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WELLS NATIONAL ESTUARINE RESEARCH RESERVE

PRODUCTION, NUTRITION, AND ECOLOGICAL HEALTH OF THE WELLS SALT MARSHES

Washington, D.C.
March 1988

U.S. DEPARTMENT OF COMMERCE / National Oceanic and Atmospheric Administration / Marine and Estuarine Management Division

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UNITED STATES DEPARTMENT OF COMMERCE / National Oceanic and Atmospheric Administration / National Ocean Service

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NOTICE

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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NATIONAL OCEAN SERVICE
OFFICE OF OCEAN AND COASTAL RESOURCE MANAGEMENT
MARINE AND ESTUARINE MANAGEMENT DIVISION
WASHINGTON, D.C.

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Production, Nutrition, and Ecological Health of the Wells Salt Marshes

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Abstract

Salt marshes are a valuable and biologically productive resource. This study provides baseline information quantifying the health and productivity of two marshes in the Wells National Estuarine Research Reserve. The little River and Drakes Island marshes were analyzed to provide a comparison of two adjacent marshes within the Reserve. Marsh productivity was measured both in terms of biomass and the nutritional value of the plant tissue. Both vegetative and reproductive tissue were analyzed for carbon, nitrogen and phosphorus content. Reproductive tissue had significantly higher nutritional value.

The Little River marsh, although not impacted by human activity, is also not characteristic of a typical New England high salt marsh because of the stress induced by its proximity to the ocean. There are many shallow pannes and ponds which are caused by wracks of dead vegetation, transport of sand across the barrier island, and ice scouring. Marsh vegetation consists of stands of mixed species composition, instead of the stands of single species characteristic of a fully developed salt marsh. Marsh surface microtopography affects plant species composition which directly correlates with marsh surface elevation. The Drakes Island marsh has been altered from a salt marsh to a brackish-water marsh by a tidal dam restriction at Drakes Island Road. The plant composition indicates a productive brackish-water marsh. However, the marsh is being lost as it evolves into an upland community with the invasion of terrestrial plant species. In this report, I propose a definition of marsh health and show that niether the Little River marsh nor the Drakes Island marsh is a healthy salt marsh based on my definition.

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Preface

My research on the productivity of the Wells National Estuarine Research Reserve salt marshes was organized and undertaken in cooperation with the synchronous salt marsh productivity study by Dr. Robert Vadas, Department of Botany and Plant Pathology, University of Maine, Orono, ME. I acknowledge the help and cooperation of Steve Meyer, the Wells Research Reserve Manager, the assistance of Edward Brainard for major contributions to the project, and the field, editorial and writing assistance of Catherine Short. Additionally, I thank Ken Toppin, Mary Halleck, and Susan Shain for there assistance in this project.

WELLS NATIONAL ESTUARINE RESEARCH RESERVE FINAL REPORT

by Frederick T. Short

1.0 General Introduction

All salt marsh is intertidal. That is, at some time during the year, salt marsh is flooded with salty ocean water. It is saline flooding that produces the typical plant species and environmental characteristics called salt marsh(Teal and Teal, 1969). The marsh at Wells, Maine is an example of "high marsh," marsh area that forms between mean high water and the upper limits of the high spring tides. Many of the classic studies on marsh environments have focused on low, regularly flooded marsh areas, but recently scientists have recognized the importance of the high marsh (Nixon, 1982) in preserving and managing marshland ecosystems generally.

Marshes along the southern coast of Maine are tidal marshes typical of what is called the "New England type" of salt marsh. The Little River marsh in Wells is not a typical New England salt marsh, but is stressed by its proximity to the open Gulf of Maine. The Drakes Island marsh has evolved from a salt marsh environment into a brackish marsh as a result of tidal restriction. Both these marshes are in the process of change from the typical New England salt marsh type as a result of very different types of environmental stress.

New England-type salt marshes developed during post-glacial submergence of land and concurrent rise in sea level. Sediments, primarily of marine origin, were deposited behind a barrier island or along tidal creeks and built up because of protection from direct impact by the sea. The sediments built up until they reached the mid-tide level. At that point, the marsh area was free of tidal waters for approximately half the day and vegetation was established in the from of cordgrass (*Spartina alterniflora)*. Cordgrass is the most immersion tolerant of the salt marsh plant species, and forms "low marsh," found along the creek banks.

As stands of cordgrass spread and thickened, the plants themselves trapped sediments; the level of the marsh rose as these trapped particles combined with decaying plant material to form marsh peat. This process, which began approximately 10,000 years ago after the last glaciation, continues today wherever *Spartina* *alterniflora* exists, including the Wells marshes. As the marsh surface level rises, the marshes develop pockets of more upland species.

When the marsh surface reaches the level of mean high tide, cordgrass is replaced by salt meadow grass (*Spartina patens*), the familiar salt hay that was so valuable to the early settlers of our coastal towns. Salt hay is one of the dominant plants of the high salt marsh, including the Wells Sanctuary marshes. It is less tolerant of salt water immersion than *Spartina alterniflora*.

No direct commercial use is made of the Wells salt marshes today. However, salt marsh and estuarine ecosystems and their related uplands are under tremendous pressure as development of the coastal strip continues. A recent article in the New York Times stated that "The Government estimates that by 1990 more than 75 percent of the nation's population will live within 50 miles of the coast." The loss of any salt marsh, whether from human-induced or natural causes, must be seen as part of the large overall loss of this valuable habitat along the east coast of the United States in recent years.

The marsh that remains along the New England coast has great value, economic and otherwise, to the towns it occupies and to the vitality of the land/sea margin as a whole. Salt marsh provides a transition zone between upland vegetation and the ocean; the role it serves in this regard, as an intermediary between the ocean and the land, is crucial to the health of both. As such, salt marsh is a sensitive predictor and indicator of the health of the coastal zone.

Primary production, the conversion of light energy and mineral elements into plant material, occurs abundantly in marshes. It is estimated that tidal marsh ecosystems may produce 10 tons of organic matter per acre per year, comparing favorably with modern wheat production, and providing a basis for the entire marsh-related ecosystem, including offshore fisheries. The marsh plant material decomposes and is then available directly as food within the marsh and offshore. The marsh is a hatchery and a nursery for oysters, crabs, shrimp, commercially valuable fish, and insects. The creatures in the marsh are attracted to it by its abundant food supply and the protection it affords.

Marshes provide a nesting ground and feeding ground for marine and other birds. Wildlife is drawn to the marsh to browse or to hunt the small mammals and reptiles that thrive there. Marshes absorb flood waters, trap sediments, and improve water quality by assimilating nutrients of upland origin, whether agricultural or industrial. Lastly, marshes provide open space in the crowded seashore environment, an asset that cannot be measured perhaps, but one of undeniable value to rapidly developing coastal areas.

The marshes studied in detail in this research are the Little River marsh and the Drakes Island marsh, adjacent but very different marshes, both located within the Wells National Estuarine Research Reserve in Wells, Maine, USA (Fig. 1). The aim of the study is to provide baseline information on the primary productivity, nutrition, and health of these two marshes. No work of this sort has been done previously within the Wells Estuarine Research Reserve. The study is complemented by the simultaneous work of Dr. Robert Vadas of the University of Maine on seasonal trends in salt marsh productivity along a gradient in the Wells Little River marsh.

Because of their location within the Estuarine Research Reserve system, the Little River and Drakes Island marshes are sure to be the subject of further study. Also, their location within the reserve system gives them a much greater chance of survival as protected ecosystems of benefit for future recreation, study and education. My aim here is to determine the current status and health of the two marshes so that future research and both present and future management decisions will have a base of information on which to proceed.

2.0 The Little River Marsh and the Drakes Island Marsh: General description and plant species

The Little River Marsh

Before launching into the main body of this report, I believe it will be helpful to give a brief description of the two marshes under study and their general characteristics. A general picture of the two marshes, their topography and plant distribution, will provide a framework for the more detailed information to follow.

As mentioned above, the Little River marsh is not typical of the New England high marsh. The marsh lies directly off the Gulf of Maine, separated only by a low barrier beach which does little to shelter the marsh from direct impact by the ocean. There are many shallow pannes and ponds distributed over the marsh surface which result from the stress caused by wracks of dead vegetation, ocean-derived debris, and by beach sand and ice damage. A complex mix of plant species is found in the Little River marsh (Table I), with only short stretches of the rather uniform, predictable mix of *Spartina patens, Juncus gerardii,* and *Distichlis spicata* which would be typical of high New England salt marsh.

The marsh surface is very irregular, because sand and other deposits elevate the marsh or kill marsh vegetation, causing depressions in the marsh surface. Marsh surface microtopography affects plant species composition; the species composition directly correlates with the marsh surface elevation (see Section 6.0). Because of the variable marsh surface, the vegetation at Little River marsh consists of stands of mixed species composition and small clumps of transition zone and sand dune plants.

The Drakes Island Marsh

The Drakes Island marsh is an enclosed pocket marsh; that is, a marsh bordered on all sides by upland barriers and having a single, and in this case restricted, connection to the ocean. The tidal flow into Drakes Island marsh is limited by a dam under the bridge on Drakes Island Road. As stated above, all salt marsh is tidal. Without the driving tidal energy and regular influx of salt water into a marsh system, the system will evolve into something which, while not necessarily unhealthy, is not salt marsh.

The plant composition of the Drakes Island marsh is indicative of a healthy brackish-to-fresh-water marsh (Table II). But the salt marsh that formerly existed here is being lost as the marsh evolves into an upland community with the invasion of terrestrial plant species.

The Drakes Island marsh is dominated by tall plant species such as *Typha angustifolia* (cattail), reeds and rushes. The marsh plants represent a low-density, high-canopy stand of upper marsh vegetation. Bushes such as blueberry and rose are invading the edge of the marsh, and extending the transition zone to terrestrial habitat typically found along a marsh edge. Small maples and pine occur at the outer fringes of Drakes Island marsh.

The habitat at Drakes Island marsh is ideal for mammals, which can graze, feed, and find refuge among the taller growth. Deer, raccoons, and foxes use Drakes Island marsh regularly.

3.0 Productivity in the Little River Marsh and Drakes Island Marsh

3.1 Introduction

Productivity here is a measure of the amount of plant material which grows on the salt marsh in a year. Salt marshes are considered to be highly productive ecosystems. A knowledge of the amount of plant material produced by a salt marsh in a year is a baseline measure of the total contribution that the marsh makes to the estuarine environment. The assessment of productivity at the Wells marshes provides the basis for comparison to other New England marshes and to future studies at Wells. There are several methods for measuring productivity; for comparative purposes, I have measured maximum standing seasonal biomass. A more complete measure of annual productivity was made by Dr. Robert Vadas in his parallel study of the Little River marsh.

3.2 Methods

Three replicate 1/16 m^2 or 1/50 m^2 quadrats, depending on plant density within each species stand, were selected for productivity sampling. Sampling locations were chosen so that the major plant communities would be represented. Plants were collected in August at the peak of the growing season. In general, samples were located along two rough tracks: one running up the river, from higher to lower salinity (I - M); another, from the marsh bank to the upland border of the marsh (N - R) (Fig. 2). Samples were taken from both the Little River and Drakes Island marshes. Plants within the plots were clipped at the marsh surface and placed in plastic bags.

In the laboratory, plants from each quadrat were analyzed separately. Plants were first sorted by species. Number of shoots and flowering parts were counted; reproductive and vegetative material were separated. Reproductive and vegetative material were dried to a constant weight at 80°C for 24 hr; the samples were then weighed and ground.

Non-destructive sediment sippers (Short et al., 1985) were used for sediment nutrient determinations at these same locations, allowing repeated sampling of the sediment interstitial water from within the plant root zone. Interstitial water 5 - 10 cm deep was sampled. Analysis of ammonium (Koroleff, 1976) and phosphate (Strickland and Parsons, 1972) in sediment pore water was measured colorimetrically.

3.3 Results

Seasonal Maximum Standing Biomass

The overall standing plant biomass was measured along two sampling transects that together formed a gradient away from the seawater source (Fig. 2). The combined plant biomass for the marsh showed a marked decrease from the low marsh (Fig. 3: I 1-3) across the high marsh to the upland edge (M-1). A marked biomass increase is then evident from the station at the inner high marsh (Fig. 3: N 1-2) to the center (R1-2) of the brackish water Drakes Island marsh.

Data for marsh plant shoot density over the same two station sets indicate a very different relationship. Low marsh plants (Fig. 3: I1-3) show low density, while the high marsh plants have the highest density at the seaward station and show a reduction in density across the high marsh toward the upland and into the brackish water marsh.

Species Abundance and Reproductive Biomass

Marsh plant samples along the two transects, described above, were analyzed for individual species density and biomass and by species for biomass of flower/seed production (Fig. 4). The density and degree of variability of plant species along each transect were examined. Shoot and flower biomass were compared and showed a high degree of variability between samples at most stations. The difference in density, and flower and shoot biomass at all stations along the transect, show the effect of environmental change within the marsh.

Sediment Salinity and Nutrients

The sediment pore water salinity and nutrients were examined along the same sampling transects (Fig. 5). The salinity in the pore water, indicative of the plants' exposure to ocean water, decreased in the progression up the tidal creek into the marsh (I-M). This dramatic drop in salinity from 30 to 8 ppt was directly associated with the observed decrease in plant biomass (Fig. 3) and was accompanied by a change in plant species (Fig. 4).

The section of the sampling transect running into the Drakes Island marsh showed a relatively constant salinity (Fig. 5) and a high diversity of brackish water plant species (Fig. 4).

Nutrient pore water concentrations of ammonium and phosphate correlated with salinity, with extremely high ammonium levels occurring in the low marsh environment (Fig. 5). Nitrate and nitrite were relatively constant except in one of the brackish water stations in the central marsh.

3.4 Discussion

The production of above ground marsh plants at the Little River marsh in Wells ranged from 50 to 1200 g dry wt/m^2/yr, based on measurements of maximum summer standing biomass. The average production for *Spartina alterniflora*, 1069 g/m^2/yr, is similar to that reported for other east coast marshes (Nixon 1982).

The only extensive high marsh monospecific stands at Little River were of *Spartina patens*, which had a maximum production of 636 g/m^2/yr. The average standing biomass of *S. patens* was somewhat below biomass measurements reported from other central and northern New England marshes (Fig. 6), due to the high degree of variability in density. Density of *S. patens* (6300 shoots/m^2) was comparable to values measured in other New Hampshire and Maine marshes; however, the variability in density (±SD; Fig. 7) was high and was similar to the variability in a stressed New Hampshire marsh in North Hampton (Short, 1983). The stands of *Spartina patens* in the Little River marsh, although as productive as similar marsh areas, show the effects of stress in low biomass and variable density (see Section 5.0).

The above ground standing biomass of combined marsh plant species (Fig. 3) at stations extending from the low marsh to the upland edge (I - M. Fig. 2) shows a dramatic drop along the sampling track. The highest biomass (greater than 1000 g/m^2) occurred at the creek bank low marsh environment. The lowest plant biomass occurred at the stations farthest from the seawater source, in shallow panne areas, and at the edge of the transition zone. The drop in plant biomass directly related to reduction in pore water salinity and sediment nutrient content along the track (Fig. 5). Concentrations of phosphorus and ammonium in the sediment pore water were directly related to plant biomass (Fig. 3).

Continuing along a track further from the seawater source, stations were examined from the south end of the Little River marsh extending into the Drakes Island marsh (N - R: Fig. 2). Biomass increased dramatically from the low-salinity salt marsh station to the stations located in the central portion of the brackish marsh. Here, the highest biomass ranged from 1000 to over 2000 g/m^2. Plants in the Drakes Island marsh were generally larger though less dense (Fig. 3) than those in the salt marsh.

Detailed examination of plant biomass and density and their variability for the major plant species along the two station tracks described above shows the dominance of specific species at each station. The tall form of *Spartina alterniflora*, in the low marsh, was found in low densities but with high biomass and a low degree of variability. Within the high marsh stations, *Spartina patens* showed the highest abundance and degree of variation. Within the brackish water stations, the most variability and highest biomass was seen in *Spartina pectinata*, or fresh water cordgrass.

Sexual reproductive biomass, or flowering biomass, was measured separately from the vegetative biomass to determine its relative importance to overall marsh productivity. In some cases in the salt marsh, such as *Spartina patens,* reproductive biomass was very important. More often, reproductive biomass was significant in the brackish marsh, where *Typha angustifolia* and *Spartina pectinata* made major contributions. Further comparison of reproductive biomass to plant abundance and its nutritional value is described in Section 5.0.

Dr. Robert Vadas and I both measured production during the same growing season, but used different methods. My figures, based on end of growing season maximum biomass, and those of Dr. Vadas, measured as maximum monthly standing crop, were similar for stands of *Spartina alterniflora* adjacent to the Little River. Additionally, my maximum productivity values for *Spartina patens*, based on surveys over a large area of the high marsh, were similar to Dr. Vadas' values, suggesting that our two methods were adequate in assessing the overall productivity of these salt marsh species.

4.0 Aerial Survey

4.1 Introduction

Aerial surveys and photographs are a valuable method for establishing the extent and condition of salt marsh areas and for providing a permanent record of the environment. Aerial methods are particularly useful in documenting stress and damage in salt marshes and dramatically show locations of human impact.

4.2 Methods

A survey of marsh plant populations was made using low level (300 and 1,000 ft) aerial photography. High speed color and infrared film was used to take photographs from a rented fixed wing aircraft. Aerial photography was used to map distribution of vegetated salt marsh areas and the locations of shallow pannes and marsh ponds in the Little River marsh. Actual mapping of salt marsh species was not feasible due to the complex mix of plant species as described in the section on marsh health below. Instead, transects of plant species distribution were surveyed relative to marsh surface elevation within the Little River marsh.

4.3 Results

Aerial photographs of the Wells National Estuarine Research Reserve from 1,000 ft.(Fig. 8) show the Little River, Laudholm Farm, and the Webhannet River. Aerial photographs of Little River marsh show the extensive shallow panne areas and the complex mix of vegetation (Fig. 9). Aerial photograph of the Drakes Island marsh shows the various groupings of brackish water vegetation (Fig. 10). A map of the distribution of shallow pannes and ponds with in the Little River marsh was developed from the low level aerial photography (Fig. 11)

4.4 Discussion

Aerial views of the Wells Estuarine Research Reserve salt marshes show an extensive vegetated strip of marsh running parallel to the shore between the heavily developed barrier island and the increasing development inland (Fig. 8). The exception is the northern end of the Research Reserve, where the Little River marsh shows an absence of human development and activity, both along the barrier island and in the upland surrounding the marsh.

Throughout the entire system, the Wells marshes are dominated by the influences of major rivers, which promote a large exchange of seawater within the marsh system. Additionally, the marsh system is close to the ocean and therefore one would expect to see quite directly the influences of tidal energy and ocean storms on the marsh. This tidal energy has created the necessity for constructing and maintaining a breachway at the mouth of the Webhannet River (Fig. 8).

From the air, the Little River marsh (Fig. 9) is seen as a dramatically meandering riverine system with numerous surface ponds and pannes. The marsh lies just behind a barrier beach, relatively unprotected from the Gulf of Maine. The surface waters on the marsh are of two types: 1) ponds, which are deeper and often contain the rooted seagrass *Ruppia maritima* and 2) shallow pannes, which have bottoms either barren of vegetation or covered with blue-green algal mats. In the lower photograph of Figure 9, the circular, connected ponds in the center and right-hand side of the photograph contain *Ruppia* ; the pannes lie along the left-hand edge of the photograph.

Drakes Island marsh (Fig. 10) is a brackish-to-freshwater marsh wedged between Drakes Island along the coast and the upland of the Laudholm Farm. The tidal flow into the marsh is restricted by a tidal dam under Drakes Island Road, seen in the center of the photograph. The former connection between Drakes Island marsh and the Little River marsh disappeared after the construction of a beach access road seen in the lower right corner of the photograph. The large area of surface water forming an extensive shallow panne to the right of the access road in the photograph was the result of tidal restriction due to the beach access road

Aerial photography has obvious benefits in documenting the environmental conditions within a salt marsh estuary at a given time. Additionally, aerial surveys provide an opportunity to see the cumulative impact of present and past human activities on the marsh ecosystem. Viewed from above, both the natural and human-induced reasons that these marshes are impacted becomes clearer, as discussed more extensively below. As the impact of human development encroaches on the narrow strips of salt marsh found along the coast of Maine, the importance of documenting and maintaining the salt marsh resource increases. A set of the original color photographs of my aerial survey of August 1986 will be preserved at the Wells Estuarine Research Reserve headquarters.

5.0 Nutrition in the Little River Marsh and Drakes Island Marsh

5.1 Introduction

Nutrition is used here to mean the availability of carbon, nitrogen and phosphorus resulting from primary salt marsh plant production to the organisms utilizing the salt marsh environment, to the bacterial populations important in decomposition and detrital cycling within the salt marsh, and to export from the salt marsh into the Gulf of Maine. My underlying hypothesis is that the reproductive portions of salt marsh vegetation, that is flowers, pollen, fruits, and seeds, constitute an important contribution to the overall nutrition of these marsh systems.

Reproductive and vegetative biomass of marsh plants were therefore measured separately at the Little River and Drakes Island marshes in August of 1986, during the period of peak biomass. The nutrient composition (carbon, nitrogen and phosphorus) of both types of biomass was then analyzed.

5.2 Methods

Plant samples were collected as part of the biomass measurements (Section 3.2) or as individual shoots selected from stands of various salt marsh species during the flowering season.

Carbon and nitrogen content of both vegetative and reproductive plant samples was analyzed with a Carlo-Erba Model 1500 Carbon-Nitrogen analyzer. Phosphorus analysis was by extraction using potassium persulfate (Menzel and Corwin, 1965). The phosphate solution was measured using colorimetric analysis, as above (Section 3.2).

5.3 Results

The chemical composition of vegetative and reproductive biomass was determined for dominant marsh species, listed in the figure on a gradient across the marsh transect (Fig. 12). The amounts of carbon, nitrogen and phosphorus are calculated as a percentage of the vegetative and reproductive biomass. The values given for each species are the mean of the three replicate samples; the error bar represents one standard deviation.

Reproductive parts showed consistently higher levels of P, N, and C than vegetative tissue. Phosphorus showed the greatest degree of difference between vegetative and reproductive material.

Two approaches were used to assess the reproductive component of overall plant productivity. Reproductive biomass was compared to vegetative biomass first on a per square meter basis and second on a per shoot basis. The per square meter method represents the minimum amount of seed production for the sample year because not all plants were in the flowering stage at the time of sampling; the per shoot method overestimates seed production, because it assumes that every shoot becomes a flowering shoot during the course of season. These two approaches were necessary because determining the actual flowering capacity of a salt marsh would have required intensive sampling too time consuming and expensive for this study. Thus, the combination of methods yeild a valid range of values for marsh reproduction.

Reproductive biomass is represented as a percent ratio of total biomass on a per square meter basis (Fig. 13). The species shown were found in relatively pure stands which enabled the calculation per square meter. Values ranged from 2% for *Triglochin maritimum* to 16% for *Typha angustifolia*. The two species of *Spartina* were intermediate in their reproductive ratios, with *Spartina patens* almost three times that of *Spartina alterniflora*.

The nutrient allocation for these same four species is displayed in Figure 14 as a ratio of the CNP located in the reproductive tissue to the CNP of the total plant. All species show a greater percentage of N and P than C in reproductive tissue. *Typha angustifolia* shows by far the largest percentage of P, with reproductive parts containing half of the plant's phosphorus.

Reproductive biomass as a percent ratio of weight on a per shoot basis is shown in Figure 15. This calculation gives the maximum possible seed production for these species. Values were available for more species, since pure stands were not needed to perform the calculation. *Juncus gerardii, Spartina patens, Panicum longifolium,* and *Typha angustifolia* all showed nearly 30% of their total weight as reproductive.

CNP allocation was then calculated on a per shoot basis for the four plant species in Figure 15 (Fig. 16). *Juncus gerardii, Spartina patens,* and *Typha angustifolia* had 50% of nitrogen and more than 60% of their phosphorus in the reproductive portion of the plants.

5.4 Discussion

Comparing the reproductive biomass of plant species on the marsh, the data, even from measurements taken at a single point in time during the summer, show there is a significant contribution by reproductive material to overall biomass. The maximum potential contribution of reproductive biomass was estimated by determining the reproductive ratio for marsh plants on a per shoot basis. This maximum value is comparable to estimates on a per meter squared basis, assuming 100% of shoots flower during a growing season. Presumably this is an overestimate, but it provides a calculation of the upper limit for reproductive material on the marsh.

Using these two methods, the range of reproductive ratios for *Spartina alterniflora* is 2 - 12%, for *Spartina patens* 6 - 28%, *Triglochin maritimum* 1 -10%, *Typha angustifolia* 16 - 35%. For other species which were not sampled in monospecific stands, *Juncus gerardii* and *Panicum longifolium*, two high marsh plants, showed 35% and 40%, respectively, of their weight as reproductive tissue.

These estimates show for the first time that reproductive biomass is a significant percentage of total biomass throughout the marsh. Examination of the nutrient composition of the reproductive and vegetative plant tissue increases the significance of this finding because both on a per square meter and a per shoot basis, phosphorus and nitrogen are concentrated in the reproductive tissue of most species. The allocation of these two nutrients is greater in reproductive tissue because seeds and flowers contain less structural material and nitrogen and phosphorus are concentrated in genetic material.

Seed production, therefore, is an important element in the overall productivity of the marsh, and indeed seeds disproportionately become the ultimate fate of phosphorus and nitrogen taken up by many plants. Since many marsh systems are considered to be nutrient limited, and because nitrogen and phosphorus provide the primary nutrition for animals, insects, and microbes in the marsh, it is apparent that seed production makes a major contribution to nutrient cycling and trophic ecology in the marsh.

6.0 Health of the Wells Marshes: Little River and Drakes Island

6.1 Introduction

While scientists often characterize a marsh as "degraded" or "unhealthy," there is no accepted definition of what constitutes health in a salt marsh ecosystem. I propose that when a salt marsh is stable, that is, when a salt marsh is maintaining itself as salt marsh, then it can be considered healthy. It is true that the evolutionary history of a salt marsh encompasses a process of formation, extension, and eventual demise, but this process occurs over thousands of years. And whereas natural salt marshes cycle through short-term periods of localized marsh formation and degradation, the overall status of such a marsh is maintenance of extensive stands of typical salt marsh plant species. The extent of tidal inundation, within the daily flooded low marsh, establishes conditions that support the growth of cordgrass, *Spartina alterniflora* ; within the high marsh the type of vegetation found, typically a mix of *Spartina patens*, *Juncus gerardii*, and *Distichlis spicata*, is also determined in part by the extent of tidal inundation and flooding. However, what all salt marsh plants have in common is their requirement for some degree of tidal flooding and draining, and when a marsh becomes unhealthy, then salt marsh plants are replaced by species whose ecology is not directly tied to tidal energy, that is, species that are not dependent on being intertidal.

In this study, I examine the salt marsh plant community in relation to environmental characteristics of elevation, salinity, and distance from marsh creeks in order to assess the stability of the present salt marsh community. Since it is already known what plant communities constitute the typical stable New England salt marsh environment, it should be possible to look at the plant species found in the Wells marshes and determine to what extent they vary from typical high marsh conditions. Finally, an examination of the marshes will show what factors produced any variations from the norm in vegetation and, therefore, what factors are affecting marsh health.

6.2 Methods

In order to investigate plant species at throughout the marsh, two transects were established on the Little River marsh (Fig. 17 and 18). Transect A ran west-to-east, extending 230 m from the upland to the Little River. Transect B, which crossed Transect A, ran north-to-south for 525 m, parallel to the Little River. Each transect terminated at the river bed. Transect A was established roughly parallel to the barrier beach, while Transect B ran perpendicular to the beach.

The marsh was surveyed on October 8, 1986, using a surveyor's transit. Plant species identifications and elevation measurements were made at 10m intervals and at the location of noticeable changes in vegetation. Species were identified in the field and samples brought back to the laboratory for verification as necessary.

The species identifications were compiled and analyzed according to elevation. Careful examination revealed distinct separation of species by elevation. Specific plant species combinations and frequencies clustered at certain elevation intervals. If each transect was divided by elevation into six zones, certain species combinations repeated themselves, always within a given zone, regardless of distance along the transect. The zones were determined as: above 1.5 m; 1.4 - 1.5m; 1.25 - 1.4m; 1.2 - 1.25m; 1.1 - 1.2m; and below 1.1 m above mean lower low water.

Species surveys were made at the seaward end and the upland end of the Drakes Island marsh. As discussed in Section 2.2, the entire marsh is dominated by brackish, freshwater, and upland plant species, relating directly to the human modification of the marsh that took place when Drakes Island Road was put in and the tidal dam was constructed.

6.3 Results

The highest elevation (greater than 1.5m above mean lower low water) was characterized by mounds of sand transported by wind, waves, and ice from the barrier beach to the marsh surface (Fig. 19 and 20). Many of the plants found within this zone were beach plants, such as *Ammophila breviligulata* (beach grass) and *Lathyrus japonicus* (beach pea), which were thriving on the marsh in the "pocket dunes" of transported sand. *Panicum longifolium* (panic grass) and *Solidago sempervirens* (seaside goldenrod) were the most prevalent plants at this elevation; other plants included *Glaux maritimum* (sea milkwort), *Aster tenuifolius* (salt marsh aster), and *Myrica pensylvanica* (bayberry), all beach dune or transition-zone plants.

The 1.4 - 1.5m zone also had *Panicum longifolium* as its most prevalent plant, but *Juncus gerardii* (black grass), a high marsh plant, replaced seaside goldenrod as the second most prevalent. Another high marsh plant, *Triglochin maritimum* (triglochin) is also found. Beach pea and bayberry, both dune plants, are absent in this lower zone.

Zone C, from 1.25 - 1.4m, showed a typical New England high marsh combination of plants. *Spartina patens* (salt hay), *Juncus gerardii* (black grass), and *Distichlis spicata* (spike grass) predominated; these plants are the familiar trio that form the dense wavy grasses that mean "high marsh" to most naturalists. *Limonium carolinianum* (sea lavender), two species of *Plantago* (seaside plantain), and *Salicornia europaea* (common glasswort) were also present in smaller quantities.

The narrowest zone, Zone D, showed a grouping of species within the 1.2 to 1.25m elevation above mean lower low water. The elevation represented a slightly depressed high marsh elevation, usually areas of saturated shallow pannes that had recently revegetated and were reestablishing a plant community. *Spartina alterniflora* (cordgrass) was present in its stunted form, the form to be expected except along creek banks. Also present were *Limonium carolinianum* (sea lavender), *Plantago* spp. (seaside plantain), and *Spartina patens* (salt hay).

The 1.1 - 1.2m elevation, Zone E, represented major depressions in the marsh surface, sometimes partially flooded and often covered with algal mats. These areas sometimes had no upright plants; when they did, *Salicornia europaea* (common glasswort), and sparse stunted cordgrass and salt hay were present.

Below 1.1m, the marsh-to-water margin occurs, and either shallow ponds or the creek bank is found. On some pond bottoms, *Ruppia maritima* (widgeon grass) is found growing extensively. *Spartina alterniflora* (cordgrass) is found along the creek banks growing, as to be expected in that location, in its tall form, and along some pond edges as well.

6.4 <u>Discussion</u>

Elevation within a salt marsh determines the extent to which ocean water floods the marsh surface as a function of daily and lunar tidal cycles. Thus, the particular elevation of any portion of marsh has a direct impact on the frequency of flooding and the extent to which the plants growing at that elevation are inundated with salt water. This acts to influence plant species composition by selecting for more or less salinity tolerant plants. Additionally, the duration of inundation and sediment saturation has a major impact on plant species occurrence.

Plant species groupings and species frequency within groupings were the same within elevation zones along both transects, A and B (Figs. 17 and 18). Neither transect was typical of New England salt marshes; both showed irregular marsh surface topography and high diversity of species along their entire lengths.

Transect A ran parallel to the barrier beach, and showed equal impact along its length from oceanic effects such as sand and debris transported by wind, waves, and ice over the barrier island. The entire transect was heavily influenced by these oceanic effects, with erratic topography formed by mounds of beach sand and depressions from debris deposited on the marsh surface. Many of the depressions had layers of sand on the bottom, evidence of a former mound of beach sand that had compacted the marsh peat and dispersed, causing subsidence of the marsh surface. The variations in elevation are directly reflected in the high diversity of plant species, with a relatively small portion of the transect having vegetation typical of New England high salt marsh.

Transect B, which ran perpendicular to the barrier beach and parallel to the tidal creek, showed ocean influences only at its seaward end. This indicates that the ocean-related stress to the marsh invades from over the barrier beach, and not up the tidal inlet. Once past the ocean-derived deposits of sand and debris, the majority of the remainder of Transect B is at or below the elevation of typical New England high marsh.

The mid-section of Transect B is riddled with slight depressions and shallow ponds, which appear to be at various stages of formation and natural restoration. Some of the ponds may be caused by debris deposited on the marsh, or by ice excavating the surface of the marsh peat. However, the cause of a number of circular shallow ponds occurring throughout the marsh is unknown (Fig. 21). Also unexplained is the subsidence of the marsh surface at the landward end of Transect B, with large areas of salt hay being flooded during neap tides and a large area of tall cordgrass apparent at the far end of the transect. A possible explanation for the extensive surface water formations is overall regional subsidence of the coast, as seen elsewhere in Maine (Jacobson et al., 1987).

My findings concerning plant species groupings and species diversity, gathered from detailed examination of the two transects, can now be compared to what we know from many previous studies to be representative New England high salt marsh characteristics. The comparison makes it possible to draw some conclusions about the health of the Little River and Drakes Island marshes.

7.0 Conclusions and Recommendations

The assessment of salt marsh species distribution, production, and nutrition as part of this research establishes baseline information for knowledge of the Wells Estuarine Research Reserve and makes it possible to draw some conclusions about the status and health of the marsh system at present. Only detailed investigation of the ecological relationships between plants and their environment can provide insight into the status the complex salt marsh-dominated estuary.

As I proposed above, a salt marsh is healthy if it tends to preserve itself as salt marsh. According to this definition of health in a salt marsh, neither the Little River marsh nor the Drakes Island marsh is a healthy salt marsh. Both are changing in ways which tend not to preserve their salt marsh characteristics, and which, though different, tend to change plant species diversity and distribution.

The Little River Marsh is experiencing fairly severe stress along its shoreward edge. Ice carries sand across the barrier island and deposits it on the marsh, causing topological changes which affect plant species diversity and distribution. When sand is deposited on the marsh surface, the resulting elevated patches are often colonized with goldenrod, aster, or dune grass. In time, the sand causes the marsh peat to subside, and these depressions become pools in the marsh surface, causing another change in topography and plant species.

The landward portion of the Little River marsh also does not reflect a healthy marsh conditions typical of a New England high marsh environment. The marsh is covered with extensive shallow pannes and deeper ponds and shows areas of marsh surface subsidence along the main tidal river. The combination of these factors gives this portion of the Little River marsh an uncharacteristic high species diversity. This area has few of the typical large monospecific stands of high marsh plants which are evident in the Webhannet River marshes to the south.

The Little River salt marsh is relatively undisturbed by human activity. Rather, the Little River marsh has the characteristics of a naturally stressed tide marsh environment. Although from a salt marsh perspective the Little River marsh is unhealthy, it may represent a type of salt marsh environment directly influenced by the ocean and no longer found in areas where ocean front development has altered the barrier islands. The various marsh characteristics, including oceanic influences, shallow panne formation, development of deeper ponds, areas of subsidence and a meandering tidal creek make the Little River marsh a valuable laboratory for more detailed examination of these coastal processes.

Shallow pannes and marsh surface ponds are not well understood, although it is evident they occur as a result of human disturbance (adjacent to the beach causeway between Little River marsh and Drakes Island marsh) and natural perturbations (as evident on the ocean side of Little River marsh). Detailed determination of the processes causing the pannes formations throughout the Little River marsh would help managers develop the expertise for diagnosing development pressures on salt marshes. There are no specific recommendations appropriate for the Little River marsh, since the factors creating the unhealthy conditions appear to be natural. My study identifies the dynamic character of this naturally stressed salt marsh; time course examination of the marsh will increase our knowledge of this type of salt marsh ecosystem.

Tidal restriction, which alters the tidal exchange, is the main cause of changes to the Drakes Island marsh. The tidal dam under Drakes Island Road has caused a major loss of tidal energy and tidal flushing in the Drakes Island marsh. The salinity regime has changed as well, and as stated before, salinity and elevation are the main factors in determining marsh plant species composition. Marked changes in plant species composition have occurred, to an extent that the Drakes Island marsh can no longer be called a salt marsh. It is, rather, a brackish- to fresh-water marsh, with many invading terrestrial species along its upland perimeters.

The loss of tidal energy and tidal flushing has increased the rate of detrital and soil build-up in the marsh, and is accelerating the process of upland encroachment on the marsh. It is likely that as the process continues, the size of the Drakes Island marsh will shrink.

Drakes Island marsh is currently highly productive, both in terms of plants and animals. The fresh and brackish water marsh plant species found in the Drakes Island marsh are characteristically taller and less dense than salt marsh plants, providing ample cover and protection for animals inhabiting the marsh. Reduction in the size of the marsh and encroachment by woody plant species will restrict the usefulness of the marsh to animals and birds, and will eventually result in loss of habitat. As woody plants invade the marsh, and alter the sediment characteristics, the marsh evolves into upland forest.

If the desire is to maintain this brackish water marsh habitat, it is important to keep human development back from the marsh and to mechanically slow the terrestrial plant encroachment by cutting back invading plants in the transition zone. Control of the invasion of terrestrial plants could be achieved by annual tractor mowing of a strip adjacent to the transition zone around the landward edge of the marsh. The tidal dam under Drakes Island Road should remain in place and be maintained in order to ensure stable tides and salinity distribution within the marsh. Taking out the tidal dam at this point in marsh development would cause a return to salt marsh conditions which would result in loss of an important wildlife habitat within the Wells Estuarine Research Reserve marsh ecosystem. Increased housing development along the barrier island is currently the largest threat to animal populations inhabiting Drakes Island marsh. Every effort should be made to create a wooded buffer in the transition zone isolating housing development from the Drakes Island marsh habitat.

The marshes of the Wells National Estuarine Research Reserve provide interesting and valuable environment for the study of dynamic estuarine processes. Further study within this ecosystem will give the badly needed information necessary to manage this and other coastal estuarine environments.

Current Literature

Adams, D.A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44:445-456

Baker, J.M. 1979. Responses of salt marsh vegetation to oil spills and refinery effluents. Pages 529-542 in R.L. Jefferies and A.J. Davy, eds. Ecological processes in coastal environments. Blackwell Scientific Publ.

Bloom, A.L. and M. Stuvier. 1963. Submergence of the Connecticut coast. Science 139:332-334.

Blum, J.L. 1968. Salt marsh spartinas and associated algae. Ecol. Monogr. 38:199-221.

Bourn, W.S. and C. Cottam. 1950. Some biological effects of ditching tidewater marshes. Res. Rep. 19. U.S. Department of the Interior, Fish and Wildlife Service. 17 pp.

Chamie, J.P. and C.J. Richardson. 1978. Decomposition in northern wetlands. Pages 115-130 in R.E. Good, D.F. Whigham, and R.L. Simpson, eds. Freshwater wetlands--ecological processes and management potential. Academic Press, New York.

Chapman, V.J. 1940. Succession on the New England salt marshes. Ecology 21:279-282.

Chapman, V.J. 1960. Salt marshes and salt deserts of the world. Interscience Publ., New York.

Cotnoir, L.J. 1974. Marsh soils of the Atlantic coast. Pages 441-447 in R.J. Reimold and W.H. Queen, eds. Ecology of halophytes. Academic Press, New York.

Daiber, F.C. 1974. Salt marsh plants and future coastal salt marshes in relation to animals. Pages 475-508 in R.J. Reimold and W.H. Queen, eds. Ecology of halopyhtes. Academic Press, New York.

Davis, C.A. 1910. Salt marsh formation near Boston and its geological significance. Econ. Geol. 5:623-639.

de la Cruz, A. 1975. Proximate nutritive value changes during decomposition of salt marsh plants. Hydrobiologia 47(3-4):475-480.

de la Cruz, A. and B.C. Gabriel. 1974. Caloric, elemental, and nutritive changes in decomposing *Juncus roemerianus* leaves. Ecology 55:882-886.

DeLaune, R.D., R.J. Buresh, and W.H. Patrick, Jr. 1979. Relationships of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. Estuarine Coastal Mar. Sci. 8:477-487

Dexter, R.W. 1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: a study in bioecology. Ecol. Monogr. 17:262-294.

Frey, R.W. and P.B. Basan. 1978. Coastal salt marshes. Pages 101-169 in R.A. Davis, Jr., ed. Coastal sedimentary environments. Springer-Verlag, New York.

Gallagher, J.L. 1978. Estuarine angiosperms: productivity and initial photosynthate dispersion in the ecosystem. Pages 131-143 in M.L. Wiley, ed. Estuarine interactions. Academic Press, New York.

Gosselink, J.G. and R.J. Baumann. 1980. Wetland inventories: wetland loss along the United States coast. Z. Geomorph. Suppl. 34:173-187.

Hampson, G.R. and E.T. Moul. 1978. No. 2 fuel oil spill in Bourne, Massachusetts: immediate assessment of the effects on marine invertebrates and a 3-year study of growth and recovery of a salt marsh. J. Fish. Res. Board Can. 35:731-744.

Harrison, E.Z. and A.L. Bloom. 1977. Sedimentation rates on tidal salt marshes in Connecticut. J. Sediment. Petrol. 47(4):1484-1490.

Hill, D.E. and A.E. Shearin. 1970. Tidal marshes of Connecticut and Rhode Island. Conn. Agric. Exp. Stn. Bull. 709.

Hopkinson, C.S. and J.P. Schubauer. 1984. Static and dynamic aspects of nitrogen cycling in the salt marsh graminoid *Spartina alterniflora*. Ecology 65:961-696.

Howarth, R.W. and J.M. Teal. 1980. Energy flow in a salt marsh. ecosystem: the role of reduced inorganic sulfur compounds. Am. Nat. 116:862-872.

Ingold, A. and D.C. Havill. 1984. The influence of sulphide on the distribution of higher plants in salt marshes. J. Ecol. 72:1043-1054.

Jacobson, H.J., G.L. Jacobson and J.T. Kelly. 1987. Distribution and abundance of tidal marshes along the coast of Maine. Estuaries 10:126-130.

Johnson, D. 1925. The New England-Acadian shoreline. Hafner Publ. Co., New York. 608 pp.

Johnson, D.S. and H.H. York. 1915. The relation of plants to tide levels. Carnegie Inst., Washington, D.C. Publ. 206. 162 pp.

Kavenagh, W.K. 1980. Vanishing tidelands: land use and law in Suffolk County, N.Y. 1650-1979. New York Sea Grant Inst. Publ. RS-80-28. 265 pp.

Keefe, C.W. 1972. Marsh production: a summary of the literature. Contrib. Mar. Sci. 16:165-181.

Keene, H.W. 1971. Postglacial submergence and salt marsh evolution in New Hampshire. Marit. Sediments 7(2):64-68.

Kjerfve, B., J.E. Greer, R.L. Crout. 1978. Low-frequency response of estuarine sea level to non-local forcing. Pages 497-513 in M.L. Wiley, ed. Estuarine interactions. Academic Press, New York.

Knight, J.B. 1934. A salt-marsh study. Am. J. Sci. 28:161-181.

Kraeuter, J.N. and P.L. Wolf. 1974. The relationship of marine macroinvertebrates to salt marsh plants. Pages 449-462 in R.J. Reimold and W.H. Queen, eds. Ecology of halophytes. Academic Press, New York.

Lagna, L. 1975. The relationship of *Spartina alterniflora* to mean high water. New York Sea Grant Inst. Publ. RS-75-002. 48 pp.

Linthurst, R.A. and R.J. Reimold. 1978. An evaluation of methods for estimating the net aerial primary productivity of estuarine angiosperms. J. Appl. Ecol. 15:919-931.

Lytle, R.W., Jr. and R.J. Hull. 1980. Photoassimilate distribution in *Spartina alterniflora* Loisel. II., Autumn and winter storage and spring regrowth. Agron. J. 72(Nov.-Dec.):938-942.

Meanley, B. and J.S. Webb. 1963. Nesting ecology and reproductive rate of the red-winged blackbird in tidal marshes of the lower Chesapeake Bay region. Chesapeake Sci. 4:90-100.

Mendelssohn, I.A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. Ecology 60:547-584.

Menzel, D.W. and N. Corwin. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fraction by persulfate oxidation. Limnol. Oecanogr. 10:280-282.

Miller, W.B. and F.E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuck tidal-marshes, Connecticut. Ecol. Monogr. 20:143-172.

Moul, E.T. 1973. Marine flora and fauna of the Northeast United States. Higher plants of the marine fringe. NOAA Tech. Rep., NMFS Circ. 384.

Niering, W.A. and R.S. Warren. 1980. Vegetation patterns and processes in New England salt marshes. BioScience 30:301-307.

Nixon, S.W. 1980. Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. Pages 437-525 in P. Hamilton and K.B. MacDonald, eds. Estuarine and wetland processes. Plenum Publishing Corp., New York.

Nixon, S.W. and C.A. Oviatt. 1973a. Ecology of a New England salt marsh. Ecol. Monogr. 43(4):463-498.

Nixon, S.W. and C.A. Oviatt. 1973b. Analysis of local variation in the standing crop of *Spartina alterniflora*. Bot. Mar. 16:103-109.

Nixon, S.W. 1982. The ecology of New England High Salt Marshes: A community Profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-81/55. 70 pp.

Odum, E.P. 1968. A research challenge: evaluating the productivity of coastal and estuarine water. Pages 63-64 in Proceedings 2nd Sea Grant Conference, Graduate School, Oceanography, University of Rhode Island, Newport.

Odum, E.P. 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling and detritus-based food chains. Pages 485-495 in V.S. Kennedy, ed. Estuarine perspectives. Academic Press, New York.

Odum, W.E. and M.A. Heywood. 1978. Decomposition of intertidal freshwater marsh plants. Pages 89-97 in R.E. Good, D.F. Whigham, and R.L. Simpson, ed. Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

Palmer, M.A., B. Kjerfve, and F.B. Schwing. 1980. Tidal analysis and prediction in a South Carolinas estuary. Contrib. Mar. Sci. 23:17-23.

Parrondo, R.T., J.G. Gosselink, and C.S. Hopkinson. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. Bot. Gaz. 139:102-107.

Phleger, F.B. 1977. Soils of marine marshes. Pages 69-77 in B.J. Chapman, ed. Wet coastal ecosystems. Elsevier Scientific Publ., New York.

Redfield, A.C. 1972. Development of a New England salt marsh. Ecol. Monogr. 42:201-237.

Redfield, A.C. and M. Rubin. 1962. The age of salt marsh peat and its relation to recent changes in sea level a Barnstable, Massachusetts. Proc. Natl. Acad. Sci. U.S.A. 48:1728-1735.

Reed, W.C. and M.C. Heath. 1974. Saltmarsh relocation restoration in Maine. Maine Department of Transportation, Augusta, ME. 48pp.

Reimold, R.J. 1977. Mangals and salt marshes of Eastern United States. Pages 157-166 in B.J. Chapman, ed. Wet coastal ecosystems. Elsevier Scientific Publ. Co., Amsterdam.

Reimold, R.J. and R.A. Linthurst. 1977. Primary Production of Minor Marsh Plants in Delaware, Georgia, and Maine. Dredge Material Research Program. U.S. Army Engineer Waterways Exp. Sta., D-77-36.

Roman, C.T., W.A. Niering, and R.S. Warren. 1984. Salt marsh vegetation change in response to tidal restriction. Environ. Manage. 8:141-150.

Ruber, E., G. Gillis, and P.A. Montagna. 1981. Production of dominant emergent vegetation and of pool algae on a northern Massachusetts salt marsh. Bull. Torrey Bot. Club. 108:180-188.

Shabman, L.A. and S.S. Batie. 1980. Estimating the economic value of coastal wetlands: Conceptual issues and research needs. Pages 3-15 in V.S. Kennedy, ed. Estuarine perspectives. Academic Press, New York.

Shanholtzer, G.G. 1974. Relationship of vertebrates to salt marsh plants. Pages 463-474 in R.J. Reimold and W.H. Queen, eds. Ecology of halophytes. Academic Press, New York.

Short, F.T. 1984. North Hampton Salt Marsh Study. Assessment of Little River and Bass Beach Marsh; The problem, recommended solution and projected outcomes. University of New Hampshire. 18pp.

Short, F.T., M.W. Davis, R.A. Gibson and C.F. Zimmermann. 1985. Evidence for phosphourus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. Estuarine, Coastal and Shelf Science. 20:419-430.

Short, F.T. 1985. Seagrass: Inorganic Chemical Constituents. In: R.C. Phillips and C.P. McRoy, eds. Seagrass research methods. UNESCO. (In Press)

Spinner, G.P. 1969. A plan for the marine resources of the Atlantic coastal zone. American Geographical Society. 80 pp.

Steever, E.Z. 1972. Productivity and vegetation studies of a tidal marsh in Stonington, Connecticut: Cottrell Marsh. M.S. Thesis. Connecticut College, New London. 74 pp.

Sullivan, M.J. and F.C. Daiber. 1975. Light, nitrogen and phosphorus limitation of edaphic algae in a Delaware salt marsh. J. Exp. Mar. Biol. Ecol. 18:79-88.

Taylor, N. 1938. A preliminary report on the salt marsh vegetation of Long Island, New York Bull. N.Y. State Museum 316:21-84.

Teal, J.M. 1959. Respiration of salt marsh crabs and its relation to their ecology. Physiol. Zool. 32:1-14.

Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.

Teal, J.M., I. Valiela, and D. Berlo. 1979. Nitrogen fixation by rhizosphere and free-living bacteria in salt marsh sediments. Limnol. Oceanogr. 24:126-132.

Tiner, R.W., Jr. 1974. The ecological distribution of the invertebrate macrofauna in the Cottrell marsh, Stonington, Connecticut. M.S. Thesis. University of Connecticut, Storrs. 76 pp.

Tiner, R.W., Jr. 1987. A field guide to coastal wetland plants of the northeastern United States. University of Massachusetts Press, Amherst.

Turner, R.E. 1976. Geographic variation in salt marsh macrophyte production: a review. Contrib. Mar. Sci. 20: 47 - 68.

Udell, H.F., J. Zarudsky, T.E. Doheny and P.R. Burkholder. 1969. Productivity and nutrient value of plants growing in the salt marshes of the Town of Hempstead, Long Island. Bull. Torrey Bot.

Club 96:42 -51.

U.S. Fish and Wildlife Service. 1977. Coastal marsh productivity - a bibliography. U.S. Fish and Wildlife Service. FWS/OBS-77/3. 300 pp.

Valiela, I. and J.M. Teal. 1974. Nutrient limitation in salt marsh vegetation. Pages 547-563 in R.J. Reimold and W.H. Queen, eds. Ecology of halophytes. Academic Press, New York.

Valiela, I. and J. M. Teal. 1979. The nitrogen budget of a salt marsh ecosystem. Nature 280:652-656.

Valiela, I., J.M. Teal, and W.J. Sass. 1975. Production and dynamics of salt marsh vegtation and the effects of experimental treatment with sewage sludge. J. Appl. Ecol. 12:245-252.

Valiela, I., J.M. Teal, and N.Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: below ground biomass. Limnol. Oceanogr. 21:245-252.

Valiela, I., J.E. Wright, J.M. Teal, and S.B. Volkmann. 1977. Growth, production and energy transformation in the salt-marsh killifish *Fundulus herteroclitus*. Mar. Biol. 40:135-144.

Van Raalte, C., W.C. Stewart, I. Valiela, and J.M. Teal. 1976. Production of epibenthic salt marsh algae: light and nutrient limitation. Limnol. Oceanogr. 21:862-872.

Welsh, B. 1980. Comparative nutrient dynamics of a marsh-mudflat ecosystem. Estuarine Coastal Mar. Sci. 10:143-164.

Wood, E.J.F., W.E. Odum, and J.C. Zieman. 1969. Influence of sea grasses on the productivity of coastal lagoons. Pages 495-502 in A.A. Castanares and F.B. Phleger, eds. Coastal lagoons. Univ. Mac. Aut. Mexico. 686 pp.

Woodwell, G.M., D.E. Whitney, C.A.S. Hall, and R.A. Houghton. 1977. The Flax Pond ecosystem study: exchanges of carbon in water between a salt marsh and Long Island Sound. Limnol. Oceanogr. 22(5):833-838.

Woodwell, G.M., R.A. Houghton, C.A.S. Hall, D.E. Whitney, R.A. Moll, and D.W. Juers. 1979. The Flax Pond ecosystem study: the annual metabolism and nutrient budgets of a slat marsh. Pages 491-511 in R.L. Jefferies and A.J. Davy, eds. Ecological processes in coastal environments . Blackwell Scientific Publ.

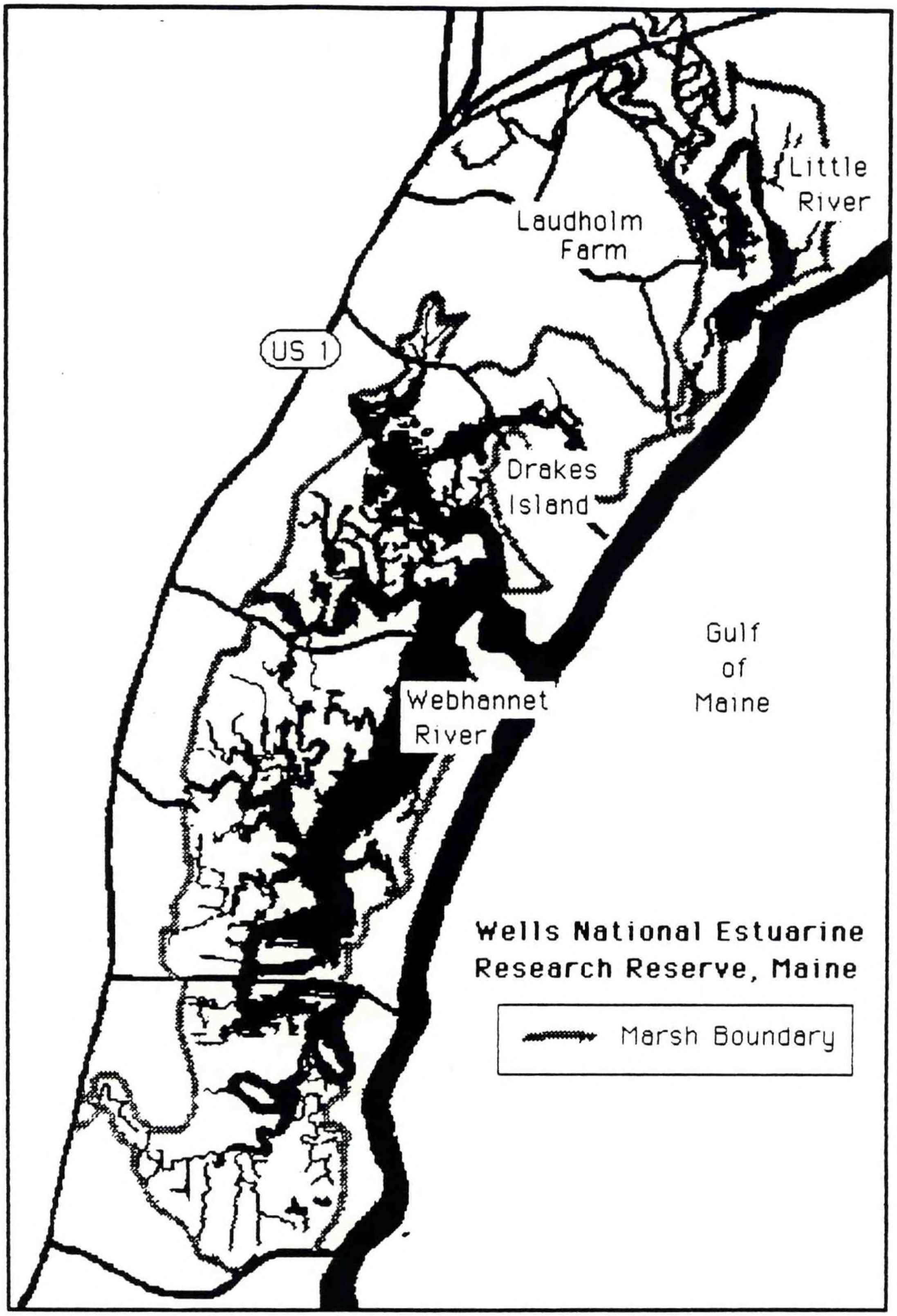


Fig 1. Map of the Wells Estuarine Research Reserve showing the marsh boundary and the two major rivers in the Reserve.

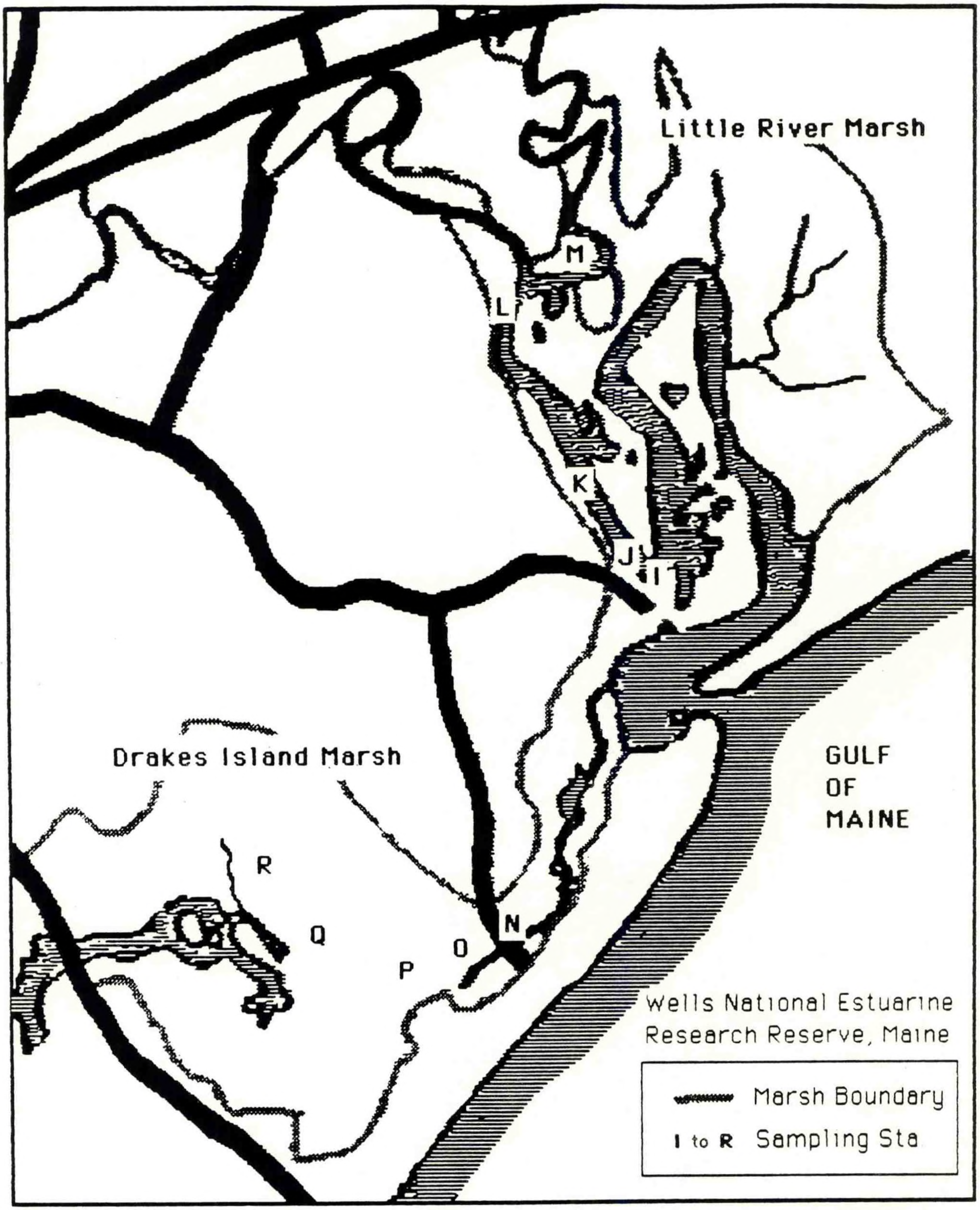


Fig. 2. Map of the Little River marsh and Drakes Island marsh in the Wells Estuarine Research Reserve. Letters depict stations sampled for plant analysis within these two marshes.

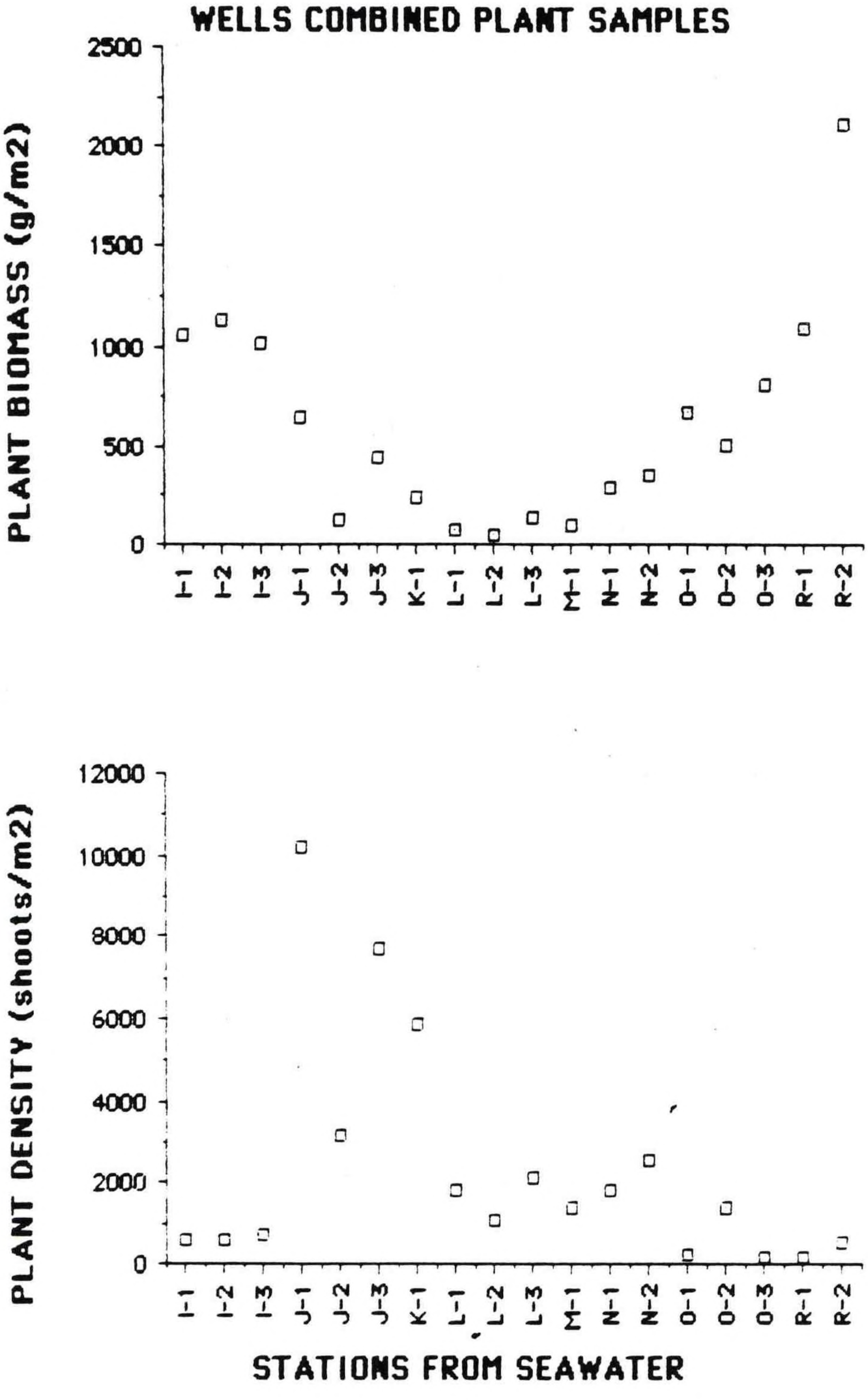


Figure 3. Combined marsh plant biomass and density for stations (see Fig. 1) in the Wells Estuarine Research Reserve.

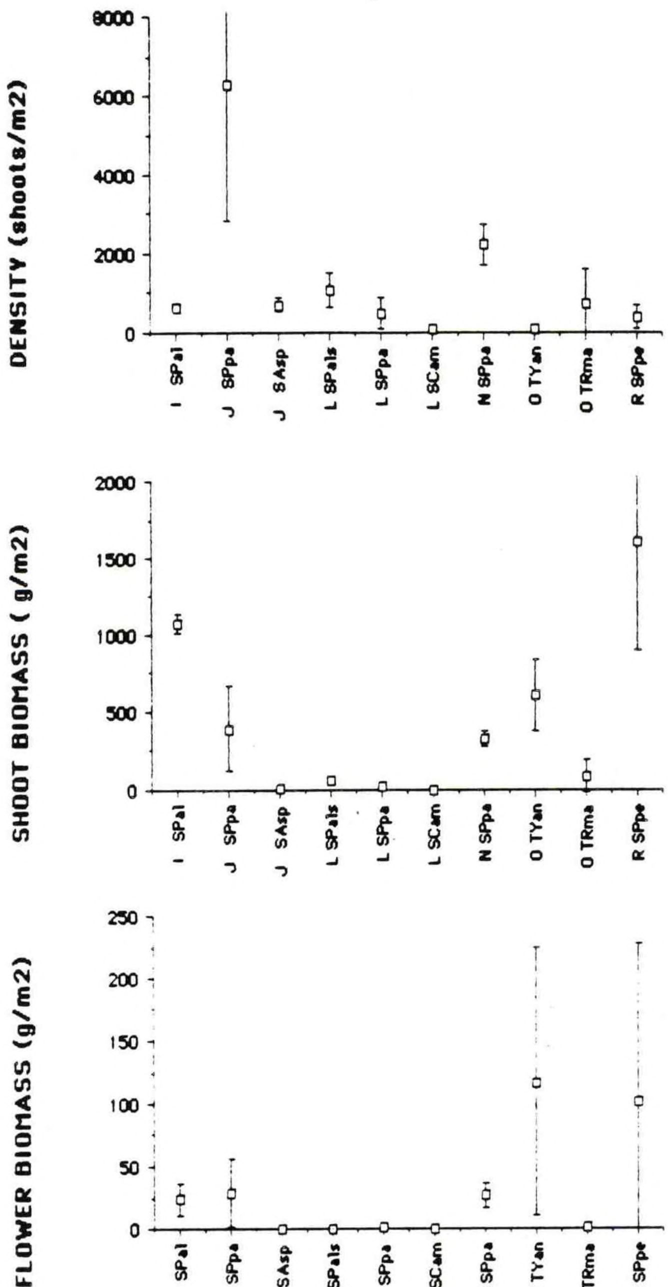


Figure 4 Marsh plant abundance for individual species (see species codes, Appendix 1) at a given station (see Fig. 1) in the Wells Estuarine Research Reserve.

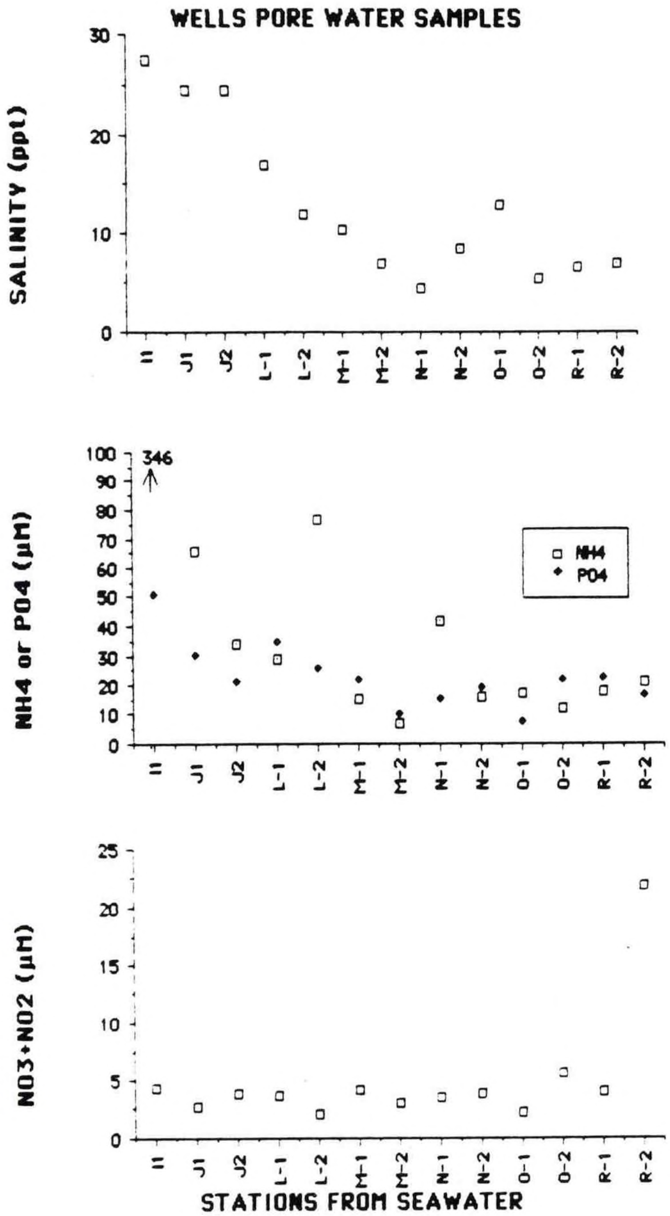


Figure 5. Marsh sediment pore water salinity, ammonium, phosphate and nitrate-plus-nitrite concentrations for stations (Fig. 1) at the Wells Estuarine Research Reserve

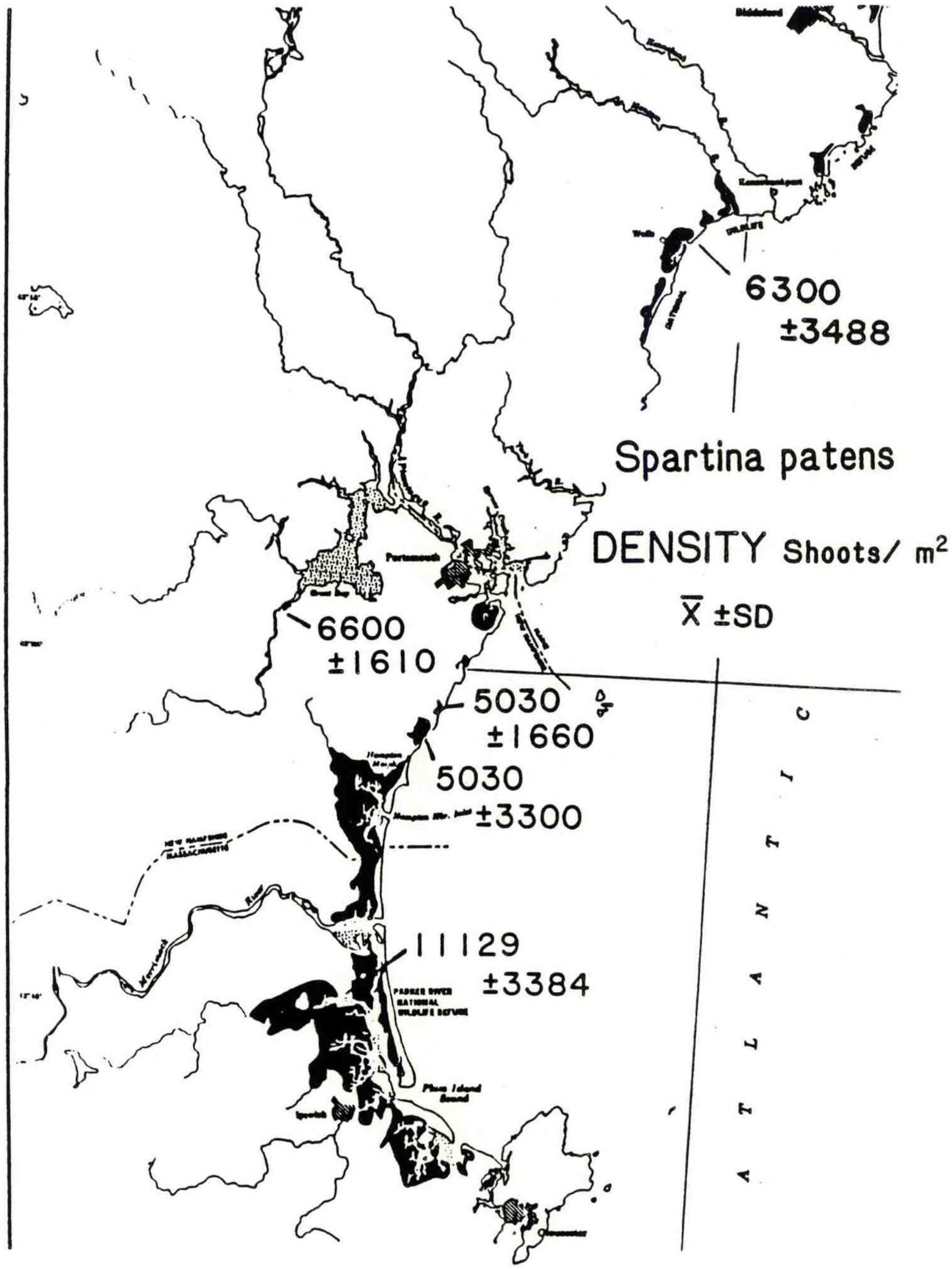


Figure 7. Density of Spartina patens (salt hay) in northern New England marshes.

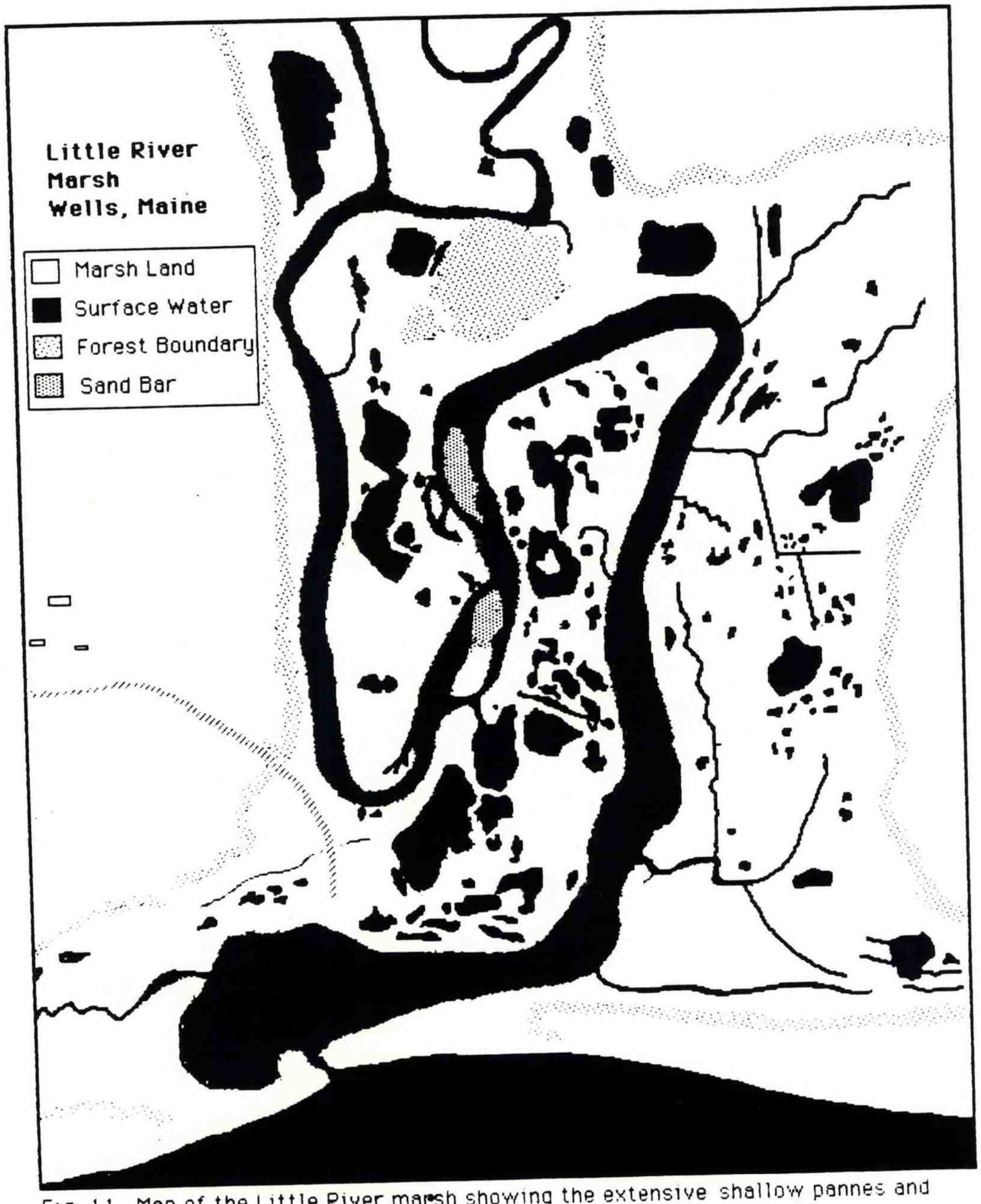


Fig. 11. Map of the Little River marsh showing the extensive shallow pannes and ponds on the marsh surface.

Figure 8. Aerial photographic overview of the salt marshes in the Wells Estuarine Research Reserve. From north to south: Little River and Laudholm Farm (top), Webhannet River breachway (middle), and Webhannet marsh (bottom).

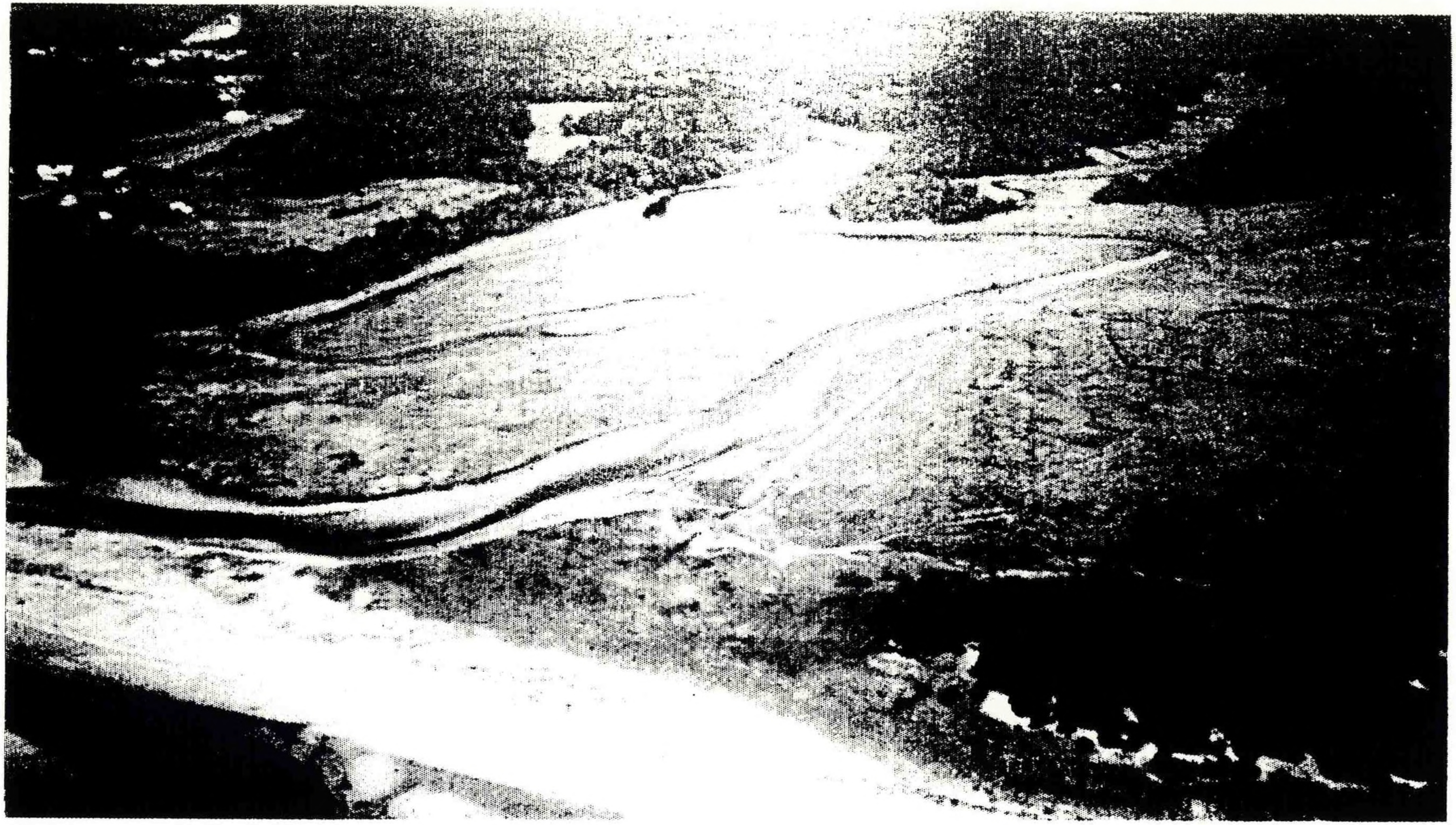


Figure 9. Aerial photographs of the Little River salt marsh. (a) overview of the river system

Figure 9. Aerial photographs of the Little River salt marsh; (b) shallow pannes and ponds on marsh surface.

Figure 1[illegible]. Aerial photograph of the Drakes Island marsh.

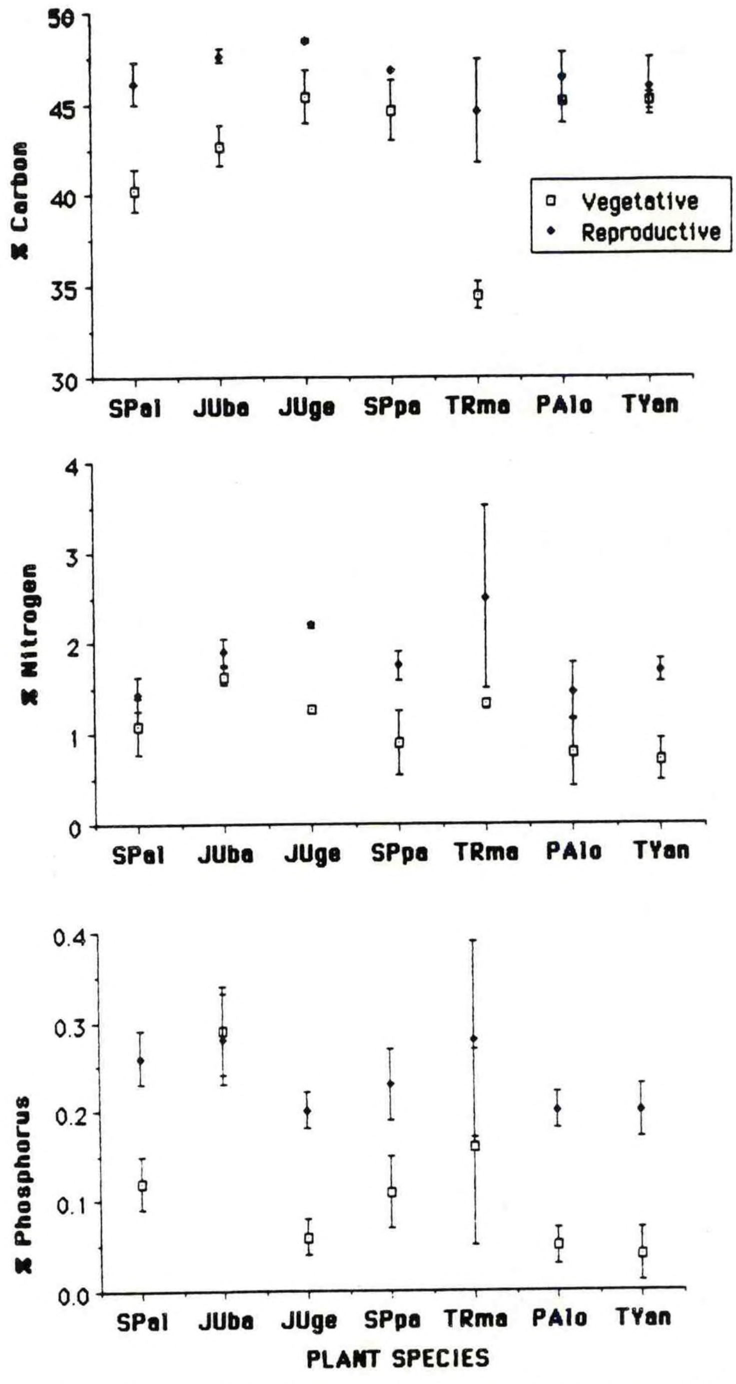


Figure 12. Chemical tissue composition of vegetative and reproductive marsh plant biomass in the Wells Estuarine Research Reserve. Marsh species (see codes in Appendix 1) were examined for carbon, nitrogen, and phosphorus.

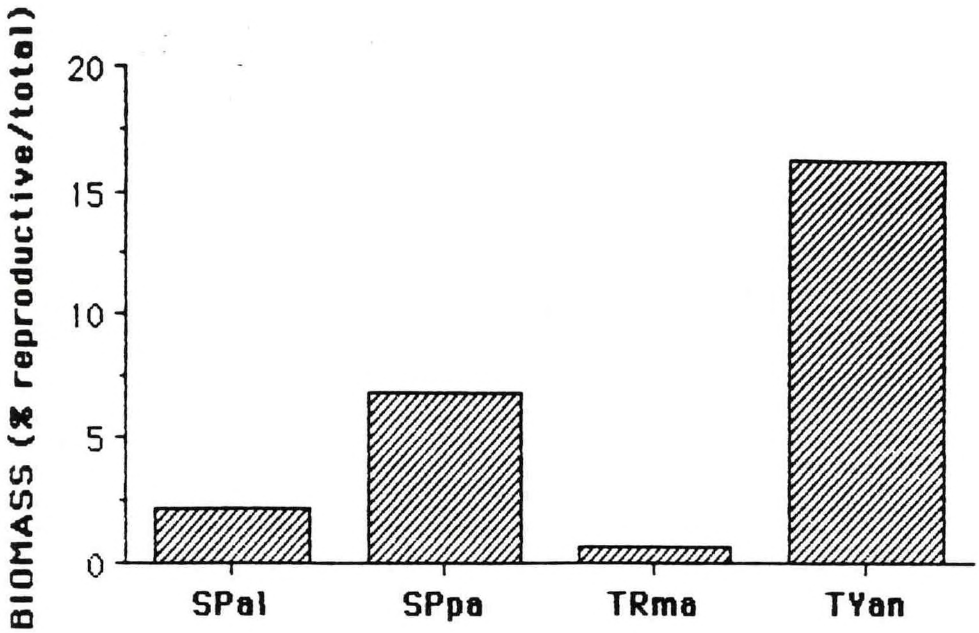


Figure 13. Reproductive biomass of specific marsh species expressed as a percentage of total biomass calculated per meter squared based on actual plant density for dominant species.

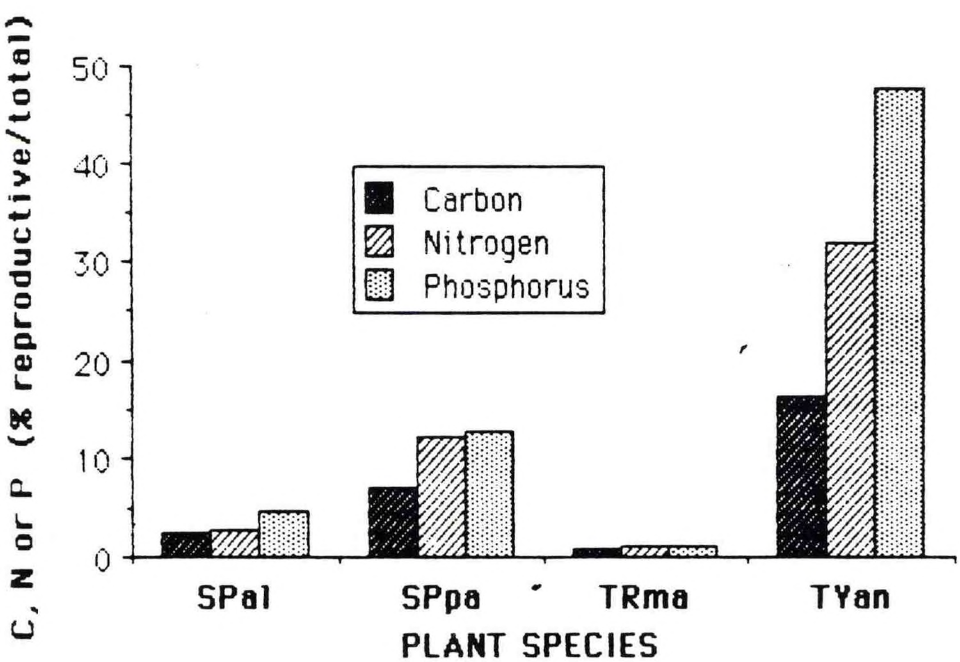


Figure 14. Nutrient allocation of carbon, nitrogen and phosphorus between reproductive and total salt marsh biomass.

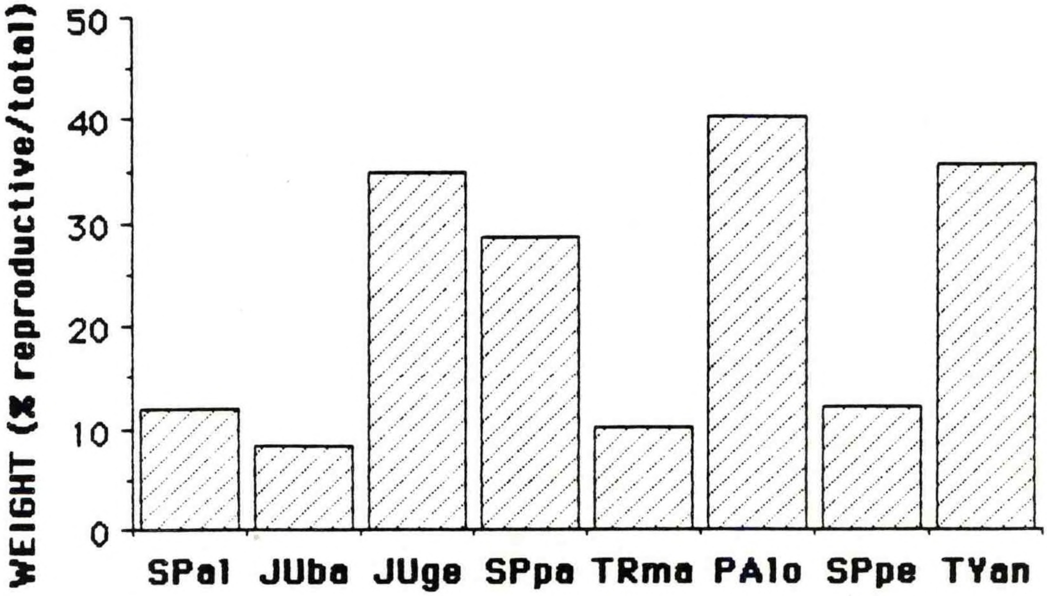


Fig. 15. Reproductive weight of specific marsh species expressed as a percentage of total plant weight calculated on a per shoot basis.

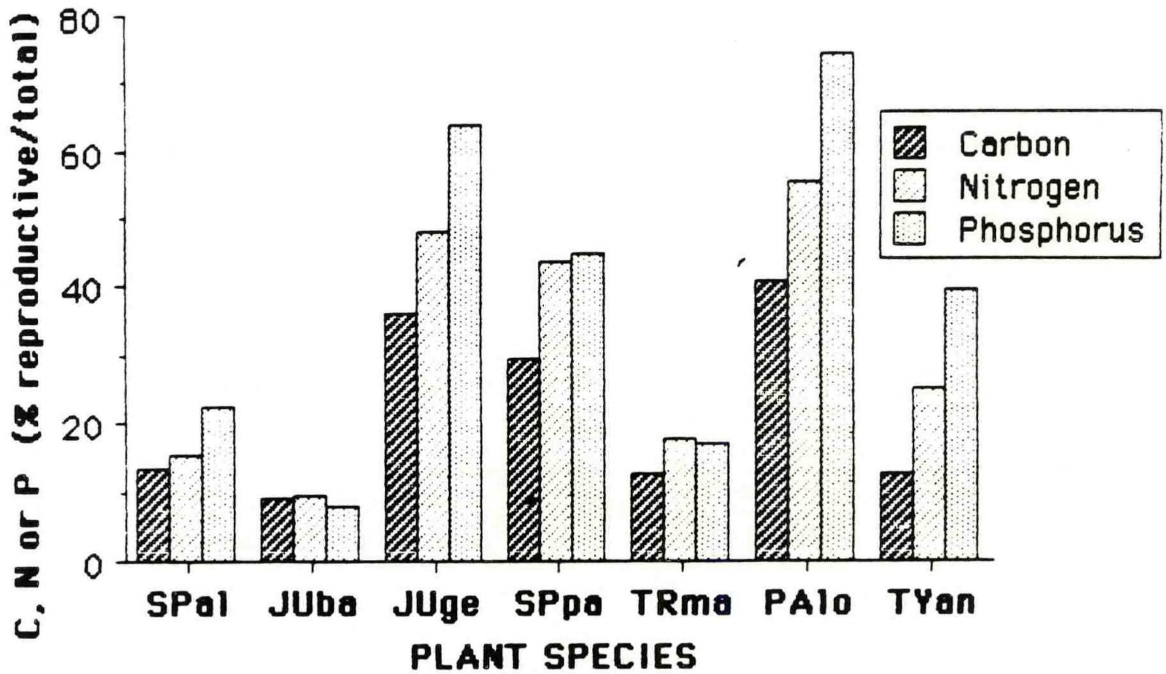


Fig. 16. Nutrient allocation of carbon, nitrogen and phorphorus between reproductive and total salt marsh plant species.

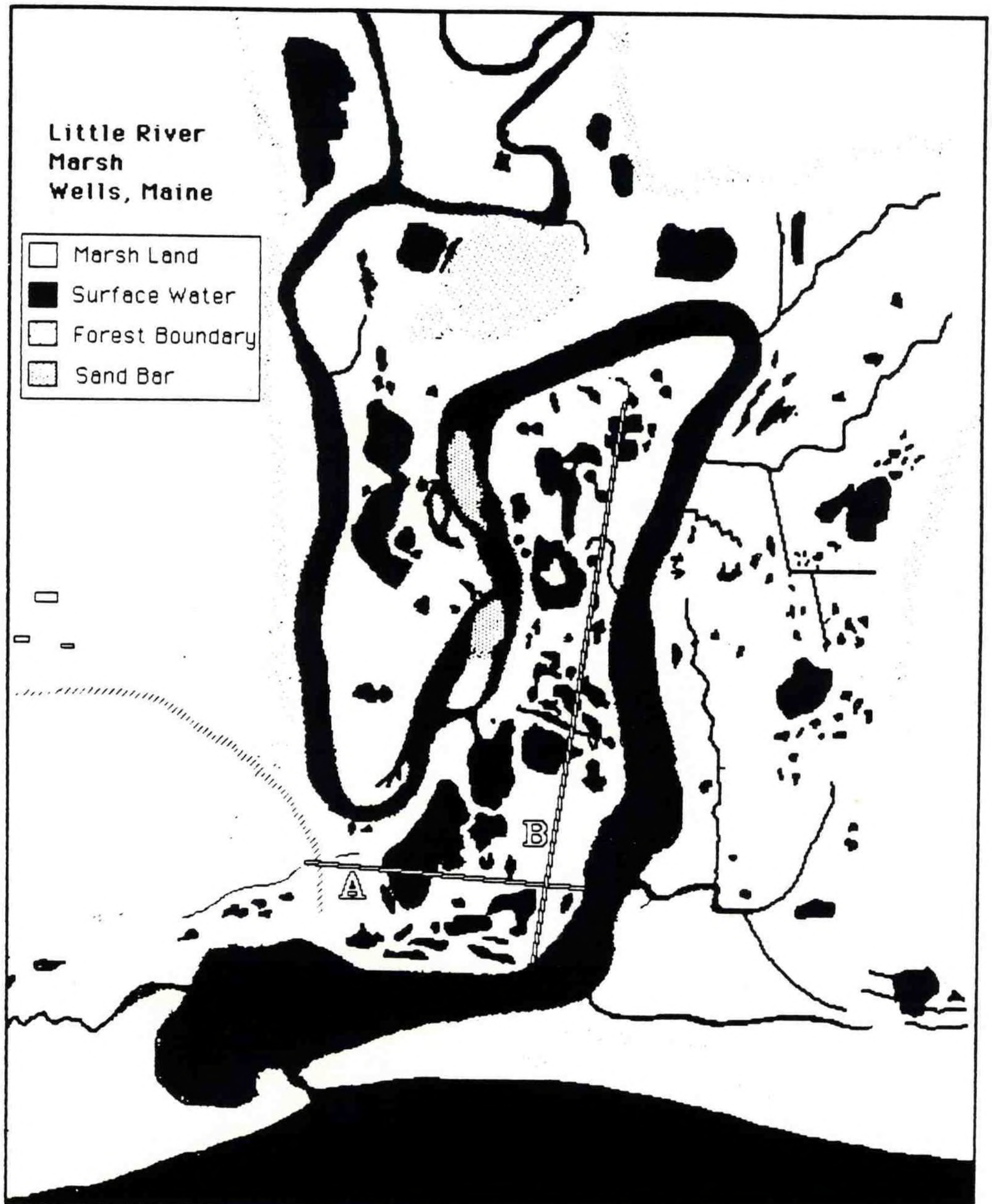


Fig 17 Map of the Little River marsh showing the location of the two elevation survey transects

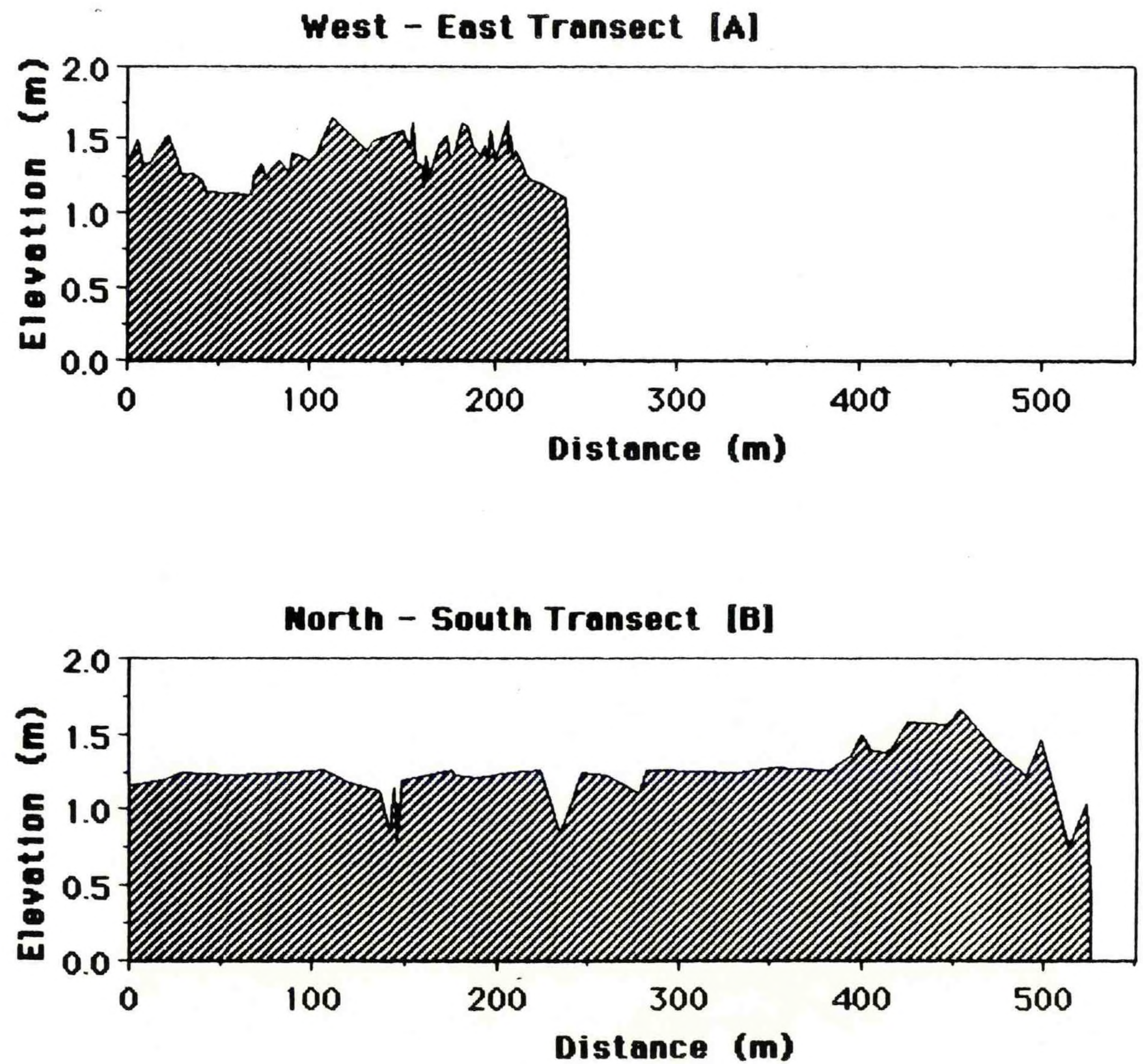
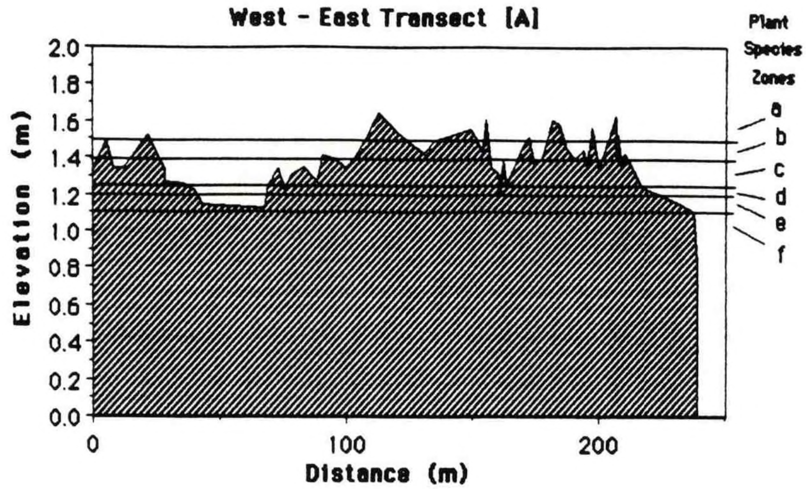


Figure 18. Marsh surface elevation surveys for two perpendicular transects in the Little River marsh. Elevation above the creek bottom is plotted vs. distance along the transect.



ZONE	SALT MARSH SPECIES	ABBRV.	COMMON NAME
a	*AMMOPHILA BREVILIGULATA*	AMbr	BEACH GRASS
	ASTER TENUIFOLIUS	ASte	SALT MARSH ASTER
	GLAUX MARITIMA	GLma	SEA MILKWORT
	LATHYRUS JAPONICUS	LAja	BEACH PEA
	MYRICA PENSYLVANICA	MYpe	BAYBERRY
	PANICUM LONGIFOLIUM	PAlo	PANIC GRASS
	SOLIDAGO SEMPERVIRENS	SOse	SEASIDE GOLDENROD
b	*GLAUX MARITIMA*	GLma	SEA MILKWORT
	JUNCUS GERARDII	JUge	BLACK GRASS
	PANICUM LONGIFOLIUM	PAlo	PANIC GRASS
	SOLIDAGO SEMPERVIRENS	SOse	SEASIDE GOLDENROD
	SPERGULARIA MARINA	SPma	SAND SPURREY
	TRIGLOCHIN MARITIMUM	TRma	SEASIDE ARROW GRASS
c	*DISTICHLIS SPICATA*	DIsp	SPIKE GRASS
	LIMONIUM NASHII	LIna	SEA LAVENDER
	SALICORNIA EUROPAEA	SAeu	GLASSWORT
	SPARTINA PATENS	SPpa	SALT HAY
d	*LIMONIUM NASHII*	LIna	SEA LAVENDER
	PLANTAGO SP	PLsp	SEASIDE PLANTAIN
	SPARTINA ALTERNIFLORA ST	SPals	STUNTED CORDGRASS
	SPARTINA PATENS	SPpa	SALT HAY
e	*SALICORNIA EUROPAEA*	SAeu	GLASSWORT
	SPARTINA ALTERNIFLORA ST	SPals	STUNTED CORDGRASS
	SPARTINA PATENS	SPpa	SALT HAY
f	*RUPPIA MARITIMA*	RUma	WIDGEON GRASS
	SPARTINA ALTERNIFLORA	SPal	CORDGRASS

Figure 19. Groupings of the dominant salt marsh plant species that characterize each of six marsh surface elevation zones (a-f) along transect A running west to east in the Little River marsh

Figure 11. Aerial photograph of circular ponds on the salt marsh surface at the Little River marsh

TABLE I PLANTS OF THE LITTLE RIVER MARSH

SALT MARSH SPECIES	ABBRV	COMMON NAME
AMMOPHILA BREVILIGULATA	AMbr	BEACH GRASS
ASTER TENUIFOLIUS	ASte	SALT MARSH ASTER
ATRIPLEX PATULA	ATpa	ORACH
BACCHARIS HALIMIFOLIA	BAha	GROUNDSEL TREE
BLUE GREEN ALGAE	b/g algae	MAT
DISTICHLIS SPICATA	DIsp	SPIKE GRASS
FESTUCA RUBRA	FEru	RED FESCUE
GERARDIA MARITIMA	GEma	SEASIDE GERARDIA
GLAUX MARITIMA	GLma	SEA MILKWORT
JUNCUS BALTICUS	JUba	BALTIC RUSH
JUNCUS GERARDII	JUge	BLACK GRASS
LATHYRUS JAPONICUS	LAja	BEACH PEA
LIMONIUM NASHII	LIna	SEA LAVENDER
MYRICA PENSYLVANICA	MYpe	BAYBERRY
PANICUM LONGIFOLIUM	PAlo	PANIC GRASS
PLANTAGO JUNCOIDES	PLju	EARLY SEASIDE PLANTAIN
PLANTAGO OLIGANTHOS	PLol	LATE SEASIDE PLANTAIN
POTENTILLA ANSERINA	POan	SILVERWEED
PUCCINELLIA MARITIMA	PUma	GOOSE GRASS
RUPPIA MARITIMA	RUma	WIDGEON GRASS
SALICORNIA EUROPAEA	SAeu	COMMON GLASSWORT
SALICORNIA VIRGINICA	SAsp	WOODY GLASSWORT
SCIRPUS MARITIMUS	SCma	SALT MARSH BULRUSH
SOLIDAGO SEMPERVIRENS	SOse	SEASIDE GOLDENROD
SPARTINA ALTERNIFLORA	SPal	CORDGRASS
SPARTINA ALTERNIFLORA ST	SPals	STUNTED CORDGRASS
SPARTINA PATENS	SPpa	SALT HAY
SPARTINA PECTINATA	SPpe	FRESH WATER CORDGRASS
SPERGULARIA MARINA	SPma	SAND SPURREY
SUAEDA MARITIMA	SUma	SEA BLITE
TRIGLOCHIN MARITIMUM	TRma	SEASIDE ARROW GRASS

TABLE 2. PLANTS AT THE DRAKES ISLAND MARSH

SALT MARSH SPECIES	ABBRV	COMMON NAME
ACER RUBRUM	ACru	RED MAPLE
BACCHARIS HALIMIFOLIA	BAha	GROUNDSEL TREE
CALYSTEGIA SEPIUM	CAse	HEDGE BINDWEED
DISTICHLIS SPICATA	DIsp	SPIKE GRASS
GERARDIA MARITIMA	GEma	SEASIDE GERARDIA
GLAUX MARITIMA	GLma	SEA MILKWORT
ILEX VERTICILLATA	ILve	ALDER
IRIS VERSICOLOR	IRve	BLUE FLAG
JUNCUS BALTICUS	JUba	BALTIC RUSH
JUNCUS EFFUSUS	JUef	SOFT RUSH
MYRICA PENSYLVANICA	MYpe	BAYBERRY
PANICUM LONGIFOLIUM	PAlo	PANIC GRASS
ROSA PALUSTRIS	ROpa	SWAMP ROSE
SCIRPUS AMERICANUS	SCam	CHAIR-MAKER'S RUSH
SOLIDAGO SEMPERVIRENS	SOse	SEASIDE GOLDENROD
SPARTINA PATENS	SPpa	SALT HAY
SPARTINA PECTINATA	SPpe	FRESH WATER CORDGRASS
TRIGLOCHIN MARITIMUM	TRma	SEASIDE ARROW GRASS
TYPHA ANGUSTIFOLIA	TYan	CATTAIL

APPENDIX 1: Plants of the Wells National Estuarine Research Reserve

SALT MARSH SPECIES	ABBRV	COMMON NAME
ACER RUBRUM	ACru	RED MAPLE
AMMOPHILA BREVILIGULATA	AMbr	BEACH GRASS
ASTER TENUIFOLIUS	ASte	SALT MARSH ASTER
ATRIPLEX PATULA	ATpa	ORACH
BACCHARIS HALIMIFOLIA	BAha	GROUNDSEL TREE
BLUE GREEN ALGAE	b/g algae	MAT
CALYSTEGIA SEPIUM	CAse	HEDGE BINDWEED
DISTICHLIS SPICATA	DIsp	SPIKE GRASS
FESTUCA RUBRA	FEru	RED FESCUE
GERARDIA MARITIMA	GEma	SEASIDE GERARDIA
GLAUX MARITIMA	GLma	SEA MILKWORT
ILEX VERTICILLATA	ILve	ALDER
IRIS VERSICOLOR	IRve	BLUE FLAG
JUNCUS BALTICUS	JUba	BALTIC RUSH
JUNCUS EFFUSUS	JUef	SOFT RUSH
JUNCUS GERARDII	JUge	BLACK GRASS
LATHYRUS JAPONICUS	LAja	BEACH PEA
LIMONIUM NASHII	LIna	SEA LAVENDER
MYRICA PENSYLVANICA	MYpe	BAYBERRY
PANICUM LONGIFOLIUM	PAlo	PANIC GRASS
PLANTAGO JUNCOIDES	PLju	EARLY SEASIDE PLANTAIN
PLANTAGO OLIGANTHOS	PLol	LATE SEASIDE PLANTAIN
POTENTILLA ANSERINA	POan	SILVERWEED
PUCCINELLIA MARITIMA	PUma	GOOSE GRASS
ROSA PALUSTRIS	ROpa	SWAMP ROSE
RUPPIA MARITIMA	RUma	WIDGEON GRASS
SALICORNIA EUROPAEA	SAeu	COMMON GLASSWORT
SALICORNIA VIRGINICA	SAsp	WOODY GLASSWORT
SCIRPUS AMERICANUS	SCam	CHAIR-MAKER'S RUSH
SCIRPUS MARITIMUS	SCma	SALT MARSH BULRUSH
SOLIDAGO SEMPERVIRENS	SOse	SEASIDE GOLDENROD
SPARTINA ALTERNIFLORA	SPal	CORDGRASS
SPARTINA ALTERNIFLORA ST	SPals	STUNTED CORDGRASS
SPARTINA PATENS	SPpa	SALT HAY
SPARTINA PECTINATA	SPpe	FRESH WATER CORDGRASS
SPERGULARIA MARINA	SPma	SAND SPURREY
SUAEDA MARITIMA	SUma	SEA BLITE
TRIGLOCHIN MARITIMUM	TRma	SEASIDE ARROW GRASS
TYPHA ANGUSTIFOLIA	TYan	CATTAIL

APPENDIX 2: Public Presentations of the Wells Salt Marsh Research

August 31, 1986. Field trip on research projects in the Reserve, by F. T. Short at The Wells National Estuarine Research Reserve Dedication, Wells, Maine

May 9, 1987. Nutrient Composition of Salt Marsh Biomass at the Wells Research Reserve, by E. C. Brainard and F. T. Short, at New England Estuarine Research Society meeting, Boothbay, Maine

June 4, 1987. Production, Nutrition and Health of the Wells Salt Marshes, by F. T. Short and E. C. Brainard, at Maine Biological and Medical Science Symposium, Bowdoin College, Brunswick, Maine.