995, Burdick et al. 1997), have inspired a number of remediation efforts. As early as 1938, resource managers sought a means to balance mosquito control with wildlife conservation. Open marsh water management ("OMWM") emerged as the premier method to utilize natural processes for mosquito reduction (Cottam 1938, Ferrigno and Jobbins 1968). Although OMWM techniques have been available for many years, they require more planning than traditional ditching and more labor than pesticide application. The methodology, however, has gained prominence in the last two decades and has been the focus of numerous fish and wildlife studies (Talbot et al. 1986, Ferrigno and McNelly 1991, Erwin et al. 1994, Grant et al. 1998).

Ditch plugging, a form of OMWM, is an experimental technique in New England. It uses peat excavated from the salt marsh surface to plug human-made ditches. Water fills the ditch upstream of the plugs and a small area adjacent to the

plugged-ditches. Areas where peat has been excavated are also flooded to form shallow pools. An on-going effort to study the effects of ditch plugging includes two marshes in southern Maine (Figure 6). Average pool coverage (174 m pool/km salt marsh) and average individual pool size (384 m²) were greater at the ditch-plugged sites compared to unditched marshes (83 m/km, 205 m²; respectively) but further examination of the field data revealed that this was due to the presence of a few large, naturally occurring pools at the plugged sites. Prior to ditch plugging, however, these pools drained substantially at low tide (personal observation). New pools formed by the excavation of plug material were relatively small and more reflective of average pool size at unditched sites. Ditch plugging did result in an increased distance to tidal flow compared to ditched and unditched marshes (53 m versus 12 m and 10 m, respectively). Ditch lengths were much reduced for plugged marshes compared to ditched sites (13 m ditch/ha salt marsh versus 217 m ditch /ha salt marsh, respectively). Average creek lengths in plugged marshes (7 m creek/ ha salt marsh) were also less than that in ditched (38 m creek/ ha salt marsh) and unditched marshes (171 m creek /ha salt marsh). This reduction in tidal pathways suggests that plugged sites may experience less tidal flushing. For this reason it is important to continue existing monitoring efforts and to extend them to other marshes where ditch plugging is proposed.

Restoration Recommendations

If increasing bird habitat is a goal of salt marsh pool restoration and creation, then the preferred pool dimensions depend upon the species under consideration and the time of year (Erwin 1996). The size recommendations given by Erwin et al. (1994) for

construction of large pools (greater than 800 - 1000 m² for autumn waterfowl and summer shorebird use) lie well within the range of pools on New England salt marshes (3 – 3786 m²). Recommended small pond sizes (less than 200 m² for autumn waterfowl) approximate the average size of pools in ditched and unditched marshes. While Erwin et al. (1994) proposed a depth of less than 15 cm, salt marsh pools in New England had a water depth range of 3 - 71 cm. Rather than build “perfect” and identical pools, managers, perhaps, should heed the variability of pool dimensions found in the field. Such variation in pool size and depth over a large number of pools ensures that at least some of them will remain desirable to birds regardless of natural fluctuations in tidal flushing, rainfall, or drought.

Comparison of New England to Other Regions

There have been very few quantitative studies of salt marsh pools. Three recent and one historic reference are provided in Table 4. Pool density ranges from a low of zero in temperate Australia (where Adam (1997) presumably expected to find pools in those grass dominated systems) to a high of 1300 pool/km² salt marsh in the unditched marshes of this study. Pool sizes documented across all regions ranged from 1m² to a high of 55 ha. An exceptionally large pool was located at 100 Acre Cove in Rhode Island where DOQ/GIS analysis estimates pool size to be approximately 35 hectares. While pools of this size have not been encountered in other New England salt marshes, evidently such large pools are found elsewhere as demonstrated by the work of Master (1992). Water depths were similar at all locations except for the historic note of a pool 1.2 m deep at an unspecified location in Rhode Island (Price 1938). In general, pools

from unditched sites in this study were well within the size and depth ranges of pools from other regions.

CONCLUSIONS

The difficulty in finding unditched sites, especially in southern New England, speaks not only to the effective efforts of early mosquito control programs and salt hay farming, but also to the need to preserve unditched salt marshes both as scientific references and as important wildlife habitats. Ditching and the resultant drainage have decreased pool density by 70% and have significantly reduced total pool surface area per hectare of marsh.

Ditch plugging as manifested in the two Maine study sites resulted in greater average values of pool coverage. Resource managers should monitor ditch-plugged sites carefully to ensure proper protection of these valuable ecosystems. While it is clear that humans are adroit at altering their surroundings, it is exceptionally difficult to reverse unintended effects, all of which calls for preserving the few remaining unditched salt marshes.

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Table 1. List of salt marshes and assessment techniques at each site included field transect surveys ("field surveys"), analysis of digital orthophotographic images ("DOQ") and color infrared images ("CIR") and other mapping or photographic base images ("Other").

Marsh Type and Location	Latitude*	Longitude*	Field Survey	DOQ	CIR	Other
<u>Ditched Marshes</u>						
Hammonasett State Park, Clinton, CT	N41°15.385'	W72°32.397'	X	X		
Grass Island 1, Guilford, CT	N41°16.100'	W72°39.326'	X	X	X	
Grass Island 2, Guilford, CT	N41°16.363'	W72°39.443'		X	X	
S. B. McKinney NWR, Hammock Dock, West Site, CT	N41°16.730'	W72°28.570'		X		
S. B. McKinney NWR, Hammock Dock, East Site, CT	N41°16.790'	W72°28.290'		X		
Great Island, Old Lyme, CT	N41°17.213'	W72°19.810'		X		
Unnamed Island, Old Lyme, CT	N41°17.115'	W72°19.315'		X		
Watts Island, Niantic, CT	N41°18.025'	W72°13.193'		X		
Barn Island Management Area (1), Stonington, CT	N41°20.330'	W71°52.390'	X	X	X	
Barn Island Management Area (3&4), Stonington, CT	N41°20.249'	W71°52.013'	X	X	X	
Sachuest Point NWR, Middletown, RI	N41°28.683'	W71°14.622'	X			**
Sapowet Wildlife Management Area, Tiverton, RI	N41°35.012'	W71°12.319'	X			**
Coggeshall Marsh, NBNERR, Portsmouth, RI	N41°39.046'	W71°20.635'	X			**
100 Acre Cove, Barrington, RI	N41°45.985'	W71°18.244'	X	X		
Felix Neck, Martha's Vineyard, MA	N41°24.967'	W70°33.561'		X		
Water Street, Essex, MA	N42°37.952'	W70°46.251'		X		
Annisquam River Marshes, Site 2, Gloucester, MA	N42°37.968'	W70°41.073'		X		
Corn Island, Essex, MA	N42°39.435'	W70°44.802'		X		

Table 1. (cont.)

	Latitude*	Longitude*	Field Survey	DOQ	CIR	Other
Moody Marsh, Wells, ME	N43°15.884'	W70°35.523'	X			***
Wells NERR, North Area, Wells, ME	N43°20.410'	W70°32.340'			X	
Granite Point, Biddeford, ME	N43°24.980'	W70°23.386'	X			***
Morse River, Phippsburg, ME	N43°45.130'	W69°49.470'		X		
Squirrel Point, Arrowsic, ME	N43°49.410'	W69°47.450'		X		
<u>Unditched Marshes</u>						
S. B. McKinney NWR, Bridgeport, CT	N41°09.376'	W73°08.297'		X		
Nauset Marsh, Eastham & Orleans, MA	N41°49.348'	W69°57.470'	X	X		
Annisquam River Marshes, Site 1, Gloucester, MA	N42°38.663'	W70°41.037'		X		
Parker River NWR, Newbury, MA	N42°43.323'	W70°47.656'	X	X		
Wells NERR, Harbor Area, Wells, ME	N43°19.050'	W70°34.290'			X	
Scarborough Marsh, Scarborough, ME	N43°33.693'	W70°19.828'	X			
Spurwink River, Pleasant Hill, ME	N43°35.264'	W70°15.767'	X			
Reid State Park, Georgetown, ME	N43°46.727'	W69°44.267'	X	X		

*From DeLorme TopoUSA NE Regional Software © 2000

** GPS map

*** Georectified aerial photograph

Table 2. Survey of salt marsh pool density in New England

Ditched Marshes	Pool Density (# of pools/km)	Unditched Marshes	Pool Density (# of pools/km)
Hammonasset State Park, Clinton, CT	0.9	S. B. McKinney NWR, Bridgeport, CT*	4.8
Grassy Island 1, Guilford, CT*	0.0	Nauset Marsh, Eastham & Orleans, MA	21.3
		Annisquam River Marshes, Site 1,	
Grassy Island 2, Guilford, CT*	0.6	Gloucester, MA*	14.6
S. B. McKinney NWR, Hammock Dock, West Site, CT*	0.0	Parker River NWR, Newbury, MA	23.1
S. B. McKinney NWR, Hammock Dock, East Site, CT*	1.9	Wells NERR, Harbor Area, Wells, ME*	7.5
Great Island, Old Lyme, CT*	1.1	Scarborough Marsh, Scarborough, ME	13.8
Unnamed Island, Old Lyme, CT*	17.6	Spurwink River, Pleasant Hill, ME	31.3
Watts Island, Niantic, CT*	2.1	Reid State Park, Georgetown, ME	24.3
Barn Island Management Area (1), Stonington, CT	3.8		
Barn Island Management Area (3&4), Stonington, CT	1.8		
Sachuest Point NWR, Middletown, RI	1.8		
Sapowet Wildlife Management Area, Tiverton, RI	7.1		
Coggeshall Marsh, NBNERR, Portsmouth, RI	1.8		
100 Acre Cove, Barrington, RI	7.4		
Felix Neck, Martha's Vineyard, MA*	4.0		
Water Street, Essex, MA*	0.0		
Annisquam River Marshes, Site 2, Gloucester, MA*	6.2		
Corn Island, Essex, MA*	11.3		

Table 2. (cont.)

Ditched Marshes	Pool Density (# of pools/km)	Unditched Marshes	Pool Density (# of pools/km)
Moody Marsh, Wells, ME (1999)	19.8		
Wells NERR, North Area, Wells, ME*	10.7		
Granite Point, Biddeford, ME (1999)	18.7		
Morse River, Phippsburg, ME*	5.5		
Squirrel Point, Arrowsic, ME*	0.4		
<i>Average Ditched Marshes (St. Dev.)</i>	<i>5(6)</i>	<i>Average Unditched Marshes (St. Dev.)</i>	<i>18 (9)</i>

* Indicates data taken from digital orthophotographic (DOQ) images

Table 3. Average values for geographic measures of pools in ditched and unditched New England salt marshes based on digital orthophotographic images and field survey analysis. Significance levels are denoted by asterisks (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

Method	Ditched Marshes		Unditched Marshes	
<i><u>Transect Data</u></i>				
Pool Cover/Transect (m/km)	31 ±	37	83 ±	47 **
Individual Pool Size (m ²) ¹	227 ±	305 (n=17)	205 ±	113 NS
Distance to Nearest Neighboring Pool (m)	15 ±	14 (n=17)	9 ±	6 NS
Distance to Tidal Flow (m)	12 ±	15 (n=17)	10 ±	5 NS
<i><u>Areal Data</u></i>				
Density (Number of Pools/ha)	4 ±	5	13 ±	7 ***
Total Pool Surface Area m ² /ha ²	229 ±	242	913 ±	489 **
Index of Dispersion	1.19 ±	2.18 (n=14)	0.33 ±	0.20 NS ²
Ditch length (m) /ha	217 ±	100	0 ±	0 **** ²
Creek length (m) /ha	38 ±	44	171 ±	89 ** ²
Average Study Size (ha) ²	19 ±	28	18 ±	10 NS
Number of Marshes Sampled (except	20		6	

¹Log transformed for analysis.

²Student t-test assuming unequal variances.

Table 4. Salt marsh pool measures from around the world.

Location	Condition	Density (#/km ²)	Size (m ²)		Depth (cm)	
			average	range	average	range
New England, USA (this study)	unditched	1300	205	3 - 3786	16	3 - 71
	ditched	400	227	4 - 3629*	15	4 - 47
Rhode Island, USA 1937 (Rich 1938)		NR	NR	3 - 20235	NR	10 - 120
New Jersey, USA (Smith 1995)**	unditched SAV	NR	44	5 - 90	46	33 - 61
	unditched no SAV	NR	28	5 - 80	38	17 - 69
New Jersey, USA (Master 1992)		810	NR	1 - 55000	NR	3 - 60
Iceland (Ingolfsson 1994)		132	318	8 - 2100	22	5 - 79
Temperate Australia (Adam 1997)		0	.	.	.	.

NR: data not reported

* An exceptionally large pool exists at 100 Acre Cove in Rhode Island. It is approximately 34 hectares in size.

** SAV = submerged aquatic vegetation; n=8 for each category (i.e. SAV, no SAV).

Figure 1. Locus map for macrophyte survey sampling sites.

Figure 2. Total pool depth was measured as the distance from the marsh surface to the bottom of a pool while water depth was simply the distance from the water surface to the pool bottom.

Figure 3. Pool density and total pool surface area versus total ditch length per hectare (14 CT sites, 7 MA sites, 5 ME sites).

Figure 4. Pool number and total pool surface area versus total creek length per hectare (14 CT sites, 7 MA sites, 5 ME sites).

Figure 5. Creek versus ditch length per hectare salt marsh.

Figure 6. The effect of ditching on total pool surface area (m²/ha) and pool density (#/ha) for paired ditched and unditched marshes.

Figure 7a. Installation of Marine Plywood as a First Step in Construction of a Ditch Plug, Moody Marsh, Wells, Maine

Figure 7b. Packing Salt Marsh Peat into Plug Area, Moody Marsh, Wells, Maine

Appendix I. Metadata

Connecticut

Black and white DOQ images were obtained over the internet from the Map and Geographic Information Center, University of Connecticut at

<http://magic.lib.uconn.edu/index.html>. These images are based on 1990 flights. The DOQs are NAD 83, state plane feet, MrSID compression with 1m/pixel.

Color infra-red photographs were obtained from Ron Rozsa at the Long Island Sound Project, CT DEP, Hartford, CT. These photographs were flown on August 1995 at a scale of 1:12,000. They were geo-rectified using the Image Analyst extension of ArcView 3.2

Rhode Island

Black and white DOQ images were obtained from the RIGIS Environmental Data Center at the University of Rhode Island. The aerial photography was flown in April 1997. The DOQs are NAD 83, state plane feet, MrSID compression with 0.6 m/pixel. Additional metadata are available from RIGIS at <http://www.edc.uri.edu>.

Massachusetts

Black and white DOQ images were obtained from the Massachusetts Geographic Information System Office at <http://www.state.ma.us/mgis/massgis.htm>. Aerial photographs were flown at a scale of 1:5000 in 1999 for the Felix Neck site and in 1994 for the other Massachusetts sites in this study. The images were converted to DOQs at NAD 83, state plane meters, MrSID compression with 0.5m/pixel.

Maine

Black and white DOQ images were obtained through the courtesy of the US Fish and Wildlife Service, Gulf of Maine Program. Aerial photographs were flown at a scale of 1:24,000 in 1997 and were converted to DOQs at NAD83, UTM Zone 19, meters, MrSID compression with 1.0 m/pixel.

A color infrared aerial photograph was used for the Wells National Estuarine Research Reserve. It was compressed as a MrSID image, UTM Zone 19, NAD 27, meters. The photograph was taken in August 1998 at a scale of 1:12000 .

A color infrared aerial photograph was used for Moody Marsh. The photograph was flown June 1992 at a scale of 1:8000. A true color aerial photograph was used for Granite Point Marsh flown on May 1986 at a scale of 1:2400. These photographs were made available by the Rachel Carson National Wildlife Refuge. Both images were digitally scanned then geo-rectified to USGS 7.5 topographic quadrangle maps using ArcView 3.2 Extension Image Analyst. Due to the low quality of the final product, analysis was limited to calculation of study site area and delineation of creeks and ditches that had been field checked.

Chapter 2:
Factors Controlling Macrophyte Distribution
Among New England Salt Marsh Pools

ABSTRACT

Salt marsh pools are soft-bottomed depressions that remain flooded throughout a tidal cycle and do not dry out as shallower pannes often do. Pools are important wildlife habitat but are much less abundant on ditched than unditched marshes. On-going management efforts to increase pool habitat in New England are proceeding without a regional benchmark for the composition and distribution of macrophytes in pools and their relationship to pool environmental conditions. The purpose of this study is to provide such a benchmark. Pool macrophytes were surveyed at 12 New England salt marshes using a 0.25m² quadrat and the Braun-Blanquet scale for coverage estimation. Eight cover types were identified with the most common being "bare" (pool bottom visible), filamentous green algae, algal flocculation, and *Ruppia maritima*. Pool cover types differed by region ($p < 0.001$, ANOSIM) with the "bare" category more prevalent at northern sites. Southern New England pools exhibited slightly more filamentous green algae, algal flocculation, and *Ruppia maritima*, accounting for 52% of the total dissimilarity between regions. Based on canonical correspondence analysis (CCA), *R. maritima*, valuable as waterfowl forage, was associated with pools that were deeper, more saline, and had less soft sediment and lower water column nitrogen than the mean values for pools in this study. Canonical correlation analysis indicated that *R. maritima* and algal flocculation coverage were separated by water depth, soft sediment depth, and water column nitrogen concentrations.

INTRODUCTION

New England salt marshes are not monotonous meadows of halophytic grasses, but rather a mosaic of vegetated and aquatic habitats. In addition to creeks and numerous human-made ditches, salt marshes also contain pools, which are soft-bottomed depressions that hold water throughout a tidal cycle and unlike the shallower pannes, do not tend to dry out (Chapman 1960). In New England, these pools are steep sided (Miller and Egler 1950) and have an average total pool depth of approximately 30 cm (Adamowicz, Chapter 1). Based on a survey of 26 marshes from Connecticut to southern Maine, they range in size from 1 m² to 35 ha and cover an average of 2% of ditched marshes and 9% of unditched marshes (Adamowicz, Chapter 1).

Pools are important habitats, supporting macrophytes (Richardson 1980, Smith 1995), nekton (Able and Fahay 1998, Raposa 2000), and foraging birds (Master 1992, Erwin et al. 1994, Erwin 1996). Macrophytes provide nekton-nesting sites (FitzGerald 1983), are associated with high fish densities (Sogard and Able 1991, Smith 1995) and elevated secondary production (Heck et al. 1989), and are important wildlife forage (Daiber 1982). Some factors influencing macrophyte species composition and abundance include salinity, water depth, nutrients, sediment composition, and sediment depth (Richardson 1980, Kantrud 1991). While some studies (Richardson 1980, Smith 1995) have examined macrophyte coverage in pools, their scope was limited to a small number of pools associated with just a few salt marshes. No work has detailed the range of conditions in pools found throughout New England, especially with respect to macrophyte coverage.

Currently, open water marsh management (OMWM) techniques are being used throughout New England and include the construction of new pool habitats.

Macrophytes in pools, however, have not been sampled in a comprehensive fashion to provide a baseline for establishing management goals. The purpose of this study is to provide a New England benchmark for macrophyte species composition, distribution, and relationships with environmental variables in order to better understand the role of pools in overall salt marsh ecosystem functioning and to provide guidelines for management efforts.

METHODS

Macrophytes were sampled during the summers of 1999 and 2000 at 12 sites from the Long Island Sound shoreline of Connecticut to southern Maine, USA (Figure 1). Macrophyte studies were carried out on two levels. A broad scale survey was conducted to determine basic physical characteristics and water quality conditions of pools throughout New England. A more intensive survey on fewer marshes enabled examination of additional water column and sediment parameters including concentration of inorganic nutrients.

Broad-Scale Survey

Twelve salt marshes throughout New England (Table 1) were part of the broad-scale survey of macrophytes in pools. Study pools were selected by establishing a series of transect lines at each salt marsh. The first transect was randomly located and

extended from the estuary/marsh edge to the marsh/upland edge. All pools falling on the transect line (a survey tape) were sampled. Subsequent transects were set parallel to the first one at 100 m intervals. At sample pools, a 0.25 m² quadrat was set along a separate transect placed on the pool's long axis. Initial quadrats were placed randomly within the first 10 m while subsequent quadrats were placed at regular intervals to obtain at least 4 sub-samples whenever pool size allowed.

Percent coverage was taken by visual estimation and recorded into cover classes according to the Braun-Blanquet scale (Kent and Coker 1992). Since identification of filamentous green algae to species was not possible in the field and the species often occurred intertwined, they were lumped into one cover category. A species list of filamentous greens was based on samples taken from northern and southern salt marsh pools identified in the laboratory (Villard-Bohnsack 1995). Besides filamentous green algae, other cover categories included "bare" (pool bottom visible), "epiphytes" (algae epiphytic on macrophytes), and "algal flocs" (algal flocculation consisting of decayed benthic algae or decayed filamentous algae). *Spartina alterniflora*, an emergent species, was included as a cover category only when individual stems grew out of the pool bottom and did not represent emergent islands or surrounding marsh surface.

Other variables measured at each quadrat included water depth and soft and total sediment depth. Both sediment depths were measured by inserting a graduated metal rod through the pool bottom. Soft sediment was defined as that surface layer with minimal resistance. At the boundary between soft sediment and lower layers, a change in resistance occurred. Insertion of the rod continued until firm resistance was

encountered or total sediment depth exceeded 140 cm. Sediment depths in excess of 140 cm were recorded as >140 cm.

Intensive Survey

Pools involved in the intensive survey were selected by the same transect method described above and were sampled once during the summer of 1999. Additional parameters examined at 33 pools on 6 marshes included water pH, salinity, dissolved oxygen, and water and surface sediment redox potential, all of which were measured at 1 m from the pool's edge and at the pool's center. A YSI-85 handheld meter provided salinity and dissolved oxygen measures. An Orion model 250A with H^+ and platinum redox electrodes yielded water pH and redox measures. These parameters were measured as pools were encountered along each transect (once during a field day of 0800 – 1800 hr). While fully cognizant that these instantaneous measurements do not capture diel patterns within pools they were intended only to provide an initial estimate of regional pool conditions.

A further subset of 12 pools from 3 Rhode Island salt marshes was sampled for sediment and water column nutrients. Sediment and water samples were taken at a pool's edge and center; water column nutrient samples were filtered in the field, all samples were stored on ice until they were placed in a freezer later in the day. Water samples were analyzed colorimetrically for inorganic nutrients (NO_2 , NO_3 , NH_3 , PO_4) on an autoanalyzer (Oviatt and Hindle 1994).

Three replicate surface sediment samples were taken to a depth of 10 cm from the center of each pool, combined, and iced until frozen later in the day. Rather than

total sediment nutrient content, sediments were analyzed for readily available nutrients. In the lab, sediment samples were thawed and homogenized thoroughly by hand mixing. A 10-gram sub-sample was then combined with 40 ml of artificial seawater. The mixture was shaken by hand for two 30-second intervals and then centrifuged at 8000 rpm for 20 minutes. The supernatant was removed by syringe, filtered, and subjected to the same nutrient analysis as the water column samples. Sediment dry weight and organic matter (loss on ignition) followed the methods of Wetzel and Likens (1991). Sediment grain-size analysis was obtained with the wet-sieve method (Folk 1974) using a series of standard sieves.

Statistical Analyses

Differences in cover type composition and abundance were analyzed using the PRIMER non-parametric randomization tests of similarity (Clarke and Warwick 1994, Roman et al. in press) applied to a similarity matrix. An analysis of similarities test (ANOSIM) was used to detect differences between groups of pools. Groups defined *a priori* included the individual marshes and the region (northern or southern) within New England. Contributions of individual cover types to dissimilarities between groups were calculated using percent similarity tests (SIMPER), with percent contribution based on Euclidean distances.

Canonical correspondence analysis (CCA) was used to relate cover types to environmental conditions for pools from all study marshes. All environmental measurements were standardized prior to analysis as suggested by Clarke and Warwick (1994). Cover types were plotted in 2-dimensional space while environmental variables

were presented as vectors. The vector's length represents the correlation between that environmental variable and the 2 ordination axes. The longer the vector is, the stronger the relationship between that variable and the community (McCune and Mefford 1999). Kent and Coker (1992) indicated that CCA is preferable over detrended correspondence analysis (DCA) where a "good set of environmental data" is available. CCA calculations and graphics were produced by PC-ORD version 4.0 (McCune and Medford 1999).

Fisher's Exact Test (Sokal and Rohlf 1981) was used to indicate whether the presence of macrophytes in one pool was linked to the presence of macrophytes in the nearest neighboring pool (also known as "contagion"). Thus Fisher's Exact Test can provide resource managers with an indication of whether macrophytes are isolated within pools or if there is a likelihood that propagules can be transferred among nearest neighboring pools. Such information is useful in restoration efforts in determining whether newly created pools can be colonized naturally.

RESULTS

Macrophytes/ Pool Cover Categories

Twelve salt marshes from Maine to Long Island Sound were surveyed resulting in eight cover types (Table 2). Four of the cover categories were for individual species, while the "filamentous green" category was composed of *Enteromorpha compressa*, *Polysiphonia lanosa*, *Rhizoclonium tortuosum*, *Cladophora sericea*, *Ulothrix flacca*, *Acrosiphonia arcta* and *Chaetomorpha linum* (scientific names and authorities are given

in Appendix I). *C. sericea* and *A. arcta* were found at both northern and southern sites. *E. compressa*, *P. lanosa*, and *R. tortuosum* were sampled only in northern marshes while *U. flacca* and *C. linum* were observed only in southern marsh pools.

Pool bottoms were mostly bare, that is, they were not covered by macroscopic vegetation of any kind (Table 2). Filamentous green algae was the next most common cover type. Algal flocs and *R. maritima* ranked third and fourth, respectively, while other individual species were less common.

For Fisher's Exact Test, samples sizes for each site were relatively small and did not produce significant results; thus, all observations were lumped for a single comparison. Despite the low coverage of macrophytes, pools did exhibit contagion ($p < 0.02$, Fisher's Exact Test) such that nearest neighboring pools both had macrophytes or both were bare.

Cover categories and abundances were the same within regions ($p > 0.17$ for southern sites, $p > 0.44$ for northern sites, ANOSIM) and between ditched and unditched marshes in the northern sites ($p > 0.24$, ANOSIM). All marshes in the southern region were ditched. Based on these findings, data were combined within regions. When comparing cover categories and abundances between regions, there were significant differences ($p < 0.001$, ANOSIM) with SIMPER results indicating that northern pools had more extensive areas of "bare", while southern pools had greater coverage of filamentous green algae, algal flocs, and *R. maritima* (Table 3).

Cover Type Canonical Correspondence Analysis

Two biplots relating cover type to pool environmental conditions were produced from the survey data. The biplots representing physical pool conditions (Figure 2) and water column nutrients (Figure 3) were linked by the placement of the *R. maritima* and algal flocs categories near opposite ends of at least one axis. The “bare” cover category tended to be close to the vector origin in each biplot due to its presence in most pools.

For the biplot with physical pool conditions (Figure 2), only axis 2 has a significant correlation to cover ordination space and a significant cover type-environment correlation ($p=0.01$, $p=0.02$, respectively; Monte Carlo test); therefore, results should be interpreted as a projection of points and vectors onto axis 2. *R. maritima* thus was correlated with deeper, more saline pools with less soft sediment than average. Alternatively, algal flocs were associated with shallower, less saline pools that had greater depths of soft sediment. Physical pool conditions and cover types plotted in Figure 2 correspond with environmental data summarized by site in Table 4.

As noted above, nutrient analyses of pool conditions were limited to three southern sites (Figure 3, Table 5). Only axis 1 in Figure 3 was significant (cover type ordination $p=0.01$, cover-environmental data $r=0.963$, $p=0.02$; Monte Carlo test) thus results should be taken as projections onto this axis. Water column nutrient conditions associated with *R. maritima* were low NO_3+NO_2 , low NO_2 and high SiO_4 concentrations (Figure 3, Table 5). Once again, the opposite situation (high NO_3+NO_2 , high NO_2 and low SiO_4 concentrations) was associated with algal flocs. Ammonia and inorganic phosphate were measured in the water column (Table 5), but their levels were not influential in the CCA analysis. Finally, while detailed data were gathered on other

pool variables (Appendix II), resulting biplots did not have significant ordination or cover-environmental correlations and are not presented.

DISCUSSION

Abundance of Macrophytes and Bare Areas

Few studies have examined macrophyte cover in salt marsh pools; most have a narrow focus, some mentioning cover types only briefly. A few common points can be elucidated, however. Macrophyte coverage initiates at the start of the growing season in May and peaks at 95 – 100% in July and August (Richardson 1980, Smith 1995). *R. maritima* (Richardson 1980, Worgan and FitzGerald 1981, Smith 1995) and *Cladophora* spp. (Nolan and Ruber 1985) are the most commonly noted species although *Enteromorpha* spp. and *Percusaria* spp. were mentioned for pools in Quebec (Worgan and FitzGerald 1981).

Surveys conducted for this study occurred from June – mid-September when macrophytes should have been abundant. While the number of cover types identified here (8) exceeded those in other pools studies (Richardson 1980, Smith 1995, Nolan and Ruber 1985, Worgan and FitzGerald 1981), the significant amount of bare area was an unanticipated result. On average, the bare category accounted for 25% of pool coverage in southern pools and 75% in northern pools (Table 4). Of additional interest are the several factors that appear to influence presence and abundance of macrophyte cover.

Factors Influencing Cover Types

Cover types were influenced by conditions at two levels: regional and between pool. Regional location determined the relative abundance of cover types (Table 4) with higher levels of vegetation in southern New England and more bare area in northern pools. At the between-pool level, the presence of macrophytes in pools was contagious – nearest neighboring pools were also likely to have macrophytes. This result offers an important suggestion to restoration managers that newly created pools can be naturally colonized by macrophytes if they are located near existing pools that already contain macrophytes. Also between pools, physical and water quality conditions produced a continuum that promoted *R. maritima* at one end and algal flocculation at the other.

Of the four physical and water quality factors that distinguish between *R. maritima* and algal floc cover, nutrient levels and soft sediment depth may indicate cover type segregation along a trophic scale. *R. maritima* would represent low nutrient conditions and algal flocs, the more enriched pools. Kantrud (1991) indicated that *R. maritima* survived best in low nutrient conditions and was out-competed at high nutrient levels. This may account for the presence of *Ruppia* in higher salinity pools when it is normally considered a brackish water species. The interaction of nutrient levels and autotrophic species has been examined extensively for other submerged aquatic vegetation systems (e.g. Dennison et al. 1993, Kinney and Roman 1998, Taylor et al. 1999) but not for salt marsh pools.

As an alternative hypothesis, the depth of soft sediment might indicate pool age, with pools accumulating soft sediment over time. *R. maritima* would occur, therefore,

in relatively young pools and algal flocs in older pools. While several theories exist for pool formation (Miller and Egler 1950, Redfield 1972, Pethick 1974), none have been demonstrated in New England salt marshes, and none address the issue of soft sediment accumulation. The process of pool formation and senescence may have a significant influence on cover types, however, and should be investigated further. Lastly, if nutrient levels and sediment accumulation were influenced by anthropogenic factors, there could be significant management implications since *R. maritima* is important waterfowl forage (Daiber 1982, Kantrud 1991).

Several factors did not distinguish among pool cover types based on CCA analysis. Water column inorganic P concentrations either were not limiting (total N:P was 2.5 – 3.6:1 (Table 5) compared to Redfield ratio of 16:1 (Valiela 1995)) or the variability among pools was too great (Table 5) to identify differences among cover types. Sediment nutrient levels, grain size, and organic content (Appendix II) also failed to distinguish among cover types, possibly due to high levels in all pools or low sample sizes.

Pool Habitat Quality

Macrophytes enhance estuarine productivity by increasing primary and secondary production (Heck et al. 1989, Sogard and Able 1991), and providing refuge from predation (Rozas and Odum 1988). As shown in this study, however, pools, especially in northern New England, have a large amount of bare area. Ruber et al. (1981), in fact, determined that pool primary productivity ($514 \text{ g/m}^2/\text{yr}$) was much less than that of the surrounding *Spartina* salt marsh and more commensurate with that of

tidal mudflats. These findings suggest that pools should be relatively unimportant habitats, although as demonstrated by the consistent nekton catches (Smith 1995, Raposa 2000, Adamowicz (Chapter 3)) and bird use (Master 1992, Erwin 1996) such is not the case.

CONCLUSION

This study documented more cover categories than did previous reports and also differs in reporting a greater predominance of bare areas in New England salt marsh pools. Several factors were associated with different cover types and abundances, including regional location and local pool conditions. Additionally, *R. maritima* and algal floc coverage were distinguished by conditions that could be indicative of pool trophic status or geomorphic condition. The role of trophic status and pool age on pool cover types has not been demonstrated and deserves further investigation. On a more immediate level, resource managers attempting to increase *R. maritima* coverage for waterfowl forage should mimic the lower nutrient concentrations, less soft sediment, greater water depths, and higher salinity conditions; factors that favor macrophytes in pools as demonstrated by CCA.

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Table 1. Locations used for pool macrophyte surveys.

	Broad-Scale Survey	Intensive Survey	Nutrient Analysis
Reid State Park, ME	X		
Spurwink River, ME	X		
Scarborough Marsh, ME	X		
Granite Point B, ME	X	X	
Moody Marsh, ME	X	X	
Parker River NWR, MA	X		
Coggeshall Marsh, RI	X	X	X
Middlebridge Marsh, RI		X	X
Sapowet Wildlife Management Area, RI	X	X	X
Sachuest Point NWR, RI	X		
Hammonasset State Park, CT	X		
Shennecossett Wildlife Management Area, CT		X	

Table 2. Braun-Blanquet cover values* averaged by site.

Site	Cover Category							
	Algal floculations	<i>Ascophyllum</i> <i>nodosum</i>	Bare	Epiphytes	Filamentous Green Algae	<i>Fucus</i> <i>spiralis</i>	<i>Ruppia</i> <i>maritima</i>	<i>Spartina</i> <i>alterniflora</i>
Southern sites								
Hammonasett State Park	0*	0.0	6.5	0.0	2.3	0.0	0.0	2.0
Barn Island Management	1.8	0.0	5.0	0.0	2.1	0.0	0.0	0.0
Middlebridge marsh	3.1	0.0	4.1	1.1	1.3	0.0	1.2	0.0
Coggeshall Marsh	0.0	0.0	6.2	1.9	0.9	0.0	1.5	0.0
Sachuest Point NWR	1.5	0.0	3.1	0.0	3.5	0.0	0.0	0.0
Sapowet Wildlife Management Area	0.0	0.0	3.8	0.0	4.0	0.0	0.9	0.0
Northern sites								
Parker River NWR	0.0	0.0	6.2	0.0	0.0	0.0	0.0	1.0
Moody Marsh	1.9	0.0	5.7	0.0	0.1	0.0	0.0	0.0
Granite Point B	0.0	0.0	6.7	0.6	0.8	0.0	0.1	0.0
Scarborough Marsh	0.0	0.0	6.9	0.0	0.2	0.0	0.0	0.4
Spurwink Marsh	0.0	0.0	6.5	0.0	0.4	0.0	0.0	1.0
Reid State Park	0.0	0.4	7.0	0.0	0.9	0.4	0.0	0.7

* Cover Category based on Braun-Blanquet Scale (Kent and Coker 1992)

B-B Score	% Cover
1	<1%
2	1-5%
3	5-10%
4	10-25%
5	25-50%
6	50-75%
7	>75%

Table 3. Percent similarity (SIMPER) results for northern versus southern salt marsh pools.

Species	Northern Pools Average Abundance (Braun-Blanquet Score)	Southern Pools Average Abundance (Braun-Blanquet Score)	Percent Contribution to Dissimilarity between Groups based on Euclidean Distances
Bare	6.63	4.81	41.68
Filamentous Green Algae	0.54	2.32	39.86
<i>Ruppia maritima</i>	0.02	0.78	7.27
Algal Flocculations	0.27	0.89	4.84
Epiphytes	0.12	0.63	3.27

Table 4. Average values for physical traits of salt marsh pools in broad-scale survey from across New England and used in CCA corresponding to Figure 3. Standard errors are in parentheses.

Site	# pools	Salt Marsh Pool Feature											
		Salinity (ppt)		Temperature (C)		Water Depth (cm)		Clarity (cm)		Total Sediment Depth (cm)		Soft Sediment Depth (cm)	
Reid State Park	15	24.9	(5.8)	23.6	(6.6)	15.6	(12.6)	15.2	(12.3)	87.1	(42.5)	20.9	(9.0)
Spurwink marsh	8	19.4	(4.2)	26.1	(1.3)	7.4	(2.9)	9.0	(5.3)	150.0	(0.00)	18.6	(14.4)
Scarborough marsh	5	26.7	(2.0)	28.0	(2.2)	7.1	(2.9)	7.0	(2.6)	148.0	(4.5)	29.7	(15.8)
Granite Point B	9	33.9	(2.2)	25.6	(2.7)	23.0	(12.1)	22.7	(12.1)	88.7	(29.1)	36.6	(21.3)
Moody marsh	1	40.3	.*	25.3	.	6.0	.	5.0	.	>140.0	.	13.8	.
Parker River NWR	2	27.2	(1.4)	22.9	(0.5)	19.0	(11.3)	14.2	(4.4)	55.0	(0.0)	19.2	(15.3)
Coggeshall marsh	4	30.8	(0.2)	28.5	(0.3)	11.8	(5.6)	11.8	(5.6)	28.9	(21.1)	20.1	(10.0)
Sapowet WMA	5	38.7	(1.0)	27.6	(1.9)	17.5	(3.4)	13.2	(4.2)	104.3	(27.3)	21.0	(18.8)
Sachuest Point NWR	2	9.4	(10.1)	25.5	(2.8)	19.5	(8.1)	9.7	(2.6)	57.2	(59.7)	13.6	(10.8)
Hammonasset State Park	2	22.4	(0.1)	19.1	(0.3)	6.5	(2.1)	6.5	(2.1)	150.0	(0.0)	20.0	(3.5)

* Only one pool from this site was used in canonical correspondence analysis biplot construction.

Table 5. Salt marsh pool water column nutrient data corresponding to Figure 4. Standard errors are in parentheses.

Nutrients	Site		
	Middlebridge	Coggeshall	Sapowet
NO ₃ +NO ₂ (μmol/L)	0.14 (0.04)	0.34 (0.08)	0.60 (0.22)
NO ₂ (μmol/L)	0.14 (0.02)	0.16 (0.03)	0.24 (0.05)
NH ₄ (μmol/L)	1.06 (0.26)	5.57 (3.27)	4.00 (2.36)
PO ₄ (μmol/L)	0.52 (0.16)	2.42 (0.64)	1.35 (0.90)
SiO ₄ (μmol/L)	25.29 (4.10)	22.03 (7.30)	5.46 (2.43)
Number of pools	4	4	4

Northern New England Macrophyte Sampling Sites

Southern New England Macrophyte Sampling Sites

Figure 1. Locus map for macrophyte survey sampling sites.

Figure 2. Biplot of pool cover types and pool physical variables. Cover types are plotted as open circles (sample pools are filled circles) in two-dimensional cover type ordination space. Environmental variables appear as vectors; a vector's length represents the correlation between that environmental variable and the two ordination axes. The minimum vector r^2 was 0.30 for this biplot. Relationships between cover types and environmental factors should be interpreted by projections onto Axis 2 since only this axis has significant correlations to cover ordination space ($p=0.01$) and a significant cover type-environment correlation ($p=0.02$).

Figure 3. Biplot of pool cover types and water column inorganic nutrient concentrations. Cover types are plotted as open circles (sample pools are filled circles) in two-dimensional cover type ordination space. Nutrient concentrations appear as vectors; a vector's length represents the correlation between that nutrient and the two ordination axes. The minimum vector r^2 was 0.30 for this biplot. Relationships between cover types and nutrients should be interpreted by projections onto Axis 1 since only this axis has significant correlations to cover ordination space ($p=0.01$) and a significant cover type-environment correlation ($p=0.02$).

Appendix I. List of scientific and common names for salt marsh pool macrophytes.

	Scientific Name	Common Name
Algae¹		
	<i>Acrosiphonia arcta</i> (Dillwyn) J. Agardh	
	<i>Chaetomorpha linum</i> (Muller) Kutzing	
	<i>Cladophora sericea</i> (Hudson) Kutzing	
	<i>Enteromorpha compressa</i> (Linnaeus) Greville	
	<i>Polysiphonia lanosa</i> (Linnaeus) Tandy	
	<i>Rhizoclonium tortuosum</i> (Dillwyn) Kutzing	
	<i>Ulothrix flacca</i> (Dillwyn) Thuret	
Angiosperms²		
	<i>Spartina alterniflora</i>	smooth cordgrass
	<i>Ruppia maritima</i>	wigeongrass

¹ Colt 1999.

² Gleason and Cronquist 1963.

Appendix II. Additional salt marsh pool water column and sediment characteristics from intensive pool survey. Standard errors are in parentheses.

Pool Parameter	Site											
	Barn Island		Middlebridge		Coggeshall		Sapowet		Moody		Granite Point	
Water Column												
Depth (cm)	24.00	(20.51)	24.50	(11.14)	14.67	(6.25)	29.63	(23.06)	35.53	(25.95)	25.68	(10.96)
Salinity (ppt)	32.51	(0.58)	30.77	(0.61)	28.97	(0.18)	32.33	(6.40)	33.05	(2.28)	35.73	(1.92)
Temp (C)	27.93	(5.76)	31.97	(1.18)	28.45	(0.16)	33.30	(1.29)	27.60	(2.31)	26.33	(2.49)
pH	6.32	(3.68)	.	.	7.20	(0.10)	8.41	(1.05)	7.68	(0.17)	8.30	(0.49)
Redox (mV)	75.55	(82.16)	24.05	(101.41)	41.07	(19.70)	-36.45	(72.52)	63.68	(47.20)	20.25	(57.78)
DO (mg/l)	6.28	(6.65)	9.70	(1.75)	4.75	(1.50)	10.25	(1.22)	7.21	(2.24)	9.58	(2.54)
Sediment												
% Organic Matter	.	.	41.67	(6.52)	14.07	(3.22)	26.49	(1.55)	.	.	.	.
% grain size <300 μ	.	.	73.09	(2.82)	68.23	(9.28)	67.16	(3.41)	.	.	.	.
Surface pH	3.02	(3.73)	.	.	6.91	(0.31)	7.04	(0.27)	6.96	(0.03)	7.21	(0.46)
Redox (mV)	-138.75	(95.82)	-330.38	(51.92)	-217.17	(52.5)	-219.46	(133.6)	-297.83	(38.52)	-259.35	(61.27)
NO ₃ +NO ₂ (μmol/L)	.	.	0.13	(0.01)	0.20	(0.06)	0.27	(0.05)	.	.	.	.
NO ₂ (μmol/L)	.	.	0.17	(0.01)	0.11	(0.01)	0.20	(0.03)	.	.	.	.
NH ₄ (μmol/L)	.	.	90.16	(15.19)	128.05	(89.60)	132.48	(116.00)	.	.	.	.
PO ₄ (μmol/L)	.	.	35.90	(14.63)	10.98	(9.23)	7.56	(6.64)	.	.	.	.
Number of pools sampled	2		4		4		4		3		10	

Chapter 3:

An Analysis of Factors Controlling Nekton Distribution Among New England Salt Marsh Pools

ABSTRACT

Salt marsh pools are soft-bottomed depressions that remain flooded throughout a tidal cycle and do not dry out as shallower pannes often do. Pools are important wildlife habitat but are much less abundant on ditched than unditched marshes. On-going management efforts to increase pool habitat in New England are proceeding without a regional benchmark for the composition and distribution of nekton in pools and its relationship to pool environmental conditions. The purpose of this study is to provide such a benchmark and specific restoration recommendations. Pool nekton communities were sampled using 1m² throw-traps at 7 marshes in 1999 and 2 marshes in 2000. Twelve fish and 4 decapod species were identified, with *Fundulus heteroclitus* comprising 80% of the fish caught. Species richness (jack-knife estimation) and density were greater in southern than in northern pools ($p < 0.005$, $p < 0.003$, respectively). In contrast to other estuarine studies, fish density was not influenced by the presence or absence of submerged aquatic vegetation (*R. maritima*) and decapod densities were higher in northern sites lacking it ($p < 0.03$). Canonical correspondence analysis indicated that different nekton species sorted by microhabitats available among salt marsh pools. For example, *Cyprinodon variegatus* was found in larger, shallower pools while *Pungitius pungitius* was associated with deeper pools that also had lower dissolved oxygen levels. Percent composition data and step-wise multiple linear regressions indicate that *F. heteroclitus* used pools as nursery habitat and potentially as refuges from predation, selecting among pools with different environmental conditions as the season progressed and juvenile size increased. These findings stress the

importance of maintaining a range of pool conditions in order to support a diverse nekton community and to accommodate the changing life history requirements of individual species.

INTRODUCTION

Salt marshes have a variety of habitats used by nekton. Creeks and human-made ditches provide habitat for resident and migrating species (Dionne et al. 1999, Fell 2000, Raposa 2000) and give access to the salt marsh surface for foraging (McIvor and Odum 1988, Rozas et al. 1988). Fish also use such small places as mussel shells and basal *Spartina alterniflora* leaves for egg deposition (Daiber 1982, Able and Fahay 1998) while larvae can grow in shallow puddles on the marsh surface (Kneib 1984). Along this continuum of nekton habitat are salt marsh pools, soft-bottomed depressions that hold water throughout a tidal cycle and do not dry out like shallower pannes (Chapman 1960). New England salt marsh pools are steep sided (Miller and Egler 1950) with an average total depth of approximately 30 cm (Adamowicz, Chapter 1). A survey of 26 marshes from Connecticut to southern Maine showed that pools range in size from 1 m² to 35 ha and cover an average of 2.3% of ditched marshes and 9.1% of unditched marshes (Adamowicz, Chapter 1).

Pools are important areas, supporting nekton (Able and Fahay 1998, Raposa 2000) and foraging birds (Master 1992, Erwin et al. 1994, Erwin 1996). While detailed studies on nekton use of pools have been conducted in neighboring regions (Quebec, FitzGerald and Wootton 1993; New Jersey, Able 1990, Smith and Able 1994, Smith 1995) New England studies have been limited in scope (Teo 1999, Halpin 2000, Raposa 2000). Work regarding the range of pool conditions throughout the region, especially with respect to nekton abundance, is lacking.

Nekton, i.e. fish and decapod crustaceans, in salt marsh pools is not only a measure of secondary production but also an important prey source for wading and other birds (FitzGerald and Dutil 1981, Master 1992, Erwin 1996), and provides a trophic link to other ecosystems (Conover and Ross 1982, Kneib 1986). Variables influencing nekton species distribution and abundance in salt marsh pools include water quality (Audet et al. 1986, Poulin and FitzGerald 1989), pool size (MacArthur and Wilson 1967), water depth (Whoriskey and FitzGerald 1989), the presence of macrophytic vegetation (Sogard and Able 1991, Heck et al. 1989, Smith 1995), and geographic conditions such as elevation (Ingolfsson 1994) and distance to tidal flow (Worgan and FitzGerald 1981).

Open water marsh management (OMWM) techniques employed throughout New England include the construction of new pool habitats. Nekton in the pools, however, has not been sampled in a comprehensive fashion to provide a baseline for establishing management goals. The purpose of this study is to provide a New England benchmark for nekton species composition, distribution, and relationships with environmental variables in order to better understand the role of pools in overall salt marsh ecosystem functioning and to provide guidelines for management efforts.

METHODS

Nekton was sampled at 3 locations in Maine and 3 locations in southern New England during 1999 (Figure 1). Nekton sampling continued at Granite Point A and Marshall Point (ME) during 2000. Species composition and abundance of nekton

(fishes and decapods) were sampled from May to October in marsh pools using a 1 m² throw trap (Rozas and Minello 1997). The dimensions of the throw trap were 1 m² x 0.5 m high and were similar to traps used elsewhere (Kushlan 1981, Sogard and Able 1991, Raposa 2000). Trapping efficiencies were estimated at 70 to nearly 100% by Kushlan (1981) and Pihl and Rosenberg (1982).

Trap construction and sampling technique followed that of Raposa (2000). The trap frame was constructed of 2.5 cm aluminum bars with 3-mm mesh-hardware cloth surrounding the four sides. The top and the bottom of the trap were open. One throw trap was outfitted with a 3-mm mesh net "skirt" on the top and bottom of the frame. The top skirt had a buoyant rope along its length while the bottom skirt had a weighted (seine-net) rope. This allowed the trap to be used in deeper pools or in newly created experimental pools where the bottom was firm, uneven peat.

Trapping was initiated once high tide had receded from a marsh and fish were restricted within pools. If a site had 24 or fewer pools, they were all sampled; otherwise 25 – 29 pools were randomly selected. Numbers of pools sampled at each site are given in Table 1.

Samples were obtained by slowly crossing the marsh surface to a randomly selected station on a pool's perimeter then tossing the trap 3 – 4 m through the air into the water while still at a distance from the pool edge. The bottom of the trap then was pushed into the sediment to ensure that no animals could escape. All animals were removed from the trap using a 1 m x 0.5 m dip net (3 mm mesh) that fit snugly into the trap. Dip-netting was conducted from at least 3 sides of the trap. Traps were considered empty when 3 consecutive uses of the dip net obtained no nekton. All

captured animals were identified to species, measured (total length for fish, carapace width for crabs), and immediately released. Whenever a species was present in large numbers, total length was measured on a subset of 15 - 30 individuals. One hundred-sixteen pools were sampled in 6 marshes in 1999. Sampling was restricted to 2 sites in Maine (Marshall Point and Granite Point A) during 2000 for a total of 13 pools, but these sites were sampled approximately monthly from May to October. Variables recorded included nekton species, abundance, and individual nekton lengths. Pool measurements included pool surface area, distance to nearest pool, and distance to tidal flow. Dissolved oxygen, salinity, and water temperature were measured with a hand-held YSI-85 DO meter at the time of nekton sampling. While fully cognizant that these instantaneous measurements do not capture diel patterns within pools they were intended only to provide an initial estimate of regional pool conditions. Water depth was measured with a meter stick from at least 3 sides of the throw trap. The presence/absence of macrophytes, particularly *Ruppia maritima*, was also recorded.

In addition to naturally existing pools, a number of pools that were created as part of ditch-plugging/marsh-restoration efforts were sampled. At Granite Point B in Biddeford, Maine, contractors excavated pools of 2 sizes (3 and 9 m diameters) at three different distances (15, 30, and 50 meters) from tidal flow. This scenario was replicated at 3 locations on the marsh. The purpose of this design was to test hypotheses concerning the influence of pool size and distance from tidal flow on use. Nekton in the created pools was also sampled with a 1m² throw trap. Pool measurements, water quality data, and the presence/absence of macrophytes also were recorded as noted

above. Data from these experimental pools were analyzed separately from the natural pools.

Statistical Analyses

Differences in nekton species richness between the northern and southern sites were determined by t-test (jack-knife estimation following Heltshe and Forrester 1983). Regional differences in nekton community were determined by non-parametric tests of similarity (PRIMER, Clarke and Warwick 1994). Differences in nekton abundance and length within a marsh over time were ascertained by t-test and ANOVA as appropriate.

The association of species to environmental variables was analyzed through canonical correspondence analysis (CCA). Kent and Coker (1992) indicated that CCA is preferable over detrended correspondence analysis (DCA) where a "good set of environmental data" is available. CCA is also appropriate since it "extracts the 'best' synthetic gradients from field data on biological communities and environmental features," and forms linear combinations of environmental variables that maximally separate species niches (ter Braak and Verdonschot 1995). CCA calculations and graphics were produced by PC-ORD version 4.0 (McCune and Medford 1999).

Canonical correspondence analysis (CCA) was executed for three different groups of salt marsh pools: southern New England sites September 1999, northern New England sites September 1999, and northern New England sites summer 2000. Due to a reduced number of sites and pools sampled in northern marshes during September 2000, the data set was expanded to include Marshall Point June and September plus Granite Point A August and September. Data for October 2000 were available for both

locations but were not included in the analysis due to potential changes in fish behavior as water temperatures declined (Raposa 2000). All fish densities were fourth-root transformed with rare species (< 10 individuals) removed as recommended by Clarke and Warwick (1994). Prior to CCA analysis, environmental measures were standardized within each variable. Nekton species were plotted in 2-dimensional space while environmental variables were presented as vectors. A vector's length represents the correlation between that environmental variable and the 2 ordination axes (ter Braak and Verdonschot 1995). The longer the vector is, the stronger the relationship between that variable and the community (McCune and Mefford 1999).

Fisher's Exact Test (Sokal and Rohlf 1981) was used to indicate whether the presence of nekton in one pool was linked to the presence of nekton in the nearest neighboring pool (also known as "contagion"). The association of nekton with submerged aquatic vegetation (specifically *R. maritima*) was determined by use of the rank-assignment/ANOVA equivalent of the Kruskal-Wallis test (SAS 1990).

In order to determine if specific pool physical or water quality conditions were associated with either high, medium, or low nekton abundance, fish density data were analyzed first by ANOVA/LS Means to determine whether there were pools with densities that remained consistently high (or low) from month to month. For marshes that had such fish density patterns, LS Means testing was used to assign pools to a category of low, medium, or high fish density. Stepwise logistic regression then was applied to environmental variables measured at each pool in order to build a model predicting fish density category. This technique was applied to each site and year combination.

Stepwise multiple linear regressions were used to evaluate which environmental conditions were associated with the greatest *F. heteroclitus* density and length at each site and sample date. This analysis was limited to *F. heteroclitus* in order to control for interspecific behavior and the species was further sub-divided into juveniles, adult males, and adult females to control for intraspecific behavioral differences. Best-fit equations presented were those with overall $p < 0.05$ and with significant coefficients ($p < 0.05$) for all variables included in the equation. Relative elevations of sample pools (obtained by laser level) were taken for only 3 sites (Moody, Granite Point A, and Granite Point B). Separate step-wise multiple linear regressions were also performed at 4 sites lacking elevation data and for comparisons sake, at the 3 sites where elevation data were available but were excluded from the regression analysis (Table 7).

The effect of biogeographical factors, such as pool size and distance to tidal flow, on nekton abundance was determined by t-test and ANOVA. Differences in abundance between created and natural pools also were identified by t-test.

RESULTS

Comparisons among Marshes and over Time

Nekton Community Characterizations. Throw-trap sampling in salt marsh pools resulted in a range of 3 to 6 fish species per site, depending upon location (Table 2).

Fundulus heteroclitus was the most geographically ubiquitous species, occurring at every site. The least common species were *F. majalis* and *Brevoortia tyrannus*, each occurring at only one site. A total of 12 different fish species were sampled throughout

the study (May 1999 – October 2000); a complete list of scientific and common names is given in Appendix I. Jack-knife estimates of species richness (Heltsh and Forrester 1983) during September (the only month when all marshes were sampled) indicated greater richness (7.0 ± 0.97 species) for the southern marshes compared to the northern marshes (5 ± 0.94 species, t-test, $p < 0.005$). In addition, fish communities were significantly different between the northern and southern sites ($p < 0.0001$, ANOSIM). Percent similarity analysis (SIMPER) indicated that southern sites possessed more *F. heteroclitus* and that *Cyprinodon variegatus* and *Lucania parva* occurred only in the southern marshes. These three species accounted for 95% of the total dissimilarity between the two regions.

During the study period, a total of 5,820 fish were caught with *F. heteroclitus* comprising 80.0% of the catch. The next most common species were *C. variegatus* at 12.3% and *Pungitius pungitius* at 3.4%. Average fish density at each site ranged from a low of 1.0 fish/m² at Moody marsh and Marshall Point, ME during June 1999 to a high of 48.8 fish/m² during September 1999 at Sapowet marsh, RI. Comparing regions based on September 1999 data (the only month when all sites were sampled), fish densities were significantly greater in southern marshes (47.7 ± 12.0 fish/m²) compared to northern sites (20.7 ± 0.1 fish/m², $p < 0.005$ square-root transformed data, t-test).

Fish density varied over time as well as across sites (Figure 2). Granite Point B and Moody marsh both had significantly higher densities later in the season (both $p < 0.0001$, square-root transformation, ANOVA/LSMeans). The southern sites were sampled only twice during 1999 so it was not possible to establish seasonal trends for these locations. There were no significant density trends in 2000. Juveniles (< 45 mm

total length) comprised greater than 65% of the *F. heteroclitus* catch on all but 3 occasions (June 1999, Moody Marsh; September 1999, Middlebridge; May 2000, Marshall Point; Table 3).

Fish Length. Average total lengths for species with significant differences between sample dates are given in Table 4. A complete listing of fish lengths by species, site, and date is provided in Appendix II.

F. heteroclitus was separated into 3 groups – juveniles, adult males, and adult females. The juveniles at Moody marsh during May 1999 were overwintering individuals from the 1998-year class. Juveniles in the 1999-year class were recruited during June and July of 1999 and increased in size through September/October, with significant between-month differences at 6 of 7 sites. The maximum change in average juvenile size (20 to 34 mm) occurred at Moody marsh. *F. heteroclitus* adults, on average, were less than 55 mm. There was only one site with significant between-month differences in length for *F. heteroclitus* males (49 – 59 mm at Moody marsh, 1999). There were 2 sites for significant differences in female lengths (49 – 71 mm at Granite Point A, 2000; 48 – 61 mm at Granite Point B, 1999).

Similar trends occurred for other species. *Menidia menidia* increased significantly over time (29.5 – 38.1 mm, $p < 0.01$) at Middlebridge marsh. *P. pungitius* increased from September to October 1999 ($p < 0.05$) at Granite Point B and from September to October 2000 ($p < 0.005$) at Granite Point A (Table 4). Sample sizes for other species were generally too low to detect significant differences.

Decapod Density. Only 4 species of decapods were sampled during 1999 – 2000 (Table 2). Of the 1369 individuals captured, 93% were *Palaemonetes pugio*, 6.3% were *Carcinus maenas*; the remainder was divided between *Crangon septemspinosa* and *Callinectes sapidus*. A list of scientific and common names is given in Appendix I. Two locations had significant differences in decapod density over time (Middlebridge, $p < 0.05$; Moody Marsh, $p < 0.005$; square-root transformation; ANOVA; Figure 3). Granite Point A and Marshall Point had a density less than 1.2 decapods/m² for each sample date in 2000 and there were no significant differences among sample dates. High densities of *P. pugio* in just a few pools accounted for the large decapod densities at Barn Island ($>150/\text{m}^2$ in 20% pools) and Sapowet ($>30/\text{m}^2$ in 44% pools) in September 1999.

Decapod Size. In distinct contrast to fish patterns of increasing length through the sampling period, *C. maenas* at Granite Point A increased in both years to a peak size during September followed by a marked decrease in size during October (Table 4). The absence of large adult *C. maenas* was very obvious as was the presence of particularly small juvenile crabs.

Canonical Correspondence Analysis. Three biplots were produced from the CCA analysis: southern New England sites September 1999 (Figure 4), northern New England sites September 1999 (Figure 5), and northern New England sites summer 2000 (Figure 6). Environmental data for each biplot are summarized by site in Figures 7 – 9.

Southern versus Northern Biplots. A CCA biplot for southern New England sites (September 1999) is given in Figure 4. Axis 1 did not have a significant species-ordination or species-environment relationship and so was not graphed. The species-ordination p-value was 0.02 (Monte Carlo test) for axis 3, but the species-environment correlation was non-significant. Only axis 2 had a significant species ordination ($p=0.01$, Monte Carlo test) and species-environment correlation ($r=0.615$, $p=0.03$; Monte Carlo test). Species-environment relationships, therefore, should be taken as projections onto axis 2. Accordingly, temperature and dissolved oxygen vectors do not play an important interpretive role since most of their lengths are directed parallel to axis 3. Pool surface area and water depth, however, do separate species as noted below.

Both axis 2 and 3 of Figure 5 (northern sites, September 1999) are significant in terms of species-ordination (axis 2 $p=0.01$, axis 3 $p=0.01$; Monte Carlo test) and species-environment correlations (axis 2 $r=0.514$, $p=0.01$; axis 3 $r=0.403$, $p=0.01$; Monte Carlo test). In this case species-environment relationships can be garnered by projecting points and vectors onto both axes. Temperature, dissolved oxygen, pool surface area, and water depth, therefore, all play a role in separating nekton species as described below.

Comparing the southern and northern sites in September 1999 (Figures 4 and 5, respectively) reveals that *F. heteroclitus* was near the origin on both biplots reflecting its presence in most pools. *Cyprinodon variegatus* was sampled only in the southern sites and appeared in larger, shallower pools. *P. pungitius* occurred only in the northern sites and was located in smaller pools of moderate depth with cooler temperatures and less dissolved oxygen. *M. menidia* was found in both regions, with

biplots indicating an association with smaller, deeper pools. *Lucania parva* and *M. beryllina* were found in southern sites only; these species were located in pools of near average depth.

Northern Biplots: 1999 versus 2000. The biplots for northern sites in 1999 and 2000 (Figures 5 and 6, respectively) have a similar arrangement of environmental vectors for dissolved oxygen, log (pool surface area), and water depth. In Figure 6, axis 2 is the only one with a significant species-ordination to axis relationship ($p=0.02$, Monte Carlo test) and species-environment Pearson correlation coefficient ($r=0.83$, $p=0.03$, Monte Carlo test). *F. heteroclitus* is close to the origin in the 1999 plot (Figure 5), while it lies slightly above the origin in the 2000 plot (Figure 6) indicating a greater association with smaller, more shallow pools within the set sampled in September 2000. In both years, *P. pungitius* were trapped in slightly deeper than average pools with lower levels of dissolved oxygen. While the position of *C. maenas* shifts somewhat between Figures 5 and 6, this did not represent a change in environmental characteristics of pools with *C. maenas* ($p>0.10$, t-tests) or in crab sizes between years ($p>0.10$, t-test). *P. pugio* was associated with somewhat deeper than average pools in each year.

Comparisons among Pools within a Marsh

Factors affecting the distribution of nekton were evaluated on several levels of complexity. At the simplest level, the presence (or absence) of fish among pools was contagious – if fish were present in one pool, its nearest neighbor also was likely to

contain fish ($p < 0.01$, $n = 99$ pools from 11 marshes throughout New England, Fisher's Exact Test). Other factors of interest included the presence of macrophytes, the consistency of fish density in a given pool over time, pool size and distance to tidal flow (biogeographical factors), and the environmental conditions in pools over time.

R. maritima Presence/Absence and Nekton Densities. Mean fish densities were greatest in pools without *R. maritima* for all sites (except for Marshall Point) although none of the differences were significant ($p > 0.05$, Kruskal-Wallis test; SAS 1990). This pattern held when the pools were grouped by region – pools lacking *R. maritima* in both the north and south had higher fish densities, but again there were no significant differences ($p > 0.05$ for both). No trends were present for decapods at individual sites. When grouped by region, the northern sites had significantly more decapods in pools without *R. maritima* ($p < 0.05$ for both 1999 and 2000).

Pool Ranking and Logistic Regression Analysis. Of the 6 marshes sampled, only Granite Point A and Sapowet had pools where fish densities remained relatively consistent from month to month ($p < 0.05$, Granite Point A; $p < 0.05$, Sapowet; ANOVA). Granite Point A data produced a statistically significant logistic regression model ($p < 0.0001$, $c = 0.761$) where fish density category (low, medium high) was best predicted by pool surface area (coefficient = -0.0126 , $p < 0.001$) followed by water depth (coefficient = 0.0819 , $p < 0.05$). Based on signs of the coefficients, the model indicated that smaller, deeper pools consistently had higher fish densities compared to other pools at the site. No statistically significant model was achieved for Sapowet.

Experimental Pools. Eighteen experimental pools were excavated at Granite Point B in Spring 2000 to test the effects of pool size (small = 7 m², large = 64 m²) and distance to tidal flow (near = 15 m, moderate = 30 m, far = 50 m) on nekton use. A total of 452 fish and 39 decapods were caught in these pools during 4 sampling periods in 2000. *F. heteroclitus* juveniles accounted for 95% of the fish captured; *Carcinus maenas* constituted 90% of the decapods. Pool size did not affect fish or decapod density ($p > 0.2$, t-test). When multiplied across the surface area of each experimental pool, however, larger pools had significantly greater numbers of total fish and decapods ($p < 0.0001$, $p < 0.0005$, respectively; log (x+1) transformed data, t-test). The second treatment in the experimental design, distance to tidal flow, did not affect fish density ($p > 0.43$, ANOVA, df= 2,6), decapod density ($p > 0.25$, ANOVA, df= 2,6), total fish abundance ($p > 0.35$, log (x+1) transformation, ANOVA, df= 2,6), or total decapod abundance ($p > 0.29$, log (x+1) transformation, ANOVA, df= 2,6).

Nekton densities in these newly created pools were compared to densities in 14 existing pools at the same site, controlling for sample date, pool size, and distance to tidal flow (Table 5). Student t-test results indicated that fish densities were significantly higher in natural compared to created pools (mean density 12.8 versus 5.0 fish/m², respectively; $p < 0.01$, square-root transformed data, t-test). *F. heteroclitus* overall, *F. heteroclitus* juveniles, and *F. heteroclitus* females were smaller in created pools ($p < 0.001$, $p < 0.001$, $p < 0.005$, respectively; t-test). Decapod densities were also significantly greater in the natural pools (0.9/m² versus 0.4/m², $p < 0.005$, square-root

transformed data, t-test). There were no significant differences in *C. maenas* carapace widths between natural and created pools ($p > 0.10$, t-test).

Step-Wise Multiple Linear Regression.

High juvenile *F. heteroclitus* density was most commonly associated with measures of water depth, salinity, and relative pool elevation (Table 6). Greater juvenile densities during May – September occurred in pools that were shallower and higher in elevation; in October, juvenile densities were greater in deeper pools that were lower in elevation. Salinity correlations with juvenile densities were mixed. *F. heteroclitus* adult densities were associated with temperature or pool size in approximately 50% of the cases reported in Table 6. Results for adult females suggest a switch to warmer waters in September/October.

When elevation data were absent, *F. heteroclitus* juvenile densities were most often modeled by salinity, pool size, distance to tidal flow, and water depth (Table 7). The best-fit equations predicted more *F. heteroclitus* juveniles in deeper pools in October; in other months juveniles were more prevalent in shallower pools. *F. heteroclitus* adult densities most frequently were correlated with temperature and pool size. For *F. heteroclitus* males, density was greater in smaller and cooler pools (June, September). *F. heteroclitus* female abundance was also greater in smaller pools overall, with those pools being warmer in October (temperature trends for other months varied). In the instances when elevation data were available but ignored, log pool surface area (in the case of adults of both sexes), distance to tidal flow (juveniles and males), and temperature (juveniles and males) entered into the regression equations.

When stepwise multiple regressions were performed on fish lengths for each class (Table 8, includes elevation data), in over 70% of the cases, larger juveniles were associated with temperature – similar to the frequent correlations between adult densities and temperature. In general, larger juveniles were correlated with lower elevation pools in all months, higher levels of dissolved oxygen, cooler pools during the summer, but warmer and deeper pools in October. Large adults tended to track pool size and dissolved oxygen levels.

When examining *F. heteroclitus* lengths at all sites without elevation data (Table 9), larger juveniles correlated with measures of water temperature and dissolved oxygen in the majority of cases. Large adults tended to track salinity and dissolved oxygen. When elevation data were available but excluded (Table 9), log pool surface area (for juveniles) and distance to tidal flow (adults) entered into the regression equations.

DISCUSSION

Nekton use of salt marsh pools is best examined on both a large and small scale. Large-scale views allow comparison among marshes and regions and reveals seasonal trends. Small-scale views address comparisons among pools within a marsh.

Large-scale Patterns

Salt marsh pools were dominated by *F. heteroclitus* and a small assemblage of species common to salt marshes (Table 2). These findings are consistent with studies of other New England salt marshes (Burdick 1997, Dionne et al. 1999, Fell et al. 2000, Raposa 2000) except that pools represent a subsample of the species caught in other

marsh habitats. This subsampling is consistent with the data of Talbot et al. (1986) in New Jersey and thus suggests ecosystem rather than local or regional processes.

Pool nekton communities were distinctly different between northern and southern New England. The greater species richness and density in southern New England exemplify the biogeographical break known to occur around Cape Cod, MA for many estuarine and marine species (Bigelow and Schroeder 1953). While examining a number of studies (e.g. Dionne et al. 1999, Fell et al. 2000, Raposa 2000) can elucidate this regional division, this is the first investigation of salt marsh pools that has used the same sampling technique in both northern and southern New England.

In terms of seasonal trends, several nekton species were shown to increase in density and size from May to October (Figure 2, Table 4). Others have noted these trends within New England (Halpin 1997, Dionne et al. 1999) and further south (Talbot et al. 1986, Smith 1995, Able et al. 2000). Rather than a steady increase in size, however, green crab (*C. maenas*) carapace width increased only from May to August (Table 4); in October, crab size fell markedly. The decreased adult density and appearance of juveniles in October may have signaled a *C. maenas* seasonal migration triggered by temperature changes as has been reported elsewhere (van der Meeren 1992, Attrill and Thomas 1996).

Small-scale Patterns

Comparison of Environmental Parameters among Pools over all Sample Dates. Nekton distribution among pools at each marsh was evaluated in several standard ways with a few unexpected results. For example, there was no significant difference in fish

densities between pools with and without *R. maritima* (the macrophyte most comparable to other studies). This finding is in sharp contrast to work in other estuarine habitats that have demonstrated higher fish abundance in areas with macrophytic vegetation (Heck et al. 1989, Sogard and Able 1991, Smith 1995). It may be that while pools are bare, fish find adequate refuge from predation (a trait associated with macrophyte cover) by burrowing in the soft sediments of pools.

Next, ANOVA/logistic regression results indicated that only one site had pools with consistent fish density levels in each pool (Granite Pool A, smaller, deeper pools had the highest fish densities). When pool size was evaluated in the experimental pools, there was no effect on fish density. It is possible that treatment levels were not extreme enough and subsequently did not affect fish colonization. This in itself is of interest since the “large” created pools (at 254 m²) were nearly 4 times the median size (64.5 m²) of existing pools and slightly less than the average area (398 m²) of pools fished at that site (Granite Point B). Additionally, the 3 distances chosen (15, 30, 50 m from tidal flow) covered most of the range for natural pools (maximum distance to tidal flow at Granite Point B was 83 m). Worgan and FitzGerald (1981), however, did find differences in fish density based on distances to estuarine waters, although they used increments of 75 m – much broader than the area available for experimental manipulation at Granite Point B.

Despite these negative results, two overall patterns were observed in nekton distribution among pools. Fisher’s Exact Test revealed contagion of fish among pools ($p < 0.01$). The demonstrated mobility of *F. heteroclitus* (Sweeney 1998, Teo 1999) and relative proximity of nearest-neighboring pools (Adamowicz, Chapter 1) ensured their

spread among pools. Additionally, when comparing newly created pools to existing ones, fish density was more than twice as great and *F. heteroclitus* were 5 – 7 mm larger in old pools (Table 5). Similar results were obtained for decapods. These findings may be linked to the poor environmental quality of newly excavated pools – during the first sampling period dissolved oxygen levels averaged 4.2 mg/l ($\pm$ 1.8 mg/l) in new pools compared to 7.8 mg/l ($\pm$ 3.0 mg/l) in old pools.

Comparison of Environmental Variables among Pools within a Sample Date: Pit-Traps Versus Fish Choice. The existence of different environmental conditions and nekton densities among pools within a marsh raises the question of whether fish (particularly *F. heteroclitus*, the dominant species) select the pools where they are sampled or if pools act merely as pit traps. Several pieces of evidence support the hypothesis that pools act as pit traps at least for small fish. First, only smaller fish colonized the newly created pools; larger fish could have evaded these and other poor quality habitats more readily due to their greater swimming ability (Kushlan 1981). Second, after hatching on flooding tides, *F. heteroclitus* larvae are known to be carried onto the high marsh where they are then found in an assortment of depressions (Able and Fahay 1998). Whoriskey et al. (1986) also suggested that *G. aculeatus* adults moved passively by ascending into the water column as water covered the marsh, traveling with wind and tide, and then settling as the tide receded. A similar behavior may apply for small juvenile *F. heteroclitus*.

Alternatively, there is evidence that larger juveniles and adult *F. heteroclitus* have the ability to choose among pools. Teo (1999) approximated individual home

ranges of *F. heteroclitus* in a New Jersey salt marsh as 15 ha at high tide, while Sweeney (1998) estimated that these fish could move 32 m across the marsh surface. Thus *F. heteroclitus* has the physical capability of traversing the distance between pools and should be able to encounter a number of pools while moving about when the marsh is flooded at high tide. Stepwise multiple regression analyses demonstrated that larger juveniles were correlated with better habitat conditions (e.g. higher levels of dissolved oxygen and lower water temperatures in summer, Table 8). One could argue that instead of fish choice, better habitat conditions facilitated greater fish growth. While this is possible, the definition of optimal conditions changed from month to month (Table 8), as did the pools that fit the description. So if larger juveniles were always in pools with the best environmental conditions, they would have to move over time.

Perhaps the strongest evidence of active site selection by larger fish is demonstrated later in the season when *F. heteroclitus* seeks pools (rather than creeks) as overwintering habitat (Smith and Able 1994, Raposa 2000). This study goes one step further, however, indicating that *F. heteroclitus* selected among pools (Tables 6 – 7). Nor is pool choice unique to *F. heteroclitus*. Adults of three species of sticklebacks (Gasterosteidae) were shown to avoid pools that dried out and to settle more often in pools that retained water, suggesting active habitat choice (Whoriskey and FitzGerald 1989).

Role of Pools In Nekton Life Histories. While fish may select among pools, why should they occupy pool habitat at all? This study has documented that pools can be devoid of vegetation and exhibit extremes in temperature and dissolved oxygen (Figures 7 – 9).

Such stressful environments seem unlikely places to support growing nekton populations. Several studies, however, have documented that food, at least, is abundant in pools (Walsh and FitzGerald 1984, Poulin and FitzGerald 1989, James-Pirri et al. 2001).

Kneib's (1987) work indicated that protection from predation is an additional incentive for pool use by juvenile fish. Adult *F. heteroclitus* foraging on flood tides restricted juveniles to the high salt marsh. When adult fish retreated to creeks with the ebb tide, juveniles remained on the marsh except in those cases where adults had been experimentally removed. In the latter circumstances, juveniles also went to the creeks. This separation of adults and juveniles was confirmed in the present study by the high relative abundance of juveniles in marsh pools (Table 3) and by larger (more predation resistant) juveniles being found in pools at lower elevations closer to open water (Table 8).

Ruiz et al. (1993) obtained similar results with shoreline fish; small fish occurred in greater numbers in shallow, unvegetated waters, in contrast to other studies where high fish densities were associated with submerged aquatic vegetation (Heck et al. 1989, Rozas and Odum 1988). Thus the preponderance of *F. heteroclitus* juveniles in pools was likely due to their use of pool habitat as a refuge from predation. As fish grew, they were able to choose among pools for improved habitat and then leave them for tidal creeks or other nearby waters when size and tides allowed, only to return to pools in fall for overwintering.

Other Species. While *F. heteroclitus* was the dominant nekton species, it was not the only one sampled in salt marsh pools; the other eleven fish and 4 decapod species sampled provide a variety of insights to pool habitat quality. For example, three- and four-spine sticklebacks (*Gasterosteus aculeatus*, *Apeltes quadracus*, respectively) were sampled only intermittently in pools at several study sites, while *P. pungitius* was more common (Tables 2 and 4). Poulin and FitzGerald (1989) found *P. pungitius* to be a pool resident unlike other sticklebacks, which stayed only for 1 tidal cycle to spawn (Whoriskey et al. 1986). The longer residence time of *P. pungitius* was thought to be due to its greater resistance to low oxygen concentrations of July and August (Poulin and FitzGerald 1989). This corroborates the correlation of *P. pungitius* to lower dissolved oxygen levels in the CCA biplots (Figures 5 and 6).

Several other fish were sampled regularly but in much reduced numbers. *Cyprinodon variegatus* were found only in southern New England sites, corresponding to the reported range of Cape Cod, Massachusetts to Florida (Robins and Ray 1986). CCA results indicated *C. variegatus* densities were correlated with larger, shallower pools (Figure 4). The association of *C. variegatus* with these particular circumstances despite the availability of more moderate pool conditions could be an indication of either competitive displacement or predation avoidance as noted above for *F. heteroclitus*.

Menidia menidia are common to marsh creeks and are intolerant of low dissolved oxygen levels (Able and Fahay 1998); therefore, their presence in pools throughout the summer may represent strandings. *Menidia beryllina* are known to use pools as nurseries (Able and Fahay 1998), though only larger young of the year (Table

4) were sampled in pools during September. Of the two *Menidia* species, *M. beryllina* is more common to fresh/ brackish waters (Robins and Ray 1986)

Incidental species included *Anguilla rostrata*, *B. tyrannus*, *F. luciae*, and *F. majalis*. *F. luciae* is a high marsh species often located in very shallow pools and puddles (Kneib 1984). Although reported only as a stray in Connecticut (Whitworth 1996), they were regularly sampled at Barn Island.

Restoration Recommendations

Restoration of salt marsh pools should proceed with caution and particular attention to detail. For example, the pool characteristics associated with high *F. heteroclitus* juvenile densities from May – September (shallower pools in higher elevations) were not the same as those in October (deeper pools, lower in elevation) (Table 6). Additionally, *C. variegatus* and *F. luciae* preferred shallow high-marsh pools whereas sticklebacks required deeper pools that were less likely to dry out (Whoriskey and FitzGerald 1989). A diversity of pool conditions, therefore, is desirable, while at the same time dissolved oxygen, temperature, and salinity levels approaching the stress limits of target species should be avoided. Managers should also acknowledge the lower species richness and nekton densities in northern New England and set their restoration goals accordingly. Given these caveats, however, results from Fisher's Exact Test indicate that new pools have a greater chance of containing fish if located near existing pools that also contain fish.

Comparison Of New England To Other Regions

Table 10 lists a number of variables available from the literature for comparing salt marsh pools from Iceland to New Jersey. Fish species richness peaked in Rhode Island at 12 (Nixon and Oviatt 1973) but species counts in New Jersey were nearly as large (9 species, Smith 1995). *F. heteroclitus* was the dominant species from Maine southward, although *G. aculeatus* was dominant in Quebec and Iceland. Based on fish species richness, density, and vegetation cover, the current study fits into the continuum reported from Iceland to New Jersey. Further work on regional comparisons would greatly enhance our understanding of salt marsh pool habitat and the role it plays in the life histories of different fishes.

CONCLUSIONS

Nekton was plentiful in pools. Nekton species composition and abundances varied from northern to southern New England and did change over time, although *F. heteroclitus* juveniles were dominant at each site and season. Interestingly, densities of *F. heteroclitus* juveniles and adults were correlated with different pool conditions over the sample period. There is some evidence that *F. heteroclitus* adults and larger juveniles were actively selecting among pools, particularly for overwintering habitat, while smaller *F. heteroclitus* juveniles may have been more passive in habitat selection. Due to different life histories of each nekton species and changing needs over the summer and fall, managers should seek to preserve and restore a variety of pool

conditions while avoiding extremes in temperature and dissolved oxygen and the physical conditions that can create them.

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Table 1. Nekton trapping locations and numbers of pools sampled for nekton in 1999 (a) and 2000 (b).

a) 1999

Location Site	Month					
	May	June	July	August	September	October
Southern						
Barn Island Management Area				6	10	
Middlebridge marsh			15		14	
Sapowet Wildlife Management Area				9	10	
Northern						
Granite Point A			4		9	9
Granite Point B			29		29	29
Marshall Point		6	4		4	4
Wedge Marsh	27	25			25	25

b) 2000

Location Site	Month					
	May	June	July	August	September	October
Northern						
Granite Point A			9	9	9	9
Marshall Point	4	4			4	4

Table 2. Nekton species trapped at sampling locations in 1999 (a) and 2000 (b).

a) 1999

Nekton Species	Site						
	Barn Island	Middle-bridge marsh	Sapowet	Moody Marsh	Marshall Point	Granite Point A	Granite Point B
<i>Anguilla rostrata</i>					X		X
<i>Apeltes quadracus</i>						X	X
<i>Brevoortia tyrannus</i>							X
<i>Cyprinodon variegatus</i>	X	X	X				
<i>Fundulus heteroclitus</i>	X	X	X	X	X	X	X
<i>F. luciae</i>	X						
<i>F. majalis</i>		X					
<i>Gasterosteus aculeatus</i>				X	X		
<i>Lucania parva</i>	X	X	X				
<i>Menidia beryllina</i>	X	X	X				
<i>M. menidia</i>	X	X	X	X			X
<i>Pungitius pungitius</i>				X		X	X
<i>Callinectes sapidus</i>	X	X					
<i>Carcinus maenas</i>	X		X	X		X	X
<i>Crangon septemspinosus</i>				X			X
<i>Paralichthys pugio</i>	X		X	X		X	X

b) 2000

Nekton Species	Site	
	Granite Point A	Marshall Point
<i>Anguilla rostrata</i>	X	
<i>Apeltes quadracus</i>		X
<i>Fundulus heteroclitus</i>	X	X
<i>Gasterosteus aculeatus</i>	X	
<i>Menidia menidia</i>	X	
<i>Pungitius pungitius</i>	X	X
<i>Crangon septemspinosus</i>	X	
<i>Paralichthys pugio</i>	X	

Table 3. Percent *F. heteroclitus* juveniles, adult males, and adult females sampled at each site and date.

Site	<i>F. heteroclitus</i> class	Sample Month-Year										
		May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Sep-00	Oct-00
Barn Island	juveniles	x*	x	x	68.5	94.0	x	x	x	x	x	x
	males	x	x	x	19.6	2.8	x	x	x	x	x	x
	females	x	x	x	11.9	3.1	x	x	x	x	x	x
Middlebridge marsh	juveniles	x	x	99.5	x	50.5	x	x	x	x	x	x
	males	x	x	0.0	x	25.2	x	x	x	x	x	x
	females	x	x	0.5	x	24.3	x	x	x	x	x	x
Sapowet	juveniles	x	x	x	97.7	94.9	x	x	x	x	x	x
	males	x	x	x	0.0	1.6	x	x	x	x	x	x
	females	x	x	x	2.3	3.5	x	x	x	x	x	x
Moody marsh	juveniles	62.5	41.7	x	x	86.1	72.8	x	x	x	x	x
	males	15.8	12.5	x	x	4.7	7.3	x	x	x	x	x
	females	21.7	45.8	x	x	9.2	19.8	x	x	x	x	x
Marshall Point	juveniles	73.3	100.0	x	x	100.0	100.0	50.0	80.0	x	89.3	100.0
	males	0.0	0.0	x	x	0.0	0.0	50.0	0.0	x	3.6	0.0
	females	26.7	0.0	x	x	0.0	0.0	0.0	20.0	x	7.1	0.0
Granite Point	juveniles	x	100.0	x	x	87.4	96.3	x	91.9	91.0	98.5	97.6
	males	x	0.0	x	x	4.0	1.2	x	4.7	4.5	0.0	0.8
	females	x	0.0	x	x	8.6	2.4	x	3.5	4.5	1.5	1.6
Granite Point	juveniles	x	91.1	x	x	81.9	83.7	x	x	x	x	x
	males	x	1.0	x	x	6.3	6.0	x	x	x	x	x
	females	x	7.9	x	x	11.9	10.3	x	x	x	x	x

*No sampling on this date.

Table 4. Average nekton length (mm) by site and sample date for cases with significant differences among months sampled.

Nekton category and site	Months Sampled												Significance Level
	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	
<i>F. heteroclitus</i>													
juveniles													
Middlebridge	x ¹	x	27.7 a ²	x	36.5 b	x	x	x	x	x	x	x	***
stdev(no. pools)			3.7 (12)		2.7(7)								
Sapowet	x	x	x	27.7 a	30.6 b	x	x	x	x	x	x	x	*
stdev(no. pools)				2.2(8)	2.5(10)								
Moody marsh	40.0 a	20.4 b	x	x	34.4 c	33.4 c	x	x	x	x	x	x	***
stdev(no. pools)	2.2(20)	7.6(4)			4.5(25)	5.7(19)							
Marshall Point	-- ⁴	15.3 a	x	x	25.8 b	27.3 b	--	24.3 a,b	x	x	33.0 b	27.8 b	*
stdev(no. pools)		(1)			1.5(2)	3.5(3)		(1)			1.5(2)	(1)	
Granite Point A	x	22.4 a	x	x	32.6 b,e	30.4 c,e	x	17.4 d	28.9 c,e	x	30.2 e	29.0 e	***
stdev(no. pools)		2.5(4)			3.2(8)	2.5(7)							
Granite Point B	x	22.1 a	x	x	32.3 b	33.4 b	x	x	x	x	x	x	***
stdev(no. pools)		5.4(14)			4.7(29)	5.2(17)							
<i>F. heteroclitus</i>													
adult males													
Moody marsh	48.6 a	51.7 a,b	x	x	58.9 b	55.3 b	x	x	x	x	x	x	**
stdev(no. pools)	3.0(15)	10.4(3)			8.4(9)	6.9(6)							

Table 4 (cont.)

Nekton category
and site

Months Sampled

Significance
Level

	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00
--	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------

F. heteroclitus

adult females

Granite Point A	x	--	x	x	49.2 a	44.7 a	x	49.0 a	55.6 a	x	45.0 a	70.5 b *
stdev(no. pools)					2.5(2)	6.6(2)		(1)	(1)		0.0(3)	(1)
Granite Point B	x	61.0 a	x	x	53.7 a,b	48.2 b	x	x	x	x	x	x *
stdev(no. pools)		12.5(3)			8.1(17)	3.8(8)						

M. menidia

Middlebridge	x	x	29.5 a	x	38.1 b	x	x	x	x	x	x	x **
stdev(no. pools)			1.3(4)		4.5(6)							

P. pugio

Granite Point A	x	--	x	x	41.0 b,c	43.7 b	x	28.5 a	33.8 a	x	35.5 a,c	40.8 b **
stdev(no. pools)					(1)	3.2(3)		(1)	1.6(4)		2.8(3)	1.8(2)
Granite Point B	x	--	x	x	37.8 a	42.9 b	x	x	x	x	x	x *
stdev(no. pools)					3.1(8)	3.7(5)						

*C. maenas*⁵

Granite Point A	x	31.0 a	x	x	39.8 b	13.0 c	x	--	24.2 d	x	40.8 b	10.0 c ***
stdev(no. pools)		(1)			2.3(3)	(1)			2.8(3)		1.1(2)	(1)

¹ No trapping on this date.² Significant differences between months within a site are signified by different lower case letters.³ Significance levels: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$ ⁴ Trapping conducted, species not in sample or length data not available.⁵ Crab size reported as maximum carapace width.

Table 5. Comparison of nekton in natural and created pools. Data are presented as average values $\pm$ 1 standard deviation (number of pools).

Nekton Parameter	Species Category	Natural Pools	Created Pools	Significance
				Level
Fish density (#/m ²)		12.8 $\pm$ 0.2 (14)	5.0 $\pm$ 0.2 (18)	** ¹
Length (mm)	<i>F. heteroclitus</i> juvenile	31.7 $\pm$ 4.7 (15)	26.6 $\pm$ 2.5 (18)	***
	<i>F. heteroclitus</i> female	52.4 $\pm$ 5.6 (10)	46.5 $\pm$ 2.6 (8)	*
	<i>F. heteroclitus</i> overall	35.3 $\pm$ 6.6 (15)	28.0 $\pm$ 2.9 (18)	***
Decapod density		0.9 $\pm$ 0.6 (15)	0.4 $\pm$ 0.5 (18)	**
Width (mm)	<i>Carcinus maenas</i>	34.4 $\pm$ 10.0 (12)	29.9 $\pm$ 5.7 (13)	NS

¹ Significance levels: *, p<0.05; **, p<0.01; ***, p<0.001

Table 6. Coefficients of significant variables used in "best fit" equations resulting from stepwise multiple linear regression of *F. heteroclitus* density versus environmental conditions including elevation data.

<i>F. heteroclitus</i> Category	Site	Date	Environmental Variables							Equation Statistics	
			Relative Elevation (m)	Temper- ature (C)	Salinity (ppt)	Dissolved Oxygen (mg/l)	Depth (cm)	Log (Pool Surface Area (m ²))	Distance to Tidal Flow (m)	Overall Significance Level	Overall R ²
<u>Juveniles (<45mm)</u>	Moody Marsh	May-99	72.63							** ¹	0.3016
	Moody Marsh	Jun-99			-0.14		-0.02		-0.05	**	0.5582
	Granite Point A	Jun-00			2.59					**	0.6792
	Granite Point A	Jul-00						-19.66		*	0.4511
	Granite Point B	Sep-99	45.20		2.99		-0.64			**	0.4191
	Granite Point A	Oct-99				7.98	2.17	-17.42		***	0.9739
	Granite Point B	Oct-99	-115.92							**	0.3192
	Moody Marsh	Oct-99					0.84		1.02	*	0.3523
<u>Male adults</u>	Moody Marsh	Jun-99		-0.12						*	0.2275
	Granite Point A	Jun-00	-5.62							*	0.4769
	Granite Point A	Sep-99	32.28			0.60			-0.26	*	0.7625
	Granite Point B	Sep-99	4.53	-0.43				-1.21		***	0.5976
	Granite Point A	Oct-99				0.27		-0.84		**	0.8681
<u>Female adults</u>	Moody Marsh	May-99						-2.57	0.28	*	0.3360
	Moody Marsh	Jun-99		-0.40						***	0.5560
	Granite Point A	Jun-00	-7.18	-1.01	-0.14		-0.12			***	0.9869
	Granite Point A	Sep-99		1.73						*	0.4900
	Granite Point B	Sep-99		-0.61				-1.14		**	0.3722
	Granite Point A	Oct-99				0.36		-1.31		*	0.7712
	Moody Marsh	Oct-99						-7.19		*	0.1778
	Granite Point A	Oct-00		0.67						*	0.6156

¹ Significance levels: *, p<0.05; **, p<0.01; ***, p<0.001

Table 7. Coefficients of significant variables used in "best fit" equations resulting from stepwise multiple linear regression of *F. heteroclitus* density versus environmental conditions *without* elevation data.

			Environmental Variables						Equation Statistics	
<i>F. heteroclitus</i> Category	Site	Date	Temperature (C)	Salinity (ppt)	Dissolved Oxygen (mg/l)	Depth (cm)	Log (Pool Surface Area (m ²))	Distance to Tidal Flow (m)	Overall Significance Level	Overall R ²
Juveniles (<45 mm)	Moody	May-99		-1.95	-1.44		-8.80	0.34	** ¹	0.6242
	Marshall Point	May-00		0.07					**	0.9962
	Moody	Jun-99		-0.15		-0.01		-0.05	**	0.5352
	Marshall Point	Jun-00				-0.11	-7.04		*	0.9977
	Granite Point A	Jun-00		2.59					**	0.6792
	Middlebridge	Jul-99		-3.96			-20.99		*	0.5027
	Granite Point A	Jul-00					-19.66		*	0.4511
	Sapowet	Aug-99		11.75					*	0.6340
	Barn Island	Sep-99	-34.81			-8.16			**	0.8291
	Granite Point B	Sep-99		1.54				-0.41	*	0.2172
	Marshall Point	Sep-00						0.58	**	0.9938
	Moody	Oct-99				0.82		0.97	**	0.3456
	Granite Point A	Oct-99			7.98	2.17	-17.42		***	0.9739
	Marshall Point	Oct-00					47.19	-0.56	*	0.9988
Male adults	Moody	Jun-99	-0.12						*	0.2231
	Granite Point A	Jun-00	-0.62			-0.06	-0.91		*	0.7878
	Barn Island	Sep-99	-1.11			-0.23			**	0.8003
	Sapowet	Sep-99			-0.23		-1.08	-0.07	*	0.7749
	Granite Point B	Sep-99	-0.32				-0.85		***	0.4869
	Granite Point A	Oct-99			0.27		-0.84		**	0.8681

Table 7 (cont.)

			Environmental Variables						Equation Statistics	
<i>F. heteroclitus</i> Category	Site	Date	Temperature (C)	Salinity (ppt)	Dissolved Oxygen (mg/l)	Depth (cm)	Log (Pool Surface Area (m ²))	Distance to Tidal Flow (m)	Overall Significance Level	Overall R ²
Female adults										
	Moody	May-99						0.26	*	0.2411
	Moody	Jun-99	-0.41						***	0.5596
	Granite Point A	Jun-00	-1.21	-0.2		-0.13	-1.1		**	0.9436
	Middlebridge	Jul-99			-0.08				***	0.6197
	Sapowet	Aug-99	0.38						*	0.3847
	Barn Island	Sep-99	-1.41			-0.31			**	0.8310
	Middlebridge	Sep-99					-3.25		**	0.4611
	Granite Point A	Sep-99	1.73						*	0.4901
	Granite Point B	Sep-99	-0.62				-1.08		**	0.3603
	Moody	Oct-99					-7.27		*	0.1856
	Granite Point A	Oct-99			0.36		-1.31		*	0.5138
	Granite Point A	Oct-00	0.67						*	0.6156

¹ Significance levels: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Table 8. Coefficients of significant variables used in "best fit" equations resulting from stepwise multiple linear regression of *F. heteroclitus* lengths versus environmental variables including elevation data.

			Environmental Variables							Equation Statistics	
<i>F. heteroclitus</i> Category	Site	Date	Relative Elevation (m)	Temper- ature (C)	Salinity (ppt)	Dissolved Oxygen (mg/l)	Depth (cm)	Log (Pool Surface Area (m ²))	Distance to Tidal Flow (m)	Overall Significance Level	Overall R ²
<u>Juveniles (<45mm)</u>											
	Moody Marsh	May-99			0.24	0.23				* ¹	0.4369
	Granite Point B	Jun-99	-38.63	-1.43			-0.2			**	0.7674
	Moody Marsh	Jun-99		-3.26		2.08				*	0.9997
	Granite Point A	Jun-00	-41.42	-4.55			0.44		0.56	**	0.9432
	Granite Point A	Jul-00		1.38	5.13	-4.28		12.5		*	0.9863
	Granite Point B	Sep-99	-22.83				0.27			**	0.4685
	Moody Marsh	Sep-99		-0.66						*	0.2450
	Granite Point A	Sep-00		-1.16		1.44				*	0.8499
	Granite Point A	Oct-99		0.92						*	0.6176
	Granite Point B	Oct-99	-16.31	2.35		1.35	0.45			*	0.5948
	Granite Point A	Oct-00	-20.46				0.32			**	0.8662
<u>Male adults</u>											
	Moody Marsh	May-99				-0.79			0.22	*	0.5758
	Moody Marsh	Oct-99				1.88		-7.90		*	0.8714
<u>Female adults</u>											
	Moody Marsh	May-99	30.67							*	0.3556
	Granite Point B	Jun-99					1.87			*	0.9960
	Moody Marsh	Jun-99						9.84		*	0.6179
	Moody Marsh	Sep-99				1.28	0.37	-7.56		*	0.5029
	Granite Point B	Oct-99	117.19					-7.06	-0.32	*	0.8623

¹ Significance levels: *, p<0.05; **, p<0.01; ***, p<0.001

Table 9. Coefficients of significant variables used in "best fit" equations resulting from stepwise multiple linear regression of *F. heteroclitus* lengths versus environmental variables *without* elevation data.

<i>F. heteroclitus</i> category	Site	Date	Environmental Variables						Equation Statistics	
			Temper- ature (C)	Salinity (ppt)	Dissolved Oxygen (mg/l)	Depth (cm)	Log (Pool Surface Area (m ²))	Distance to Tidal Flow (m)	Overall Significance Level	Overall R ²
Juveniles (<45mm)	Moody	May-99		0.21	0.23				* ¹	0.4082
	Moody	Jun-99	-3.26		2.08				*	0.9997
	Granite Point B	Jun-99	-1.8		1.42				**	0.6835
	Granite Point A	Jul-00	1.38	5.13	-4.28		12.51		*	0.9864
	Sapowet	Aug-99	1.07						*	0.5960
	Middlebridge	Sep-99			-1.37	-0.41			*	0.8813
	Sapowet	Sep-99	1.53	-0.78			-5.78	-1.45	*	0.8855
	Moody	Sep-99	-0.66						*	0.2463
	Granite Point B	Sep-99	-2.30		1.13	0.49			*	0.4996
	Granite Point A	Sep-00	-1.16		1.44				*	0.8499
	Granite Point A	Oct-99	0.93						*	0.6176
	Granite Point B	Oct-99					-3.85		*	0.2825
	Granite Point A	Oct-00				0.37	-2.79		**	0.7921
Male adults	Moody	May-99			-0.80			0.22	*	0.5757
	Barn Island	Sep-99		18.46				0.99	*	0.9992
	Sapowet	Sep-99		-0.73	3.47				*	0.9998
	Moody	Oct-99			1.88		-7.90		*	0.8714
Female adults	Moody	May-99	0.91	-0.78			-3.56		*	0.6141
	Granite Point B	Jun-99				1.87			*	0.9996
	Sapowet	Sep-99						-0.24	*	0.6720
	Middlebridge	Sep-99		-15.71					**	0.8590
	Moody	Sep-99			1.28	0.37	-7.57		*	0.5029

¹ Significance levels: *, p<0.05; **, p<0.01; ***, p<0.001

Table 10. Comparison of salt marsh pools from different regions.

Characteristic	Site					
	Iceland ¹	Isle Verte Quebec	New England		Rhode Island Bissel Cove	New Jersey
			Northern	Southern		
	<i>G.</i>	<i>G.</i>	<i>F.</i>	<i>F.</i>	<i>F.</i>	<i>F.</i>
Dominant fish species	<i>aculeatus</i> ¹	<i>aculeatus</i> ²	<i>heteroclitus</i> ⁴	<i>heteroclitus</i> ⁴	<i>heteroclitus</i> ⁵	<i>heteroclitus</i> ⁶
Total number of fish species reported	1 ¹	3 ²	7 ⁴	7 ⁴	12 (summer) ⁵	5 ⁶ , 9 ⁷
Average fish density (#/m ²)	NA	7.2 ³	12.4 ⁴	36.9 ⁴	NA	48 ⁷

1. Ingolfsson 1994.

2. Poulin and FitzGerald 1989.

3. Whoriskey et al. 1986; seine netting, n=2 pools, repeated samples, 2 years, May - July.

4. This study, 1m² throw trap, 2 years, May - October.

5. Nixon and Oviatt 1973.

6. Talbot et al. 1986.

7. Smith 1995; 0.25m² throw trap, 1 year, June - November.

Northern New England
Nekton Sampling Sites

Southern New England
Nekton Sampling Sites

Figure 1. Locus map for nekton sampling sites.

Figure 2. Average fish densities in 1999 and 2000. Significant differences within sites identified by different letters.

Figure 3. Average decapod densities in 1999 and 2000. Significant differences within sites identified by different letters.

Figure 4. Biplot of nekton species and pool physical variables for southern sites in September 1999. Species are plotted as open circles, sample pools as solid circles, in two-dimensional ordination space. Environmental variables appear as vectors; a vector's length represents the correlation between that environmental variable and the two ordination axes. The minimum vector r^2 was 0.35 for this plot. Relationships between nekton species and environmental factors should be interpreted as projections onto Axis 2 since only this axis has significant correlations to nekton species ordination space ($p=0.01$) and between nekton and the environment ($p=0.03$).

Figure 5. Biplot of nekton species and pool physical variable for northern sites in September 1999. Species are plotted as open circles with sample pools as solid circles in two-dimensional ordination space. Environmental variables appear as vectors; a vector's length represents the correlation between that environmental variable and the two ordination axes. The minimum r^2 for this biplot was 0.35. Relationships between nekton species and environmental factors should be interpreted as projections onto both Axis 2 and 3 since they both have significant correlations to nekton species ordination space ($p=0.01$, both Axis 2 and Axis 3) and between nekton and the environment ($p=0.01$, both Axis 2 and Axis 3).

Figure 6. Biplot of nekton species and pool physical variables for northern sites in summer 2000. Species are plotted as open circles with sample pools as solid circles in two-dimensional ordination space. Environmental variables appear as vectors; a vector's length represents the correlation between that environmental variable and the two ordination axes. The minimum vector r^2 for this biplot was 0.20. Relationships between nekton species and environmental factors should be interpreted as projections onto Axis 2 since only this axis has significant correlations to nekton species ordination space ($p=0.02$) and between nekton and the environment ($p=0.03$).

Figure 7. Mean values for salt marsh pool environmental variables, southern sites, September 1999, corresponding to Figure 4. Bars indicate 1 standard deviation except for water depth which is 1 standard error.

Figure 8. Mean values for salt marsh pool physical variables, northern sites, September 1999, corresponding to Figure 5. Bars indicate 1 standard deviation except for water depth which is 1 standard error.

Figure 9. Mean values for salt marsh pool environmental variables, northern sites, summer 2000, corresponding to Figure 6. Bars correspond to 1 standard deviation except for water depth which is 1 standard error.

Appendix I. List of scientific and common names.

Category	Scientific Name	Common Name
Fish¹		
	<i>Anguilla rostrata</i> (Lesueur, 1817)	American eel
	<i>Apeltes quadracus</i> (Mitchill, 1815)	fourspine stickleback
	<i>Brevoortia tyrannus</i> (Latrobe, 1802)	menhaden
	<i>Cyprinodon variegatus</i> Lacepede, 1803	sheepshead minnow
	<i>Fundulus luciae</i> (Baird, 1855)	spotfin killifish
	<i>F. majalis</i> (Walbaum, 1792)	striped killifish
	<i>F. heteroclitus</i> (Linnaeus, 1766)	mummichog
	<i>Gasterosteus aculeatus</i> Linnaeus, 1758	threespine stickleback
	<i>Lucania parva</i> (Baird & Girard, 1855)	rainwater killifish
	<i>Menidia beryllina</i> (Cope, 1866)	inland silverside
	<i>Menidia menidia</i> (Linnaeus, 1766)	Atlantic silverside
	<i>Pungitius pungitius</i> (Linnaeus, 1758)	ninespine stickleback
Decapods²		
	<i>Callinectes sapidus</i> (Rathbun, 1896)	blue crab
	<i>Carcinus maenas</i> (Linnaeus, 1758)	green crab
	<i>Palaemonetes pugio</i> (Holthuis, 1949)	daggerblade grass shrimp
	<i>Crangon septemspinosa</i> Say, 1818	seven-spined bay shrimp

¹ Robins et al. 1991.

² William et al. 1989.

Appendix II. Average nekton length (mm) by species, site, and sample date.

Nekton category and site		Months Sampled												
<i>F. heteroclitus</i>														Significance
juveniles	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	Level	
Barn Island	x ¹	x	x	28.2	30.8	x	x	x	x	x	x	x	NS	
stdev(no. pools)				4.9(6)	9.0(9)									
Middlebridge	x	x	27.7 a ²	x	36.5 b	x	x	x	x	x	x	x	*** ³	
stdev(no. pools)			3.7(12)		2.7(7)									
Sapowet	x	x	x	27.7 a	30.6 b	x	x	x	x	x	x	x	*	
stdev(no. pools)				2.2(8)	2.5(10)									
Moody marsh	40.0 a	20.4 b	x	x	34.4 c	33.4 c	x	x	x	x	x	x	***	
stdev(no. pools)	2.2(20)	7.6(4)			4.5(25)	5.7(19)								
Marshall Point	-- ⁴	15.3 a	x	x	25.8 b	27.3 b	--	24.3 a,b	x	x	33.0 b	27.8 b	*	
stdev(no. pools)		(1)			1.5(2)	3.5(3)		(1)			1.5(2)	(1)		
Granite Point A	x	22.4 a	x	x	32.6 b,e	30.4 c,e	x	17.4 d	28.9 c,e	x	30.2 e	29.0 e	***	
stdev(no. pools)		2.5(4)			3.2(8)	2.5(7)		4.3(9)	3.0(7)		2.2(8)	3.6(9)		
Granite Point B	x	22.1 a	x	x	32.3 b	33.4 b	x	x	x	x	x	x	***	
stdev(no. pools)					4.7(29)	5.2(17)								
<i>F. heteroclitus</i> adult males														
Barn Island	x	x	x	56.1	44.1	x	x	x	x	x	x	x	NS	
stdev(no. pools)				7.6(2)	16.1(4)									
Middlebridge	x	x	--	x	56.9	x	x	x	x	x	x	x	no model	
stdev(no. pools)					8.0(5)									
Sapowet	x	x	x	--	53.9	x	x	x	x	x	x	x	no model	
stdev(no. pools)					5.5(4)									
Moody marsh	48.6 a	51.7 a,b	x	x	58.9 b	55.3 b	x	x	x	x	x	x	*	
stdev(no. pools)	3.0(15)	10.4(3)			8.4(9)	6.9(6)								

Appendix II (cont.)
Nekton class and site

	Months Sampled												Significance
	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	Level
Marshall Point	--	--	x	x	--	--	46.0	--	x	x	46.0	--	no model
stdev(no. pools)							(1)				(1)		
Granite Point A	x	--	x	x	53.0	53.0	x	56.0	60.6	x	--	45.0	NS
stdev(no. pools)					0.0(2)	(1)		5.7(2)	(1)			(1)	
Granite Point B	x	56.0	x	x	49.3	52.2	x	x	x	x	x	x	NS
stdev(no. pools)		(1)			5.4(13)	4.9(8)							
<i>F. heteroclitus</i> adult females													
Barn Island	x	x	x	55.4	47.7	x	x	x	x	x	x	x	NS
stdev(no. pools)				14.7(2)	2.0(2)								
Middlebridge	x	x	45.0	x	53.7	x	x	x	x	x	x	x	NS
stdev(no. pools)			(1)		7.4(6)								
Sapowet	x	x	x	46.7	50.5	x	x	x	x	x	x	x	NS
stdev(no. pools)				2.1(3)	3.9(6)								
Moody marsh	52.2	53.2	x	x	53.2	49.1	x	x	x	x	x	x	NS
stdev(no. pools)	4.6(17)	5.9(8)			9.2(16)	3.6(12)							
Marshall Point	53.0	--	x	x	--	--	--	50.0	x	x	68.0	--	no model
stdev(no. pools)	(1)							(1)			(1)		
Granite Point A	x	--	x	x	49.2 a	44.7 a	x	49.0 a	55.6 a	x	45.0 a	70.5 b	*
stdev(no. pools)					2.5(2)	6.6(2)		(1)	(1)		0.0(3)	(1)	
Granite Point B	x	61.0 a	x	x	53.7 a,b	48.2 b	x	x	x	x	x	x	*
stdev(no. pools)		12.5(3)			8.1(17)	3.8(8)							

Appendix II (cont.)
Nekton class and site

Months Sampled

													Significance
<i>A. rostrata</i>	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	Level
Granite Point B	x	55.3	x	x	--	--	x	x	x	x	x	x	NA
stdev(no. pools)		66.8(2)											
<i>A. quadracus</i>													
Marshall Point	--	--	x	x	--	--	29.1	--	x	x	--	--	NA
stdev(no. pools)							(1)						
Granite Point A	x	21.0	x	x	--	--	x	--	--	x	28.0	--	no model
stdev(no. pools)		(1)									(1)		
<i>B. tyrannus</i>													
Granite Point B	x	--	x	x	58.0	--	x	x	x	x	x	x	NA
stdev(no. pools)					(1)								
<i>C. variegatus</i>													
Barn Island	x	x	x	24.4	26.7	x	x	x	x	x	x	x	NS
stdev(no. pools)				5.6(3)	6.5(9)								
Middlebridge	x	x	22.6	x	26.7	x	x	x	x	x	x	x	NS
stdev(no. pools)			6.7(13)		5.9(13)								
Sapowet	x	x	x	26.8	28.9	x	x	x	x	x	x	x	NS
stdev(no. pools)				5.4(7)	3.7(9)								
<i>F. luciae</i>													
Barn Island	x	x	x	35.0	35.0	x	x	x	x	x	x	x	NS
stdev(no. pools)				(1)	0.1(2)								

Appendix II (cont.)
Nekton class and site

<i>F. majalis</i>	Months Sampled												Significance
	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	Level
Middlebridge	x	x	20.4	x	47.0	x	x	x	x	x	x	x	NS
stdev(no. pools)			(1)		5.7(2)								
<i>G. aculeatus</i>													
Moody marsh	30.4	--	x	x	--	--	x	x	x	x	x	x	NA
stdev(no. pools)	20.8(5)												
Marshall Point	23.8	--	x	x	--	--	--	--	x	x	--	--	NA
stdev(no. pools)	(1)												
Granite Point A	x	--	x	x	--	--	x	19.7	--	x	--	28.0	NS
stdev(no. pools)								4.3(2)				(1)	
<i>L. parva</i>													
Barn Island	x	x	x	--	25.0	x	x	x	x	x	x	x	NA
stdev(no. pools)					3.4(4)								
Middlebridge	x	x	--	x	24.1	x	x	x	x	x	x	x	NA
stdev(no. pools)					1.9(7)								
Sapowet	x	x	x	20.0	25.2	x	x	x	x	x	x	x	NS
stdev(no. pools)				(1)	3.2(8)								
<i>M. beryllina</i>													
Barn Island	x	x	x	--	35.0	x	x	x	x	x	x	x	NA
stdev(no. pools)					(1)								
Sapowet	x	x	x	--	(1)	x	x	x	x	x	x	x	NA
stdev(no. pools)													
Granite Point A	x	--	x	x	32.8	--	x	--	--	x	--	--	NA
stdev(no. pools)					(1)								

Appendix II (cont.)
Nekton class and site

	Months Sampled												Significance
	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	Level
<i>M. menidia</i>													
Barn Island	x	x	x	--	37.8	x	x	x	x	x	x	x	NA
stdev(no. pools)					3.9(2)								
Middlebridge	x	x	29.5 a	x	38.1 b	x	x	x	x	x	x	x	**
stdev(no. pools)			1.3(4)		4.5(6)								
Sapowet	x	x	x	38.0	35.2	x	x	x	x	x	x	x	NS
stdev(no. pools)				(1)	3.7(2)								
Moody marsh	--	55.0	x	x	69.8	--	x	x	x	x	x	x	no model
stdev(no. pools)		(1)			(1)								
Granite Point A	x	--	x	x	--	--	x	26.0	38.0	x	--	--	NS
stdev(no. pools)								14.1(2)	(1)				
Granite Point B	x	31.1	x	x	50.0	--	x	x	x	x	x	x	NS
stdev(no. pools)		8.7(3)			11.3(2)								
<i>P. pugitius</i>													
Moody marsh	--	--	x	x	41.0	47.8	x	x	x	x	x	x	NS
stdev(no. pools)					1.4(2)	4.6(2)							
Marshall Point	27.0	--	x	x	--	--	32.2	--	x	x	34.4	--	no model
stdev(no. pools)	(1)						(1)				(1)		
Granite Point A	x	--	x	x	41.0 b,c	43.7 b	x	28.5 a	33.8 a	x	35.5 a,c	40.8 b	**
stdev(no. pools)					(1)	3.2(3)		(1)	1.6(4)		2.8(3)	1.8(2)	
Granite Point B	x	--	x	x	37.8 a	42.9 b	x	x	x	x	x	x	*
stdev(no. pools)					3.1(8)	3.7(5)							

Appendix II (cont.)
Nekton class and site

C. sapidus ⁵	Months Sampled												Significance
	May-99	Jun-99	Jul-99	Aug-99	Sep-99	Oct-99	May-00	Jun-00	Jul-00	Aug-00	Sep-00	Oct-00	Level
Barn Island	x	x	x	--	15.0	x	x	x	x	x	x	x	NA
stdev(no. pools)					(1)								
Middlebridge	x	x	35.3	x	--	x	x	x	x	x	x	x	NA
stdev(no. pools)			37.1(2)										
<i>C. maenas</i> ⁵													
Barn Island	x	x	x	45.0	--	x	x	x	x	x	x	x	NA
stdev(no. pools)				(1)									
Sapowet	x	x	x	--	30.0	x	x	x	x	x	x	x	NA
stdev(no. pools)					0.0(2)								
Moody marsh	19.2	25.3	x	x	28.7	19.6	x	x	x	x	x	x	NS
stdev(no. pools)	5.0(6)	5.6(9)			3.2(3)	17.3(5)							
Granite Point A	x	31.0 a	x	x	39.8 b	13.0 c	x	--	24.2 d	x	40.8 b	10.0 c	***
stdev(no. pools)		(1)			2.3(3)	(1)			2.8(3)		1.1(2)	(1)	
Granite Point B	x	23.8	x	x	36.4	26.9	x	x	x	x	x	x	NS
stdev(no. pools)		4.0(6)			7.5(2.3)	15.9(5)							

¹ No trapping on this date.

² Significant differences between months within a site are signified by different lower case letters.

³ Significance levels: NA, not applicable; NS, not significant; 'no model' indicates sample size too small for testing; *, p<0.05; **, p<0.01; ***, p<0.001.

⁴ Trapping conducted, species not in sample or length data not available.

⁵ Crab size reported as maximum carapace width.

Chapter 4:
Initial Effects of
Surface Water Habitat Enhancement Efforts
on Nekton Use of Salt Marsh Pools

ABSTRACT

Ditched New England salt marshes have fewer pools (steep-sided, permanently flooded depressions) than unditched marshes. Ditch plugging, a form of open marsh water management, was employed at three marshes on the Rachel Carson National Wildlife Refuge in southern Maine, USA, to increase surface water habitat and thus fish and wildlife use. A BACI (Before-After-Control-Impact) study design was used to assess the initial effects of ditch plugging on pool nekton populations. Throw-trap sampling indicated a total of 7 fish and 3 decapod species used pools; *Fundulus heteroclitus* was the dominant species at each site accounting for 89% of all fish caught. After controlling for natural variation through the BACI design, few changes in nekton use were attributed to the effects of ditch plugging. Nekton community remained unaltered at Moody and Granite Point as did total fish density. Species richness, however, decreased at Granite Point experimental area (12 – 9 species, $p < 0.001$). The physical barriers created by ditch plugs and reduced fish access are thought to be responsible. Estimates of total fish abundance indicated a possible decrease in fish density; direct monitoring of plugged ditches is recommended to resolve this with other density measures. “Before” data were not available for the Marshall Point study site. Comparisons of the experimental area (where all pools had been created) to an adjacent control indicated substantial increases in pool habitat and nekton use. Both fish and decapods occupied newly created pools within weeks, and within months nekton densities were not different from those in old pools at Marshall Point or Moody marsh. Comparisons of old, enlarged, and newly created pools at Granite Point indicated greater nekton use (species richness, density, *F. heteroclitus* length) in old pools. This

study documents only initial nekton responses to ditch plugging; additional monitoring is necessary to ensure achieving management goals.

INTRODUCTION

Salt marshes are intertidal vegetated habitats that occur along much of the New England shoreline (Chapman 1960). They are considered one of the most productive ecosystems in the world (Whittaker, 1975) and are thought to be important to estuarine and nearshore production (Nixon and Oviatt 1973, Valiela 1995, although see Nixon 1980). Salt marshes, however, are also known as mosquito breeding areas and the serious diseases that mosquitoes sometimes carry have made their control a public policy issue. With the aid of the Civil Works Program during the 1930's, nearly 90% of the coastal marshes from Maine to Virginia were ditched in order to drain mosquito-breeding areas (Bourn and Cottam 1950). Some ditching was also done during Colonial times and afterwards to facilitate salt hay farming (Daiber 1986, Rozsa 1995).

Ditching has affected marshes far beyond the original intents of agricultural improvements and mosquito control. Miller and Egler (1950) in their study of a Connecticut salt marsh gave this scathing review, "...ditching, at best a violent activity which, though it destroys the mosquitoes, also destroys the permanent pools so valuable to wildlife, completely rearranges the mosaic of natural plant communities, and eventually produces other pools of the same kind that the ditches were designed to eliminate." Adamowicz (Chapter 1) quantified the high correlation between ditching intensity (m of ditch/ha marsh) and reduction of salt marsh pools. Clarke et al. (1984)

and Wolfe (1996) reviewed numerous articles describing the deleterious effects of ditching on wildlife ranging from invertebrates to birds.

Despite the difficulties attendant with ditching, alternative mosquito control measures such as the application of pesticides, have proven less desirable. It was in this milieu that another method, Open Marsh Water Management (OMWM), came into use during the second half of the last century (Ferrigno and Jobbins 1968). It was determined that OMWM could be used not only to control mosquitoes by providing larvivorous fish access to mosquito breeding areas, but also to enhance fish and wildlife habitat (Wolfe 1996).

Following this reasoning, in 1998 the US Fish and Wildlife Service began an intensive salt marsh management program at Rachel Carson National Wildlife Refuge in southern Maine. The objective was to employ ditch plugging (a form of OMWM) to restore pools and other low-lying areas that had been drained (Taylor 1998). Ditch-plugging involves inserting marine plywood across a ditch, usually near the mouth where the ditch joins a natural creek, then surrounding the plywood with peat excavated from the surface of the marsh. The peat is packed down and water is allowed to back-flood behind the plug. In this process, several types of pools are created: basins from which peat had been excavated to form the plug, drained pools that now retain water, portions of ditches now back-flooded behind plugs, formerly existing pools that were enlarged through peat excavation, and formerly existing ("old") pools. The purpose of the current study is to evaluate the effect of ditch plugging on nekton use of altered and controlled sites as well as to compare nekton use of old, enlarged, and newly created pools.

METHODS

Study Site

The Rachel Carson National Wildlife Refuge is located along the coast of southern Maine, USA. Three locations were identified by resource managers for application of the ditch-plugging technique (Figure 1): Moody marsh in Wells (N43° 16.01' W70° 35.55'); Marshall Point in Cape Porpoise (N43° 22.75' W70° 25.99'); and Granite Point in Biddeford, Maine (N43° 24.89' W70° 23.35'). These sites are typical New England salt marsh complexes (Nixon 1982, Chapman 1960) with *Spartina patens*, *Juncus gerardii*, and *Distichlis spicata* in the high marsh, while *Spartina alterniflora* occupies low marsh positions.

BACI Study Design

Each study site was divided into a control and experimental area as part of a BACI (Before-After-Control-Impact) study design (Stewart-Oaten et al. 1986). Control refers to areas unaltered during the course of the study while impact (i.e. experimental) areas were ditch-plugged. Control areas at Granite Point and Marshall Point (Figures 2 and 4) were contiguous sections of marsh set at a short distance from experimental areas. At Moody marsh, the control area was established in the portion of the marsh downstream of ditch plugs (Figure 3). This situation was not ideal for a control but adjacent marsh areas previously had been altered with berms and road crossings or were

not owned by the Rachel Carson National Wildlife Refuge and so were precluded from use as controls.

Salt marsh pools at both control and impact areas at each of the three marshes were sampled nearly monthly from May – October in 1999 and again in 2000. During April 2000, ditch plugs were installed at Moody marsh and from May – June 2000 at Granite Point. Thus sampling occurred at these sites “Before” ditch plugging and “After.” Marshall Point had been ditch-plugged in the fall of 1998 prior to project initiation but it was sampled in 1999 and 2000 to provide a longer time frame for assessing “After” conditions. Sampling during 2000 was carefully timed to occur on the same portion of the tidal cycle as sampled in 1999. If a study area had less than 20 pools, they were all sampled; otherwise up to 29 pools were randomly selected. The number of sample pools at the Granite Point and Moody experimental areas was increased in 2000 in order to monitor newly created pools. The numbers of pools sampled on each survey date and at each site are given in Table 1.

Pool Sampling

Salt marsh pool sampling included measurement of pool physical parameters, water quality conditions (salinity, temperature, dissolved oxygen), and nekton species composition and abundance. Nekton was sampled at salt marsh pools using a 1-m² throw trap with 3mm mesh sides (Rozas and Minello 1997). Trap construction and sampling technique followed that of Raposa (2000).

Trapping was initiated once high tide had receded from a marsh and fish were restricted within pools. Samples were obtained by slowly crossing the marsh surface to

a randomly selected station on a pool's perimeter then tossing the trap 3-4 m through the air into the water while still at a distance from the pool edge. After landing in the pool, the trap was rapidly pushed further into the sediment so as to prevent animals from escaping from under the bottom of the trap frame. All animals were removed from the trap using a 1 m x 0.5 m dip net (3mm mesh) that fit snugly into the trap. Dip netting was conducted from at least 3 sides of the trap. Traps were considered empty when 3 consecutive uses of the dip net obtained no nekton. Captured nekton were identified to species, measured (total length for fish, carapace width for crabs), and immediately released. Variables recorded included species, abundance, and individual organism lengths (up to 30 individual for each species). Water quality measures obtained with a YSI-85 hand-held dissolved oxygen meter included dissolved oxygen (mg/l), salinity (ppt), and temperature (C). Water depth was recorded from 3 sides of a deployed throw-trap using a meter stick. Pool size (m^2) was estimated by measuring the major and minor axes of regularly shaped pools (Ingolfsson 1994) and applying the formula of an ellipse. Irregularly shaped pools were subdivided into simple geometric shapes, with appropriate data taken to calculate surface area. All pool sizes were re-measured following ditch plugging and whenever water levels expanded or contracted the pools from their well-defined margins. Distances of pools to nearest tidal flow (creeks, open ditches, estuarine shoreline) were measured with a standard metric survey tape. Further details of methodologies are provided in Adamowicz (Chapter 3).

Statistical Analyses

Differences in nekton community were analyzed using the PRIMER non-parametric randomization tests of similarity (Clarke and Warwick 1994, Roman et al. in press) applied to a similarity matrix calculated from the Bray-Curtis similarity index. An analysis of similarities test (ANOSIM) was used to detect differences between groups of pools in the BACI design ("Before-Control, After-Control, Before-Impact, After-Impact) for each site. Contributions of individual nekton species to dissimilarities between groups were calculated using percent similarity tests (SIMPER). It should be noted that for all the BACI comparisons, regardless of statistical test used, the data sets were limited to containing sampling from the same months in both years (May, June, September, October).

At Granite Point and Moody marsh, changes in nekton densities and sizes were assessed with ANOVA with least squared means (LSMeans, SAS 1985) post-hoc testing of the interaction term (site x time). In a BACI design, there is a time element between "Before" and "After." One might argue that the difference between "Before" and "After" was simply due to time. Thus the interaction term was used to examine the change from "Before" to "After" at the control area and compare it with the change from "Before" to "After" for the impact (experimental) area. If the interaction term was not significant, then natural variability was considered the cause of change rather than the site alterations.

Testing the interaction term also was used to compare physical (e.g. water depth, pool size) and water quality data (e.g. salinity, dissolved oxygen). Nekton densities

were square root transformed ($\sqrt{(x+0.5)}$) and pool sizes were log transformed ($\log(x+1)$) prior to analyses in order to achieve normality (Sokal and Rohlf 1981).

A comparison of species richness among the BACI groups for each site was made using the jack-knife estimate procedure of Heltshe and Forrester (1983). In order to test for the interaction term a modified t-test was used as noted below:

$$t = \frac{|S_{bc} - S_{bi} - S_{ac} + S_{ai}|}{(s_{bc}^2/n_{bc} + s_{bi}^2/n_{bi} + s_{ac}^2/n_{ac} + s_{ai}^2/n_{ai})^{0.5}}$$

where

S_{bc} is the jack-knife estimate of species richness for the "Before-Control" group, (similarly the subscripts bi = "Before-Impact"; ac = "After-Control"; ai= "After-Impact"),

s_{bc}^2 is the jack-knife estimate of the square of the standard error $((se)^2)$ of S_{ij} ,

the decision rule is to reject H_0 if $|t| > t_{\alpha/2, n_{bc} + n_{bi} + n_{ac} + n_{ai} - 4}$.

At Marshall Point, comparisons were made between the control and experimental sites during 1999 and 2000 through ANOVA and post-hoc LS Means testing. An interaction term was not used in the ANOVA model for Marshall Point.

The effect of pool type (old, enlarged, new) on nekton species richness, density, nekton size, and pool characteristics was determined by t-tests and ANOVA/ LSMeans testing as appropriate.

GIS/GPS Mapping

The total amount of surface water at each study area was determined through geographic information system (GIS) and global positioning system (GPS) techniques. Pre-ditch-plugging conditions were mapped by scanning aerial ortho-photographs at 600 dots per inch. Photograph dates and scales are as follows: Moody marsh 1992 (1:8000), Marshall Point 1992 (1:8000), Granite Point 1986 (1:2400). The scanned images were georectified with Erdas Imagine 8.4 (geometric correction module) in conjunction with GPS-ed ground control points and were fitted with a polynomial function. ArcView (version 3.2) software was used to map pools and ditches on the imported images. Post-plugging conditions were mapped in the field in 2001 using a Trimble Pathfinder with differential correction resulting in sub-meter post-processing accuracy. Site and individual pool areas were determined in ArcView. The level of accuracy obtained by GIS mapping, however, could not match that of field surveying with the GPS unit; for example, field mapping recognized connections between pools that were not visible on the aerial photographs. As a result, only broad comparisons were made between total pool surface area at each site and not on individual pool sizes. Clearly it would have been preferable to GPS the study areas and their pools in conjunction with the nekton sampling.

Total Fish Abundance Calculations

Changes in total fish abundance in the "Before" and "After" experimental areas were calculated two ways. First, the average fish density for all pools was multiplied by the total surface water area (pools and plugged ditches) based on September 1999 and

September 2000 nekton data at Granite Point and Moody marsh. September data were used since it represented the peak summer abundance. Surface water area used was that calculated from aerial photographic ("Before") and GPS ("After") mapping. Resulting "Before" – "After" differences in total fish abundance were expressed as a percent increase or decrease relative to the total fish abundance of both years. Second, the same method (surface water area x average fish density) was applied to all sample months during the "Before" and "After" periods. Monthly averages from 1999 and 2000 were subjected to paired t-testing. Data at Marshall Point was similarly subjected to paired t-testing, although groups were control versus experimental areas paired by month for 2000 data. All data were $\log(x+1)$ transformed prior to analysis to achieve normality (Sokal and Rohlf 1981).

RESULTS

Throw-trap sampling was initiated in May 1999 with 4 sample periods through October, resuming in May of 2000 with 5 sampling periods through October of that year. A total of 244 throw-trap samples was taken in 1999 and 395 in 2000 (Table 1). Seven fish and 3 decapod species were sampled in the two years (Table 2). Of the 7822 fish caught over the course of the study, 89% were *F. heteroclitus* (mummichog); the next most common fish was *P. pungitius* (nine-spine stickleback) at 7%. *Apeltes quadracus* (four spine stickleback), *Anguilla rostrata* (American eel), and *Brevoortia tyrannus* (menhaden) were the least common fish species. Among the decapods, *Palaemonetes pugio* (daggerblade grass shrimp) was most common overall accounting

for 54% of the 666 decapods caught. A complete list of scientific and common names is given in Appendix Table I.

“Before” and “After” Comparisons at Granite Point and Moody Marsh

At Granite Point, the nekton community remained unchanged in both control and experimental area pools from before to after ditch plugging ($p > 0.05$, both, ANOSIM). The same results were obtained for Moody marsh (Table 3). Similarly total fish and total decapod densities at Granite Point were not altered due to ditch plugging ($p > 0.05$, both; ANOVA). Again, the same results occurred at Moody marsh (Table 3, Appendix II).

Despite these similarities between “Before” and “After” conditions at the two study sites, there were some differences. Species richness decreased by 3 species at the Granite Point experimental area (Bonferroni adjusted alpha 0.025, $p < 0.001$, Table 3) despite an increase of 5.9 species at the control area. At Moody marsh there was no change in species richness due to ditch plugging ($p > 0.05$, Bonferroni adjusted alpha 0.025, Table 3).

At both Moody marsh and Granite Point, there were few differences among the BACI comparisons when the data were evaluated for each species. Of the 10 nekton species sampled at Granite Point and Moody marsh, there were no significant changes in nekton sizes among the BACI comparisons for each site. Density changes occurred in only 2 individual species. *F. heteroclitus* juveniles density decreased by 5.4 fish/m² at the Moody experimental area despite no significant change in the control area (Appendix II). At Granite Point, the only individual species that changed from the

“Before” to “After” condition was *P. pugio* which decreased significantly at pools in the control area ($p < 0.05$, ANOVA, Appendix II).

Marshall Point Control and Experimental Area Comparisons

Since the Marshall Point site was ditch plugged prior to this project, it is only possible to compare the experimental and control areas for the 2 years following plug installation. Additionally, since all the pools at the experimental site were created, it is assumed that whatever nekton occurred in created pools was a result of the site alteration.

Nekton communities between the control and experimental areas began the same, but differed over time. In 1999, the nekton community was the same between experimental and control area pools ($p > 0.05$, ANOSIM) but not in 2000 ($p < 0.05$, ANOSIM). The species most responsible for differences in the experimental and control area in 2000 were *F. heteroclitus* (39%), *C. maenas* (22%), and *P. pugio* (8%) in the experimental area and the sticklebacks *P. pungitius* (20%) and *A. quadricus* (8%) in the control area (Table 4).

Experimental area nekton communities also differed between 1999 and 2000 ($p < 0.01$, ANOSIM). The majority of the difference (57%) was due to greater *F. heteroclitus* density in 1999. The three other species, *C. maenas*, *P. pungitius*, and *P. pugio*, all had greater densities in 2000 (Table 4).

Marshall Point control and experimental areas also differed in almost all other measures of nekton use (Table 5). Experimental area pools had greater species richness

($p < 0.001$, both years; Bonferroni adjusted alpha 0.025; t-test), total fish density ($p < 0.001$, 1999; ANOVA), and total decapod density ($p < 0.001$, both years; ANOVA).

Individual species density patterns reflected that of total density. *F. heteroclitus* juveniles (and *F. heteroclitus* overall) were denser at control area pools in 1999 but not in 2000 ($p < 0.001$, ANOVA; Appendix II). *C. maenas* was also denser in experimental area pools in 1999 and 2000 compared to control area pools ($p < 0.001$, ANOVA; Appendix II). *P. pugio* and *C. maenas* densities increased in experimental area pools from 1999 to 2000 ($p < 0.05$, $p < 0.001$, respectively; ANOVA) while *F. heteroclitus* densities fell during the same time period ($p < 0.001$; ANOVA). In terms of nekton size only *C. maenas* were larger in experimental area pools in 2000 compared to 1999 ($p < 0.05$, ANOVA; Appendix III).

Environmental Conditions

Following ditch plugging, the only pool environmental parameter that changed was distance to tidal flow (Table 6). At the Moody experimental site, this distance increased 7.4 m after ditch plugging, while at the Granite Point experimental area, the increase was 21.2 m. Distance to tidal flow values remained the same at the associated control areas ($p > 0.05$, both; ANOVA, Appendix IV). All other environmental parameters (water temperature, salinity, dissolved oxygen, water depth, and pool size) remained constant among the BACI comparisons (Table 6, Appendix IV).

At Marshall Point (Table 7), again there were no pools at the experimental area prior to ditch plugging. After ditch plugging, however, experimental area pools, on average, were only 5 m from tidal flow compared to over 50 m at the control area. In

2000, experimental area pools were 4.7 C cooler ($p < 0.001$, ANOVA), 5 ppt more saline ($p < 0.01$, ANOVA), and nearly 8 m² larger ($p < 0.05$, ANOVA) than control area pools. Experimental area pools, however, decreased in size from 1999 to 2000 ($p < 0.05$; ANOVA; Appendix IV).

Comparisons of Old, Enlarged, and New Pools

The excavation of new pools and enlargement of existing pools in the experimental areas of Moody marsh and Granite Point allowed a comparison of new, enlarged, and old (pre-existing) pools during 2000. New and enlarged pools at Moody marsh were excavated during April 2000 with sampling beginning in May 2000. At Granite Point, pools were excavated during May – June 2000 with sampling beginning once equipment left the site in June 2000. At both sites, there was greater species richness in the old pools ($p < 0.01$), with an equal or intermediate number at enlarged pools, and the lowest values in new pools (Table 8). Nekton densities were also greater at old pools for 7 of 8 species where there were differences (Granite Point, Table 9). Interestingly, there was only one difference in species density at Moody; *C. maenas* density was greatest at enlarged pools ($p < 0.05$, Table 9). In terms of nekton size, only *F. heteroclitus* juveniles and *F. heteroclitus* overall differed among pool types, being larger in old pools at Granite Point (Table 10).

While attempts were made to control for pool size and distance to tidal flow, at Granite Point, enlarged pools were both larger and further from tidal flow than old or new pools ($p < 0.001$, $p < 0.01$, respectively; Table 11). The exceptional average size of enlarged pools was due in part to the fact that contractors expanded already large pools.

At Moody marsh, there was no difference in pool size among the three pool types; however, old pools were 12.2 m further from tidal flow than new pools ($p < 0.01$, Table 11). Interestingly, at both sites new pools were 15 – 20 cm shallower compared to old or enlarged pools ($p < 0.001$ for both sites).

Habitat Availability and Total Fish Abundance

Maps of pre-existing and post-plugging surface water are provided in Figures 2 - 6. The total area of surface water (pools and plugged ditches) for each site and study area are listed in Table 12. Percent of marsh occupied by surface water increased for the experimental sites following ditch plugging ($p < 0.05$, t-test), while the control sites remained the same ($p > 0.05$, t-test). Plugged ditches constituted the majority of new surface water at each site followed by new pools and enlarged pools (Table 13).

Total fish abundance (average fish density per month $\times$ total surface water habitat area) did not vary from Before to After for either Moody marsh or Granite Point. Paired t-tests (sample months in each year as a pair) did not result in differences for “Before” versus “After” conditions at the Moody experimental area ($p > 0.05$, $n=4$) and there was no change in control area pools over the same period ($p > 0.05$, $n=4$). The same results held for Granite Point: there was no change in total fish abundance at either the experimental ($p > 0.05$, $n=3$) or control area pools ($p > 0.05$, $n=3$) from before to after ditch plugging. Similarly, there were no differences in decapod total abundances at Moody or Granite Point experimental areas (both $p > 0.05$; $n=4$, $n=3$, respectively; paired t-test) or at their controls. At Marshall Point, however, fish and decapod total abundances both were significantly greater at the Marshall Point experimental area in

2000 ($p < 0.01$, $n=4$, paired t-tests) compared to control area pools due to the greater area of surface water and the higher nekton densities at the experimental area compared to the control.

Using just September fish densities, however, total fish abundance at the Moody experimental area declined by 12% from the "Before" to the "After" condition. In contrast, total fish abundance was 13% greater in the "After" (versus "Before") condition at Granite Point experimental area pools. Over the same time, total fish abundances increased from 9 – 11% at the Moody and Granite Point control areas, respectively.

DISCUSSION

The success of ditch plugging efforts should be assessed using a variety of indicators. Nekton use is one category of such indicators and is particularly beneficial on two levels. First, nekton has been shown to respond quickly to salt marsh alterations (Burdick et al. 1997, Able et al. 2000, Roman et al. in press). Second, nekton use integrates a number of other factors such as water quality and food availability (Fell 2000). Thus initial levels of nekton use can be used as an early indicator of habitat function.

Nekton Community and Density Measures

Given the rapid response of nekton in other salt marsh projects where tidal flow had been restored (Burdick et al. 1997, Able et al. 2000, Roman et al. in press), it was

surprising to find very little change in nekton use of pools at Moody marsh and Granite Point following ditch plugging. At these two Maine sites nekton community, total fish density, and total decapod density (Table 3) were not influenced by ditch plugging. A possible explanation for this apparent inconsistency may lie in the different types of marsh alteration – restoration of tidal flow versus ditch plugging.

Upon restoration of tidal flow to a marsh where it had been severely restricted, Raposa (2000) found that *F. heteroclitus* followed the leading edge of water into the most upstream portions of newly created tidal channels. In this case it was both the restoration of tidal flow and fish behavior that resulted in increased nekton use in the recovering marsh.

Experimental area pools in this study, however, differ from the tidally restored marsh just described in 2 important ways. First, except for distance to tidal flow, average environmental conditions (dissolved oxygen, salinity, temperature, water depth; Table 6) across experimental area pools did not change as a result of ditch plugging. Secondly, not only were nekton present in these pools prior to ditch plugging, but significantly, the dominant species, *F. heteroclitus*, overwintered in the pools and thus already were present (unaffected by ditch plugging) and able to spawn and produce the juveniles that were sampled in the following weeks and months. While these two factors can account for a lack of an initial change in nekton use of pools, several nekton parameters (species richness, *F. heteroclitus* juvenile density, and total fish abundance) did vary indicating effects that may become more prominent over a longer span of time.

Species Richness

While at least some *F. heteroclitus* successfully overwintered in pools and provided a starting population for the post-plug sampling period, other species are known to overwinter in deeper waters outside the marsh (Conover and Ross 1982, Whoriskey et al. 1986, Whoriskey and FitzGerald 1989, Able and Fahay 1998). Due to the relatively low numbers of these other species, impacts associated with ditch plugging would not necessarily be seen in density measures (Table 5, Appendix II) but were detected by the presence/absence-based measure of species richness.

After controlling for natural variability through the BACI design, species richness decreased at the Granite Point experimental area while there was no change at Moody marsh (Table 3). These opposing trends can be resolved by understanding how fish gain access to salt marsh pools and by comparing alterations at both sites. Just as other studies have documented a rapid increase in nekton following removal of tidal barriers (Simenstad and Thom 1996, Burdick et al. 1997, Able et al. 2000, Roman et al. in press), the rapid decrease in species richness at the Granite Point experimental area may be a result of imposing tidal barriers. The ditch plugs used in Maine salt marshes were up to 0.3 m above the marsh surface and extended across the marsh for several meters by small berm "wings." Thus ditch plugs created a physical barrier to nekton movement onto the marsh in addition to their designed capacity to retain water.

Neill and Turner (1987) and Herke et al. (1992) documented that canal plugging and low-level weirs in Louisiana decreased fish movement to and from marshes. Both obstructions resulted in decreased numbers of migrant species using the marshes and could account for the declined species richness at Granite Point. But why wasn't there

also a decline at Moody? In the Louisiana papers, the canal plugs and weirs were placed at the primary access points where tidal flow (and fish) entered the study areas. At the Maine study sites, each marsh had a long interface (through ditches, creeks, and shoreline) with tidal flow.

Since fish gain access to the salt marsh surface (and thence to pools) through creeks and channels on flood tides (Kneib 1984, Rozas et al. 1988), elimination of these tidal interfaces denies fish ready access to the marsh interior. Ditch plugging eliminates from the tidal interface that portion of a ditch lying upstream from a plug. At Moody marsh, ditch plugs obstructed only 19% of the site's original tidal interface. In most instances, plugs were placed close to breached pools leaving most of the northern, eastern, and a third of the southern tidal interfaces unaltered (Figure 3). This evidently was sufficient to maintain species richness. At Granite Point, however, the experimental area had an extensive network of ditches (Figure 2) and ditch plugging eliminated 51% of the original tidal interface. This large decrease in conjunction with the physical obstruction of plugs and "wings" along portions of the remaining interface could account for the decreased nekton species richness in the Granite Point experimental area.

Another obstacle to nekton use of pools was indicated by the distance to tidal flow. At both the Moody and Granite Point experimental areas, this distance was much greater after ditch plugging. At Granite Point, however, the value was nearly twice that found at Moody (Table 6).

F. heteroclitus Juvenile Density and Total Fish Abundance

One full season after ditch plugging, *F. heteroclitus* juvenile density at Moody experimental area pools decreased relative to the “Before” condition. This decrease was interpreted as the result of ditch plugging after controlling for natural variability using the BACI design. *F. heteroclitus* densities may have decreased by spreading out across newly created pools and plugged/flooded ditches.

In fact, that total fish abundance did not increase either at Moody or at Granite Point despite the increase in habitat area (Table 12) suggests that the new habitat areas could be “diluting” the existing population of fish on the marsh. Nekton use of plugged ditches was not evaluated in this study, but would be a useful addition to pool sampling to determine more definitively whether ditch plugging increases total fish numbers on the entire marsh. This is a particularly important matter since one of the motivations of the marsh project was to enhance bird foraging habitat. Steady or decreased total fish abundances despite increased surface water habitat could result in increased foraging effort by target bird species.

Marshall Point

At Marshall Point, control area pools lay far from the creeks and ditches. In contrast, the experimental area was fairly narrow and bisected by a large, unobstructed tidal creek (Figure 4). While the experimental area was narrow to start with, this creek restricted placement of new pools to areas adjacent to ditch plugs – only a short distance from tidal flow (Table 7). Given both the small distance to tidal flow and the large

bisecting creek (a nekton source), it was not surprising to find greater species richness and densities in experimental area pools compared to the control.

Pool environmental conditions also differed markedly between the experimental and control areas. Water temperatures were cooler and salinities were higher at the experimental area (Table 7) reflecting proximity to tidal flow. These factors together may have been responsible for the differences in nekton community (ANOSIM, Table 7) between the control and experimental areas.

Effect of Pool Type on Nekton Use and Survival

Since post-alteration nekton sampling proceeded almost immediately after construction of ditch plugs at Granite Point, this study was able to capture the earliest stages of nekton response. At Granite Point, old (naturally existing) pools were better nekton habitat as indicated by a number of nekton use parameters (species richness, nekton density, and nekton size; Tables 8, 9, 10). While not directly measured, habitat conditions in new pools may be harsh. Excavation of new pools exposes anoxic peat to oxic conditions, prompting radical changes in redox conditions, pH, and chemical states of minerals such as sulfur and iron (Portnoy 1999). Being relatively shallow (Table 11), new pools are subject to extremes in temperature. New pools also have no vegetation in contrast to old pools, which have some amount of filamentous green algae or macrophytes (Adamowicz, Chapter 2).

At the experimental area in Moody marsh, however, several weeks had passed between ditch plugging and the first nekton sampling. This evidently was a long enough period to allow amelioration of initial, potentially harsh conditions in excavated

pools so that overall there was no significant difference among pool types. Marshall Point sampling began several months after site alteration and revealed that the experimental area had significantly more nekton use than the control area (Table 5). Thus within a year's time, nekton use of new pools at Moody marsh and Marshall Point had equaled or exceeded use of old pools.

Fish not only occupy newly restored sites (including pools), but as other studies have documented with gut content analysis, they are able to find food there (Allen et al. 1994, James-Pirri et al. 2001). Pool fish feed on a variety of planktonic organisms (Poulin and Fitzgerald 1989, James-Pirri et al. 2001), which are readily conveyed by flood tides. Thus the successful establishment of nekton communities in salt marsh pools can occur rapidly and represents the integration of 2 highly mobile trophic levels.

Future Management Recommendations

Evaluating the success of habitat enhancement requires determining to what extent nekton use changes over time. Marshall Point experimental pools have already demonstrated some changes in nekton community (Table 4), individual species densities (Appendix II), individual species size (Appendix III), and pool size (Appendix IV) during the 2 years since their creation. Fell et al. (2000) have documented that different marsh functions return at different rates. Future monitoring would indicate whether the initial responses recorded here were short-lived phenomena or indicators of long-term trends (Simenstad and Thom 1996). Additionally, nekton use of plugged ditches must be assessed since they form a significant percentage of the total permanent surface water created on the marsh site. Project success should also be evaluated in

terms of trophic exchanges, i.e. whether nekton productivity transfers to target organisms are enhanced or hindered in the newly created habitats. Finally, changes in sediment geochemistry and elevation levels should be closely monitored given the findings of Portnoy (1999) and in light of the severe consequences of rising sea level.

CONCLUSIONS

Ditch plugging is an intensive form of habitat enhancement. At Moody and Granite Point there were few initial differences between the "Before" and "After" conditions of nekton use at experimental area pools that could be attributed to the plugging itself. New pools, however, were not as good habitat as old pools, at least at the outset. Alterations across plugged areas (i.e. decreased species richness, decreased *F. heteroclitus* juvenile density, and increased distance to tidal flow) deserve further investigation. All that said, ditch plugging did increase surface water on the marshes and thus provides the potential for an increase in total nekton abundance. Such was the case at Marshall Point where nekton use did increase at the experimental area. Managers, however, should carefully balance potential direct and indirect effects of ditch plugging on a site-by-site basis prior to adopting it as the best way to amend the effects of drainage ditches.

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Table 1. Number of salt marsh pools sampled at each location and study area 1999 - 2000.

Location	Area	Year									
		1999					2000				
		May	June	September	October	May	June	August	September	October	
Granite Point	Control		4		9		9		9		9
	Experimental		29		29		46		46		46
Moody marsh	Control	4	3		4	4	4		4		4
	Experimental	17	16		15	19	19		19		19
Marshall Point	Control	4	4		2	4	4		.		4
	Experimental	10	11		11	11	11		.		11

Table 2. Species collected from throw-trap samples 1999, 2000.

Species	1999					
	Granite Pt. Ctrl	Granite Pt. Exp	Moody Ctrl	Moody Exp	Marshall Pt. Ctrl	Marshall Pt. Exp
<i>Fundulus heteroclitus</i>	X	X	X	X	X	X
<i>Menidia menidia</i>		X	X			
<i>Gasterosteus aculeatus</i>				X	X	X
<i>Apeltes quadracus</i>	X	X				
<i>Pungitius pungitius</i>	X	X	X	X		X
<i>Anguilla rostrata</i>		X			X	X
<i>Brevoortia tyrannus</i>		X				
<i>Palaemonetes pugio</i>	X	X	X	X		X
<i>Crangon septemspinosa</i>		X				X
<i>Carcinus maenas</i>	X	X	X	X		X
Total number of species collected in 1999	5	9	5	5	3	7
Species	2000					
	Granite Pt. Ctrl	Granite Pt. Exp	Moody Ctrl	Moody Exp	Marshall Pt. Ctrl	Marshall Pt. Exp
<i>Fundulus heteroclitus</i>	X	X	X	X	X	X
<i>Menidia menidia</i>	X	X		X		
<i>Gasterosteus aculeatus</i>	X	X	X	X		X
<i>Apeltes quadracus</i>	X	X	X	X	X	X
<i>Pungitius pungitius</i>	X	X	X	X	X	X
<i>Anguilla rostrata</i>	X	X				X
<i>Palaemonetes pugio</i>	X	X	X	X		X
<i>Crangon septemspinosa</i>	X	X		X		
<i>Carcinus maenas</i>	X	X	X	X		X
Total number of species collected in 2000	9	9	6	8	3	7

Table 3. Comparison of nekton variables before and after ditch plugging at Granite Point and Moody marsh, Maine. Data listed as average values $\pm$ 1 standard deviation (sample size). Significance levels are indicated by asterisks (*, $p<0.05$; **, $p<0.01$; ***, $p<0.001$).

		Before				After
		Experimental				Experimental
Nekton variable	Location	1999				2000
Species richness						
	Granite Point	12±1(87)				9±0(184) ***
	Moody	6±1(63)				10±2(95) NS
Nekton community --ANOSIM test statistic ¹						
	Granite Point	(51)	-0.01	(84)	NS	
	Moody	(69)	0.03	(166)	NS	
Density						
Total fish/m ²						
	Granite Point	10.5±19.5(87)				11.4±27.3(138) NS
	Moody	14.0±18.7(63)				8.3±14.9(76) NS
Total decapods/m ²						
	Granite Point	0.9±1.5(87)				0.6±1.6(138) NS
	Moody	1.4±3.2(63)				0.6±1.6(76) NS

¹ An error term is not applicable to the ANOSIM test statistic.

Table 4. Percent similarity (SIMPER) results for significant ANOSIM comparisons at Marshall Point control and experimental areas¹.

	Control 2000	Experimental 2000			
Nekton species	Average density		Average dissimilarity	% Contribution	Cumulative %
<i>F. heteroclitus</i>	4.3	13.6	27.3	39.2	39.2
<i>C. maenas</i>	0.0	1.9	15.5	22.3	61.5
<i>P. pungitius</i>	1.6	1.5	13.5	19.5	81.0
<i>A. quadracus</i>	1.3	0.1	5.7	8.3	89.3
<i>P. pugio</i>	0.0	0.6	5.2	7.5	96.7

Nekton species	Experimental 1999	Experimental 2000	Average dissimilarity	% Contribution	Cumulative %
	Average density				
<i>F. heteroclitus</i>	23.0	13.6	32.9	56.6	56.6
<i>C. maenas</i>	0.8	1.9	11.1	19.1	75.7
<i>P. pungitius</i>	0.3	1.5	5.2	8.9	84.6
<i>P. pugio</i>	0.1	0.6	4.7	8.0	92.7

¹ ANOSIM $p=0.036$ for Control 2000 vs. Experimental 2000; $p=0.002$ for Experimental 1999 vs. Experimental 2000. ANOSIM and SIMPER based on Bray-Curtis Similarity Index.

Table 5. Comparison of Marshall Point control and experimental areas in 1999 and 2000. Data listed as average values ± 1 standard deviation (sample size). Significance levels are denoted by asterisks (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

Nekton variable	Year	Control	Experimental	
Species richness				
	1999	3 $\pm$ 0(14)	9 $\pm$ 2(43)	***
	2000	4 $\pm$ 1(16)	7 $\pm$ 0(44)	***
Nekton community --ANOSIM test statistic ¹				
	1999	(8)	0.2	(39) NS
	2000	(9)	0.2	(39) *
Density				
Total fish (#/m ²)				
	1999	8.0 $\pm$ 16.2(14)	21.3 $\pm$ 29.9(43)	***
	2000	4.1 $\pm$ 6.2(16)	13.6 $\pm$ 38.3(44)	NS
Total decapods (#/m ²)				
	1999	0 $\pm$ 0(14)	0.9 $\pm$ 1.3(43)	***
	2000	0 $\pm$ 0(16)	2.0 $\pm$ 3.0(44)	***
Size (mm)				
<i>C. maenas</i>				
	1999	--	21.0 $\pm$ 10.2(21) ²	*
	2000	--	28.7 $\pm$ 10.4(25) ²	

¹ An error term is not applicable to the ANOSIM test statistic.

² Error term is ± 1 standard error.

Table 6. Comparison of water quality and physical variables measured at throw-trap pools before and after ditch plugging at Granite Point and Moody marsh, ME. Data listed as average values $\pm$ 1 standard deviation (sample size). Significance levels are denoted by asterisks (ANOVA; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

Pool Variable	Location	Before	After	
		Experimental 1999	Experimental 2000	
Water temperature (C)				
	Granite Point	20.6±8.7(87)	19.9±7.9(137)	NS
	Moody marsh	21.8±6.0(63)	20.1±5.5(76)	NS
Salinity (ppt)				
	Granite Point	29.0±4.8(87)	30.6±3.5(136)	NS
	Moody marsh	27.7±8.0(61)	23.9±8.0(76)	***
Dissolved oxygen (mg/l)				
	Granite Point	7.0±2.3(87)	6.9±2.7(137)	NS
	Moody marsh	7.6±3.9(63)	5.6±2.3(76)	***
Water depth (cm) ¹				
	Granite Point	30.7±10.3(87)	25.3±11.4(137)	**
	Moody marsh	32.2±24.0(63)	33.1±12.8(76)	NS
Pool size (m ²)				
	Granite Point	398.0±957.1(87)	262.0±674.1(138)	NS
	Moody marsh	176.2±250.0(60)	137.0±193.4(76)	NS
Distance to tidal flow (m)				
	Granite Point	24.2±23.4(87)	45.1±37.6(138)	***
	Moody marsh	15.2±10.4(60)	28.6±21.7(76)	***

¹ Error term is $\pm$ 1 standard error.

Table 7. Comparison of water quality and physical variables measured at throw-trap pools at Marshall Point control and experimental areas in 1999 and 2000. Data listed as average values $\pm$ 1 standard deviation (sample size). Significance levels are denoted by asterisks (ANOVA; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

Pool Variable	Year	Control	Experimental	
Water temperature (C)	1999	18.0 $\pm$ 10.3(14)	22.3 $\pm$ 8.1(43)	NS
	2000	23.7 $\pm$ 7.3(16)	19.0 $\pm$ 7.8(44)	***
Salinity (ppt)	1999	26.3 $\pm$ 19.6(14)	27.0 $\pm$ 6.0(43)	NS
	2000	18.7 $\pm$ 9.9(16)	23.7 $\pm$ 9.7(44)	***
Dissolved oxygen (mg/l)	1999	8.6 $\pm$ 4.0(12)	10.2 $\pm$ 3.0(32)	NS
	2000	8.8 $\pm$ 3.6(16)	8.9 $\pm$ 3.2(44)	NS
Water depth (cm) ¹	1999	20.7 $\pm$ 33.2(14)	17.0 $\pm$ 7.6(41)	NS
	2000	16.2 $\pm$ 9.2(16)	14.5 $\pm$ 6.1(44)	NS
Pool size (m ²)	1999	37.3 $\pm$ 24.8(14)	34.9 $\pm$ 16.7(33)	NS
	2000	22.7 $\pm$ 8.9(16)	30.0 $\pm$ 17.4(44)	NS
Distance to tidal flow (m)	1999	51.4 $\pm$ 9.6(14)	4.9 $\pm$ 6.4(33)	***
	2000	54.4 $\pm$ 10.5(16)	5.2 $\pm$ 5.9(44)	***

¹ Error term is $\pm$ 1 standard error.

Table 8. Estimates of species richness $\pm$ 1 standard deviation using the jack-knife estimate in different pool types at two sites in Maine.

Lowercase letters indicate significant differences at $p < 0.01$ (t-tests).

Bonferroni adjusted alpha equals 0.0167.

Site	Paired old pools	Enlarged pools	New pools
Granite Point			
	9.0 $\pm$ 1.0a	9.0 $\pm$ 1.0a	8.0 $\pm$ 1.4b
(n)	52	28	72
Moody marsh			
	7.9 $\pm$ 1.3 a	4.0 $\pm$ 0.0 b	3.9 $\pm$ 1.3 b
(n)	24	5	15

Table 9. Comparison of nekton densities ($\#/m^2$) $\pm$ 1 standard deviation among different pool types. Significant differences among pool types are indicated by lower case letters. Significance levels are denoted by asterisks (ANOVA; *, $p < 0.05$; **, $p < 0.01$; *** $p < 0.001$).

Nekton category	Granite Point							Moody marsh						
	Paired old		Enlarged		New			Paired old		Enlarged		New		
<i>F. heteroclitus</i> juvenile	13.1 $\pm$	26.7	7.1 $\pm$	13.4	6.0 $\pm$	7.1	NS	3.3 $\pm$	3.8	7.8 $\pm$	8.1	4.1 $\pm$	5.1	NS
<i>F. heteroclitus</i> male	1.0 $\pm$	3.1 a	0.1 $\pm$	0.4 b	0.1 $\pm$	0.4 b	**	0.7 $\pm$	1.6	0.8 $\pm$	1.8	0.2 $\pm$	0.6	NS
<i>F. heteroclitus</i> female	2.4 $\pm$	9.7 a	0.2 $\pm$	0.4 b	0.2 $\pm$	0.4 b	**	1.7 $\pm$	3.2	2.0 $\pm$	2.0	0.4 $\pm$	0.8	NS
<i>M. menidia</i>	0.2 $\pm$	0.8	0.4 $\pm$	1.2	0.0 $\pm$	0.1	NS	0.0 $\pm$	--	0.0 $\pm$	--	0.0 $\pm$	--	--
<i>G. aculeatus</i>	0.3 $\pm$	1.2 ab	0.4 $\pm$	1.1 a	0.0 $\pm$	-- b	*	0.1 $\pm$	0.4	0.0 $\pm$	--	0.0 $\pm$	--	NS
<i>A. quadracus</i>	0.0 $\pm$	0.1 a	0.4 $\pm$	0.9 b	0.0 $\pm$	--	***	0.0 $\pm$	--	0.0 $\pm$	--	0.0 $\pm$	--	--
<i>P. pungitius</i>	1.8 $\pm$	5.5 a	2.0 $\pm$	6.1 a	0.0 $\pm$	0.2 b	**	0.6 $\pm$	1.3	1.4 $\pm$	1.7	0.2 $\pm$	0.8	NS
All fish	18.8 $\pm$	42.5 a	10.5 $\pm$	15.5 ab	6.3 $\pm$	7.4 b	**	6.4 $\pm$	8.0	12.0 $\pm$	8.2	4.9 $\pm$	5.8	NS
<i>P. pugio</i>	0.5 $\pm$	1.7 a	0.4 $\pm$	0.9 ab	0.0 $\pm$	0.2 b	*	0.9 $\pm$	2.6	1.2 $\pm$	2.2	0.3 $\pm$	0.8	NS
<i>C. septemspinosa</i>	0.1 $\pm$	0.4	0.0 $\pm$	--	0.0 $\pm$	0.1	NS	0.0 $\pm$	0.2	0.0 $\pm$	--	0.0 $\pm$	--	NS
<i>C. maenas</i>	0.7 $\pm$	1.0	0.4 $\pm$	0.8	0.5 $\pm$	1.0	NS	0.2 $\pm$	0.4 a	0.6 $\pm$	0.9 b	0.0 $\pm$	-- a	*
All decapods	1.3 $\pm$	1.8 a	0.7 $\pm$	1.2 ab	0.5 $\pm$	1.0 b	*	1.1 $\pm$	2.6	1.8 $\pm$	8.2	0.3 $\pm$	0.8	NS
Sample size (n)	52		28		72			24		5		15		

Table 10. Comparison of average nekton sizes (mm) $\pm$ 1 standard error among different pool types at Granite Point and Moody marsh, ME. Significant differences among pool types are indicated by lower case letters. Significance levels are denoted by asterisks (ANOVA; *, $p < 0.05$; ***, $p < 0.001$).

Nekton category	Granite Point			
	Paired old	Enlarged	New	
<i>F. heteroclitus</i> juvenile	31.1 $\pm$ 5.7(37)a	32.1 $\pm$ 10.0(19) a	26.5 $\pm$ 4.9(56) b	***
<i>F. heteroclitus</i> male	53.6 $\pm$ 5.2(12)	46.0 $\pm$ -- (1)	49.8 $\pm$ 9.8(6)	NS
<i>F. heteroclitus</i> female	52.5 $\pm$ 6.1(15)	52.4 $\pm$ 8.0 (4)	47.1 $\pm$ 2.9(9)	NS
<i>F. heteroclitus</i> overall	34.8 $\pm$ 9.5(41)a	34.5 $\pm$ 9.0(20) a	28.1 $\pm$ 7.1(58) b	***
<i>M. menidia</i>	31.0 $\pm$ 5.6(3)	31.9 $\pm$ 6.5(4)	33.0 $\pm$ -- (1)	NS
<i>G. aculeatus</i>	22.7 $\pm$ 8.8(4)	26.7 $\pm$ 6.2(4)	.	NS
<i>A. quadracus</i>	30.0 $\pm$ -- (1)	25.9 $\pm$ 1.4(5)	.	NS
<i>P. pungitius</i>	36.5 $\pm$ 4.1(14)	36.5 $\pm$ 5.7(11)	37.3 $\pm$ 4.7(3)	NS
<i>A. rostrata</i>	.	8.0 $\pm$ -- (1)	.	.
<i>C. maenas</i>	32.2 $\pm$ 8.9(20)	34.7 $\pm$ 17.0 (6)	29.8 $\pm$ 6.8(21)	NS

Nekton category	Moody marsh			
	Paired old	Enlarged	New	
<i>F. heteroclitus</i> juvenile	32.2 $\pm$ 6.3(18)	27.8 $\pm$ 8.6(4)	28.7 $\pm$ 5.2(9)	NS
<i>F. heteroclitus</i> male	50.5 $\pm$ 6.0(6)	51.5 $\pm$ -- (1)	53.3 $\pm$ 4.6(2)	NS
<i>F. heteroclitus</i> female	51.6 $\pm$ 7.4(9)	47.9 $\pm$ 4.9(4)	56.1 $\pm$ 6.3(4)	NS
<i>F. heteroclitus</i> overall	37.3 $\pm$ 11.4(20)	34.0 $\pm$ 12.4(5)	33.1 $\pm$ 10.6(10)	NS
<i>M. menidia</i>	.	.	.	.
<i>G. aculeatus</i>	21.5 $\pm$ -- (1)	.	.	.
<i>A. quadracus</i>	.	.	.	.
<i>P. pungitius</i>	42.0 $\pm$ 5.6(6)	41.7 $\pm$ 6.4(3)	43.7 $\pm$ -- (1)	NS
<i>A. rostrata</i>	.	.	.	.
<i>C. maenas</i>	34.7 $\pm$ 5.0(3)	27.5 $\pm$ 3.5(2)	.	NS

Table 11. Comparison of water quality and physical variables measured three different pool types at Granite Point and Moody marsh, ME. Data listed as average $\pm$ 1 standard deviation (standard error for water depth). Significance levels are denoted by asterisks (ANOVA; **, $p < 0.01$; ***, $p < 0.001$).

Pool Variable	Granite Point							Moody marsh						
	Paired old		Enlarged		New			Paired old		Enlarged		New		
Temperature (C)	20 $\pm$	6.9	18.9 $\pm$	6.8	21 $\pm$	6.8	NS	19.4 $\pm$	4.7	18.6 $\pm$	4.8	21.4 $\pm$	4.8	NS
Salinity (ppt)	30 $\pm$	3.1	29.0 $\pm$	5.5 ¹	29 $\pm$	5.4	NS	25.2 $\pm$	6.4	26.3 $\pm$	6.6	26.4 $\pm$	4.7	NS
Dissolved oxygen (mg/l)	7.0 $\pm$	2.7	7.3 $\pm$	5.0	6.6 $\pm$	4.6	NS	5.7 $\pm$	1.7	5.5 $\pm$	1.4	5.0 $\pm$	2.5	NS
Depth (cm)	33 $\pm$	9.0 a	35.3 $\pm$	12.6 a	17 $\pm$	5.3 b	***	37.6 $\pm$	11.2 a	40.6 $\pm$	9.3 a	20.0 $\pm$	6.4 b	***
Pool size (m ²)	34 $\pm$	17.4 a	621.4 $\pm$	605.6 b	37 $\pm$	29.2 a ²	***	82.7 $\pm$	99.1	81.8 $\pm$	2.4	40.8 $\pm$	16.7	NS
Distance to tidal flow (m)	37.0 $\pm$	32.5 a	52.5 $\pm$	45.9 b	32 $\pm$	14.3 a ³	**	27.6 $\pm$	19.6 a	19.7 $\pm$	4.0 a	15.4 $\pm$	6.1 b	**
Sample size (n)	52		28		71			24		5		15		

¹ Sample size = 27.

² Sample size = 72.

Table 12. Area of surface water at control and experimental sites before and after ditch plugging.

Location	Study area	Area of surface water ¹ (m ²)	Total marsh area (m ²)	Percent of total marsh occupied by surface water
Granite Point				
Control	Before	2426	13201	18.4
	After	2726		20.7
Experimental	Before	17038	87604	19.4
	After	25666		29.3
Moody marsh				
Control	Before	246	7618	3.2
	After	248		3.3
Experimental	Before	3718	24672	15.1
	After	5425		22.0
Marshall Point				
Control	Before	224	15302	1.5
	After	208		1.4
Experimental	Before	2	15215	0.0
	After	1112		7.3

¹ Surface water in the "Before" condition refers to pools only. See Table 13 for breakdown of surface water in the "After" condition.

² Estimated from aerial photographs and site visits.

Table 13. Categories of surface water identified in the "Experimental-After" study areas in Table 12.

Location	New pools (m ²)	Plugged ditches (m ²)	Enlarged pools and remainder (m ²)*	Total altered surface water (m ²)
Granite Point	2829	3195	2604	8628
Moody marsh	492	895	320	1707
Marshall Point	357	754	0	1112

* "Enlarged pools" refers to those pre-existing pools that were directly altered through use of excavation equipment. "Remainder" refers to pools that were GPS'ed in the field but not found on photograph of pre-existing conditions and any differences between pools delineated on photograph and those GPS'ed in the field.

Figure 1. Salt marsh study sites

Figure 2. Granite Point marsh showing surface water before and after ditch plugging. Control area lies to southwest; experimental area lies to northeast. Tidal flow enters each area from the west; a barrier beach and upland separates the marsh from the Atlantic Ocean to the east.

Figure 3. Moody marsh showing surface water before and after ditch plugging. Control area lies on the eastern half of the site; experimental area lies on the western portion of the site. A tidal creek flows unimpeded on the northern boundary; a tidal ditch/plugged ditch lies on the southern boundary.

Figure 4. Marshall Point showing surface water before and after ditch plugging. Control area lies to the west; experimental area lies to the east. Tidal water enters each area from the south.

Appendix I. List of scientific and common names.

Category	Scientific Name	Common Name
Fish¹		
	<i>Anguilla rostrata</i> (Lesueur, 1817)	American eel
	<i>Apeltes quadracus</i> (Mitchill, 1815)	fourspine stickleback
	<i>Brevoortia tyrannus</i> (Latrobe, 1802)	menhaden
	<i>Cyprinodon variegatus</i> Lacepede, 1803	sheepshead minnow
	<i>Fundulus luciae</i> (Baird, 1855)	spotfin killifish
	<i>F. majalis</i> (Walbaum, 1792)	striped killifish
	<i>F. heteroclitus</i> (Linnaeus, 1766)	mummichog
	<i>Gasterosteus aculeatus</i> Linnaeus, 1758	threespine stickleback
	<i>Lucania parva</i> (Baird & Girard, 1855)	rainwater killifish
	<i>Menidia beryllina</i> (Cope, 1866)	inland silverside
	<i>Menidia menidia</i> (Linnaeus, 1766)	Atlantic silverside
	<i>Pungitius pungitius</i> (Linnaeus, 1758)	ninespine stickleback
Decapods²		
	<i>Callinectes sapidus</i> (Rathbun, 1896)	blue crab
	<i>Carcinus maenas</i> (Linnaeus, 1758)	green crab
	<i>Palaemonetes pugio</i> (Holthuis, 1949)	daggerblade grass shrimp
	<i>Crangon septemspinosa</i> Say, 1818	seven-spined bay shrimp

¹ Robins et al. 1991.

² William et al. 1989.

Appendix II. Average nekton densities (#/m²) for 1999 and 2000 throw-trap sample pools $\pm$ 1 standard deviation. Granite Point and Moody marsh ANOVA models included an interaction term to test for effect of ditch plugging. Marshall Point ANOVA model examined treatment effect (control versus experimental) only for 1999 and 2000. Significance levels are denoted by asterisks (ANOVA; *, p<0.05; **, p<0.01; ***, p<0.001). Results of post-hoc LSMeans testing are given where applicable.

Nekton category	Granite Point										LSMeans for Interaction Term	
	1999					2000					Significant?	
	Ctrl		Exp			Ctrl		Exp		BACI p-value	Control 1999-2000	Experimental 1999-2000
<i>F. heteroclitus</i>												
Juvenile	15.1 $\pm$ 15.4		8 $\pm$ 15.2			14.5 $\pm$ 15.9		8.6 $\pm$ 18.5		NS		
Male	0.4 $\pm$ 1.2		0.6 $\pm$ 1.3			0.2 $\pm$ 0.5		0.4 $\pm$ 1.8		NS		
Female	0.9 $\pm$ 2.1		1.1 $\pm$ 2.5			0.3 $\pm$ 0.7		1 $\pm$ 6		NS		
Overall	16.4 $\pm$ 17.5		9.6 $\pm$ 16.6			15 $\pm$ 16.1		9.9 $\pm$ 25.3		NS		
<i>M. menidia</i>	0.0 $\pm$ 0.0		0.1 $\pm$ 0.4			0.1 $\pm$ 0.3		0.2 $\pm$ 1.2		NS		
<i>G. aculeatus</i>	0.0 $\pm$ 0.0		0.0 $\pm$ 0.0			0.4 $\pm$ 1.2		0.4 $\pm$ 2.3		NS		
<i>A. quadracus</i>	0.1 $\pm$ 0.4		0.1 $\pm$ 0.6			0.1 $\pm$ 0.4		0.1 $\pm$ 0.6		NS		
<i>P. pungitius</i>	0.2 $\pm$ 0.4		0.7 $\pm$ 3.7			1.2 $\pm$ 3		0.7 $\pm$ 2.9		NS		
<i>A. rostrata</i>	0.0 $\pm$ 0.0		0.04 $\pm$ 0.2			0.04 $\pm$ 0.2		0.002 $\pm$ 0.2		NS		
<i>B. tyrannus</i>	0.0 $\pm$ 0.0		0.01 $\pm$ 0.1			0.0 $\pm$ 0.0		0.0 $\pm$ 0.0		NS		
Total fish	16.6 $\pm$ 17.6		10.5 $\pm$ 19.5			16.7 $\pm$ 17.2		11.4 $\pm$ 25.0		NS		
<i>P. pugio</i>	3.2 $\pm$ 7.9		0.6 $\pm$ 1.2			0.7 $\pm$ 1.5		0.3 $\pm$ 1.1		*	Y	N
<i>C. septemspinosa</i>	0.0 $\pm$ 0.0		0.01 $\pm$ 0.1			0.04 $\pm$ 0.2		0.02 $\pm$ 0.2		NS		
<i>C. maenas</i>	0.3 $\pm$ 0.6		0.3 $\pm$ 0.8			0.1 $\pm$ 0.5		0.4 $\pm$ 0.8		NS		
Total decapod	3.5 $\pm$ 7.9		0.9 $\pm$ 1.5			0.9 $\pm$ 1.7		0.8 $\pm$ 1.3		**	Y	N
Sample size (n)	22		87			27		138				

Appendix II. (cont.)

Appendix II. (cont.)		Moody marsh								BACI p-value	LSMeans for Interaction Term	
		1999				2000					Significant?	
		Ctrl		Exp		Ctrl		Exp			Control 1999- 2000	Experimental 1999-2000
Nekton category												
<i>F. heteroclitus</i>												
	Juvenile	4.7 ±	11.1	11.0 ±	14.5	7.1 ±	13.4	5.1 ±	10.2	*	N	Y
	Male	1.1 ±	2.6	0.9 ±	2.4	0.8 ±	1.4	0.4 ±	0.9	NS		
	Female	2.2 ±	4.4	2.1 ±	5.1	1.3 ±	2.5	1.0 ±	1.8	NS		
	Overall	8.1 ±	13.3	14.0 ±	18.7	9.1 ±	15.9	6.5 ±	10.8	NS		
<i>M. menidia</i>		0.1 ±	0.3	0.0 ±	0.0	0.0 ±	0.0	0.05 ±	0.3	NS		
<i>G. aculeatus</i>		0.0 ±	0.0	0.0 ±	0.1	0.4 ±	0.9	1.4 ±	10.1	NS		
<i>A. quadracus</i>		0.0 ±	0.0	0.0 ±	0.0	0 ±	0	0.01 ±	0.1	NS		
<i>P. pungitius</i>		0.1 ±	0.3	0.1 ±	0.3	3.1 ±	9.6	0.4 ±	1	*	Y	N
Total fish		8.2 ±	13.1	14.0 ±	18.7	12.5 ±	24.8	8.3 ±	14.9	NS		
<i>P. pugio</i>		1.3 ±	1.9	1.1 ±	3.1	1 ±	1.6	0.4 ±	1.5	NS		
<i>C. septemspinosa</i>		0.0 ±	0.0	0.0 ±	0.0	0.0 ±	0	0.01 ±	0.1	NS		
<i>C. maenas</i>		0.9 ±	2.1	0.3 ±	0.6	0.8 ±	0.8	0.1 ±	0.3	NS		
Decapod total		2.1 ±	3.2	1.4 ±	3.2	1.8 ±	1.8	0.6 ±	1.6	NS		
Sample size (n)		15		63		16		76				

Appendix II. (cont.)

Appendix II. (cont.)		Marshall Point								LSMeans for Treatment		
		1999				2000				Significant?		
		Ctrl		Exp		Ctrl		Exp		Treatment p-value	Control - Experimental 1999	Control - Experimental 2000
Nekton category		Ctrl		Exp		Ctrl		Exp		Treatment p-value		
<i>F. heteroclitus</i>												
	Juvenile	2.6 ±	6.1	18.3 ±	27.0	2.1 ±	4.3	8.1 ±	17.5	***	Y	N
	Male	0.0 ±	0.0	0.8 ±	1.4	0.1 ±	0.3	0.8 ±	3.6	NS		
	Female	0.2 ±	0.6	1.8 ±	3.6	0.2 ±	0.5	3.1 ±	17.7	NS		
	Overall	2.9 ±	36.7	20.9 ±	29.9	2.4 ±	4.8	12.0 ±	36.7	***	Y	N
<i>G. aculeatus</i>		1.4 ±	3.7	0.1 ±	0.4	0.0 ±	0.0	0.2 ±	0.9	NS		
<i>A. quadracus</i>		0.0 ±	0.0	0.0 ±	0.0	0.8 ±	3.0	0.1 ±	0.3	NS		
<i>P. pungitius</i>		3.8 ±	12.1	0.3 ±	1.4	0.9 ±	2.0	1.3 ±	4.2	NS		
<i>A. rostrata</i>		0.0 ±	0.0	0.1 ±	0.3	0.0 ±	0.0	0.1 ±	0.3	NS		
Total fish		8.0 ±	16.2	21.3 ±	29.9	4.1 ±	6.2	13.6 ±	38.3	**	Y	N
<i>P. pugio</i>		0.0 ±	0.0	0.1 ±	0.6	0.0 ±	0.0	0.6 ±	1.6	*	N	Y
<i>C. septemspinosa</i>		0.0 ±	0.0	0.02	0.2	0.0	0.0	0.0	0.0	NS		
<i>C. maenas</i>		0.0 ±	0.0	0.7 ±	1.0	0.0 ±	0.0	1.6 ±	2.3	***	Y	N
Decapod total		0.0 ±	0.0	0.9 ±	1.3	0.0 ±	0.0	2.2 ±	3.0	***	Y	N
Sample size (n)		14		43		16		44				

Appendix III. Average fish lengths (mm) and crab widths (mm) for 1999 and 2000 throw-trap data. Data listed as average values $\pm$ 1 standard error. Granite Point and Moody marsh ANOVA models included an interaction term to test for effect of ditch plugging. Marshall Point ANOVA model examined treatment effect (control versus experimental) only for 1999 and 2000. Significance levels are denoted by asterisks (ANOVA; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). None of the applicable post-hoc LS Means tests were significant and therefore are not listed.

Nekton category	Granite Point										BACI p-value		
	1999					2000							
	Ctrl		Exp			Ctrl		Exp					
<i>F. heteroclitus</i>													
Juvenile	29.7 ±	4.8	(19)	30.2 ±	6.7	(60)	25.4 ±	6.8	(33)	29.3 ±	7.2	(94)	NS
Male	53.0 ±	0.0	(3)	50.7 ±	5.3	(22)	52.3 ±	7.5	(4)	51.0 ±	6.7	(15)	NS
Female	46.9 ±	4.8	(4)	52.9 ±	8.3	(28)	50.9 ±	11.1	(6)	49.8 ±	5.7	(25)	NS
Overall	30.3 ±	5.5	(19)	33.6 ±	9.1	(62)	27.2 ±	7.9	(33)	32.4 ±	9.8	(105)	NS
<i>M. menidia</i>	.	.		38.7 ±	13.3	(5)	26.0 ±	14.1	(3)	27.7 ±	4.7	(6)	NS
<i>G. aculeatus</i>	.	.		.	.		22.5 ±	5.7	(3)	25.9 ±	8.1	(12)	NS
<i>A. quadracus</i>	21.0 ±	na	(1)	.	.		28.0 ±	na	(1)	25.2 ±	3.5	(6)	NS
<i>P. pungitius</i>	43.0 ±	2.9	(4)	39.8 ±	4.1	(13)	36.1 ±	4.9	(10)	36.4 ±	4.7	(29)	NS
<i>A. rostrata</i>	.	.		55.3 ±	66.8	(2)	.	.		8.0 ±	na	(1)	NS
<i>B. tyrannus</i>	.	.		58.0 ±	na	(1)	.	.		.	.		.
<i>C. maenas</i>	32.7 ±	11.8	(5)	29.3 ±	10.9	(18)	30.5 ±	17.8	(6)	32.5 ±	8.7	(37)	NS

Appendix III (cont.)

Nekton category	Moody marsh										BACI p-value
	1999					2000					
	Ctrl		Exp			Ctrl		Exp			
<i>F. heteroclitus</i>											
Juvenile	35.2 ± 3.9 (7)	33.8 ± 7.2 (41)	32.9 ± 8.7 (9)	31.3 ± 7.3 (48)	NS						
Male	63.2 ± 6.4 (4)	52.7 ± 7.4 (19)	55.2 ± 8.1 (4)	50.0 ± 3.4 (17)	NS						
Female	56.1 ± 9.9 (7)	51.8 ± 5.9 (32)	58.8 ± 5.2 (4)	51.9 ± 7.3 (27)	NS						
Overall	45.8 ± 11.3 (10)	38.2 ± 9.9 (47)	39.8 ± 12.8 (12)	36.6 ± 11.5 (58)	NS						
<i>M. menidia</i>	55.0 ± na (1)	.	.	84.3 ± 50.6 (2)	NS						
<i>G. aculeatus</i>	.	67.0 ± na (1)	33.9 ± 21.4 (2)	28.3 ± 17.2 (4)	NS						
<i>A. quadracus</i>	.	.	.	33.0 ± na (1)	.						
<i>P. pungitius</i>	40.0 ± na (1)	43.3 ± 1.8 (2)	40.2 ± 5.9 (6)	43.2 ± 4.6 (15)	NS						
<i>A. rostrata</i>	.	.	.	.	.						
<i>B. tyrannus</i>	.	.	.	.	.						
<i>C. maenas</i>	15.8 ± 9.6 (5)	23.3 ± 6.6 (12)	30.9 ± 16.0 (9)	29.6 ± 10.0 (7)	NS						

Appendix III (cont.)

Nekton category	Marshall Point												Treatment p-value
	1999						2000						
	Ctrl			Exp			Ctrl			Exp			
<i>F. heteroclitus</i>													
Juvenile	24.8 ±	5.3	(6)	32.4 ±	6.8	(34)	29.5 ±	4.3	(4)	32.3 ±	6.7	(28)	NS
Male	.	.		50.3 ±	4.3	(14)	46.0 ±	0.0	(2)	51.9 ±	7.3	(10)	NS
Female	53.0 ±	na	(1)	50.3 ±	3.9	(14)	59.0 ±	12.7	(2)	51.3 ±	4.6	(15)	NS
Overall	28.9 ±	11.6	(7)	43.0 ±	4.2	(10)	36.6 ±	10.0	(6)	37.0 ±	10.0	(32)	NS
<i>M. menidia</i>	.	.		.	.		.	.		.	.		.
<i>G. aculeatus</i>	23.8 ±	na	(1)	48.3 ±	27.2	(3)	.	.		24.3 ±	6.7	(2)	NS
<i>A. quadracus</i>	.	.		.	.		29.1 ±	na	(1)	34.7 ±	9.3	(3)	NS
<i>P. pungitius</i>	27.0 ±	na	(1)	27.4 ±	9.3	(3)	33.3 ±	1.6	(2)	36.4 ±	4.7	(9)	NS
<i>A. rostrata</i>	.	.		65.0 ±	na	(1)	.	.		95.7 ±	49.9	(3)	NS
<i>B. tyrannus</i>	.	.		.	.		.	.		.	.		.
<i>C. maenas</i>	.	.		21.0 ±	10.2	(21)	.	.		28.7 ±	10.4	(25)	*

na: not applicable since n=1.

Appendix IV. Average pool characteristics for 1999 and 2000 throw-trap sample pools $\pm$ 1 standard deviation (standard error for water depth). Granite Point and Moody marsh ANOVA models included an interaction term to test for effect of ditch plugging.

Marshall Point ANOVA model examined treatment effect (control versus experimental) only for 1999 and 2000. Significance levels are denoted by asterisks (ANOVA; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Results of post-hoc LSMeans testing are given where applicable.

Pool Variable	Granite Point								LSMeans for Interaction	
	1999				2000				Term Significant?	
	Ctrl		Exp		Ctrl		Exp		BACI p-value	Control Experimental
									1999-2000	1999-2000
Water temperature (C)	20.0 $\pm$ 6.5 (22)		20.6 $\pm$ 8.7 (87)		22.4 $\pm$ 9.5 (27)		19.9 $\pm$ 7.9 (137)		NS	
Salinity (ppt)	29.8 $\pm$ 4.3 (22)		29.0 $\pm$ 4.9 (87)		31.2 $\pm$ 4.7 (27)		30.6 $\pm$ 3.5 (136)		NS	
Dissolved oxygen (mg/l)	7.1 $\pm$ 2.4 (22)		7.0 $\pm$ 2.3 (87)		8.3 $\pm$ 3.4 (27)		6.9 $\pm$ 2.7 (137)		NS	
Water depth (cm)	32.9 $\pm$ 7.3 (21)		30.7 $\pm$ 10.3 (87)		27.8 $\pm$ 8.8 (26)		25.3 $\pm$ 11.4 (137)		NS	
Pool size (m ²)	162 $\pm$ 164 (22)		398 $\pm$ 957 (87)		136 $\pm$ 129 (27)		262 $\pm$ 674 (138)		NS	
Distance to tidal flow (m)	17.2 $\pm$ 8.3 (22)		24.2 $\pm$ 23.4 (87)		17.3 $\pm$ 6.8 (27)		45.1 $\pm$ 37.6 (138)		*	N Y

Appendix IV. (cont.)

Pool Variable	Moody Marsh										LSMeans for Interaction	
	1999					2000					Term Significant?	
	Ctrl		Exp			Ctrl		Exp			BACI	Control
											p-value	1999-2000
												Experimental
												1999-2000
Water												
temperature (C)	19.9 ±	4.9 (15)	21.9 ±	5.8 (63)		19.7 ±	5.8 (20)	20.1 ±	5.5 (76)	NS		
Salinity (ppt)	30.4 ±	4.4 (15)	27.7 ±	8.0 (61)		27.8 ±	2.7 (20)	23.9 ±	8.0 (76)	NS		
Dissolved oxygen												
(mg/l)	7.2 ±	1.5 (15)	7.3 ±	2.6 (63)		6.4 ±	1.7 (20)	5.6 ±	2.3 (76)	NS		
Water depth (cm)	34.9 ±	9.7 (15)	32.2 ±	24.0 (63)		38.1 ±	6.2 (20)	33.1 ±	12.8 (76)	NS		
Pool size (m ²)	61 ±	45 (15)	176 ±	250 (60)		54 ±	41 (20)	137 ±	193 (76)	NS		
Distance to tidal												
flow (m)	6.6 ±	3.0 (15)	15.2 ±	10.4 (60)		6.6 ±	2.9 (20)	28.6 ±	21.7 (76)	*	N	Y

Appendix IV. (cont.)

Pool Variable	Marshall Point										LSMeans for Treatment Significant?		
	1999					2000					Treat- ment p- value	Control -	
	Ctrl		Exp			Ctrl		Exp				Experi- mental 1999	Control - Experimental 2000
Water temperature (C)	18.0 ±	10.3 (14)	22.3 ±	8.1 (43)	23.7 ±	7.3 (16)	19.0 ±	7.8 (44)	***		N	Y	
Salinity (ppt)	26.6 ±	9.6 (14)	27.0 ±	6.0 (43)	18.7 ±	9.9 (16)	23.7 ±	9.7 (44)	***		Y	N	
Dissolved oxygen (mg/l)	8.6 ±	4.0 (12)	10.2 ±	3.0 (32)	8.8 ±	3.6 (16)	8.9 ±	3.3 (44)	NS				
Water depth (cm)	20.7 ±	33.2 (14)	17.0 ±	7.6 (41)	16.2 ±	9.2 (16)	14.5 ±	6.1 (44)	NS				
Pool size (m ²)	37 ±	25 (14)	35 ±	17 (33)	23 ±	9 (16)	30 ±	17 (44)	NS				
Distance to tidal flow (m)	51.4 ±	9.6 (14)	4.9 ±	6.4 (33)	54.4 ±	10.5 (16)	5.2 ±	5.9 (44)	***		Y	Y	

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