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An Inventory of Distribution and Variation in Salt Marshes from Different Settings along the Maine Coast

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ABSTRACT

Planimetry studies of maps of coastal geology prepared by the Maine Geological Survey show that over 3000 separate tidal marshes, encompassing approximately 79 km^2, lie along the coast of Maine. The distribution of tidal marshes as well as their size and vegetation are shown to be related to geologic setting, sediment supply, and developmental history, all of which vary greatly along the 5970 km long coast. Systematic surveys of vegetation in 18 marshes reveal much variability in species composition, species richness, and zonation patterns. Species composition is influenced by freshwater input. Species richness is higher in older marshes situated in stable geologic settings. Zonation patterns represent a transition between those of southern New England and those of the Bay of Fundy region.

INTRODUCTION

Salt marshes of the eastern seaboard of North America can be separated into three types that are named for the region in which they occur: Bay of Fundy-type, New England-type, and Atlantic Coastal Plain-type (Johnson, 1925; Chapman, 1974; Frey and Basan, 1978). Bay of Fundy-type marshes are closely associated with estuarine clay flats. In the scheme of marsh maturation proposed by Frey and Basan (1978), these could be described as developmentally young marshes, in which meandering watercourses are common. Their sediments consist of soft, red, clayey mud, and hard-caked silt with scattered bits of vegetal remains; they are sometimes overlain by a surficial veneer of peat. Silts tend to be homogeneous with no visible stratigraphy and no primary structure (Johnson, 1925; Klein, 1963; Klein and Sanders, 1964; Chapman, 1974).

Vegetation of marshes in New Brunswick and Nova Scotia was described initially by Ganong (1903) and Chapman (1937), and more recently by Pielou and Routledge (1976), Reimold (1977), Thomas (1983), and Gordon and others (1985). *Spartina alterniflora* Loisel., *Spartina patens*, (Ait.) Muhl., and *Juncus balticus* Willd. are the dominant plant species in those Bay of Fundy marshes.

New England-type salt marshes, on the other hand, are predominantly high-marsh meadow, with low-marsh plants occurring mostly along borders of tidal creeks (Miller and Egler, 1950; Nixon, 1982). These marshes are developmentally mature, with steep banks at the seaward edge, low sedimentation rates, and mosaic patterns in the vegetation. The predominant plant taxa in marshes of southern New England are *Spartina, Juncus*, *Distichlis*, and *Panicum* (Johnson, 1925; Chapman, 1940a, 1940b, 1974; Miller and Egler, 1950; Redfield, 1972; Niering and Warren, 1980; Nixon, 1982; Bertness and Ellison, 1987). Sediments therein usually consist of horizontally-bedded grayish or brownish "springy" marine peat (Chapman, 1974), which is composed of roots, stems, and leaves of grasses (Nixon and Oviatt, 1973). The peat also includes variable amounts of silt, although inorganic material is generally less available to

these marshes than to those farther north. Marsh sediments are often underlain by black, brackish-to-freshwater peat, sand, till, or bedrock (Johnson, 1925; Redfield, 1972).

By comparison with marshes in the regions described above, only a few of Maine's salt marshes have received significant attention in the literature (exceptions include e.g. Hill, 1923; and Chapman, 1974). The coast of Maine is in many ways a transition zone between the Bay of Fundy and southern New England. Thus, we have here an opportunity to study transitional characteristics of marsh vegetation in the context of strong gradients in surface-water temperature, tidal range, wave energy, available sediments, and local terrain.

For example, in the summer months surface-water temperatures range from 18°C to 9°C in a southwest to northeast gradient (Larsen, 1985). Tidal amplitude ranges from around 2.5 m in southern Maine to around 6.5 m in eastern Maine (Fefer and Schettig, 1980). Regional patterns of bedrock composition and structure, abundance and composition of Quaternary sediment, as well as differential rates of change in sea-level all result in considerable variability in geologic settings (Kelley, 1987). One of those geologic variables, namely the differential rates of change in sea level (Tyler and Ladd, 1980; Anderson and others, 1984; several papers in this volume) has special consequences for salt marshes. The apparently rapid rise in sea level in eastern Maine is probably unmatched elsewhere in New England or the Bay of Fundy. Yet these fundamental environmental changes may well be having significant effects on the development and stability of marshes bordering that segment of the Gulf of Maine. Significant changes in the nature or abundance of salt marshes can, of course, have serious consequences for nearshore marine ecosystems.

Given the lack of information about salt marshes in Maine, we recognize four areas of basic research necessary for understanding the implications of rising sea level on our salt marsh resource; the first two are necessary to provide a context for either of the others: (1) inventory of distribution and abundance of salt marshes in different regions of the coast of Maine; (2) characterization of vegetation and its variability along this geographic gradient; (3) analysis of marsh development, particularly in the context of changing sea-level; and (4) analysis of productivity in these different marshes, and of how this productivity contributes to nearshore marine ecosystems.

In this paper we present a summary of work we have completed on the first two topics. Additional information and detail about this work is available in Jacobson and others (1987), Jacobson and Jacobson (1989), and Kelley and others (1988).

METHODS

Inventory of Marshes

Primary sources of data for this portion of the study were maps (1:24,000) of marine geology prepared by the Maine State Department of Conservation (Timson, 1977). Those maps were prepared from aerial photographs, and delineate supratidal, intertidal (marsh, beach, and flat), and subtidal (flat and channel) environments.

Using a Numonics (brand) electronic digital planimeter, for each marsh shown on the maps we measured both the total area and the length of the low-marsh/mud interface. Areas of salt marsh separated by either a tidal creek or a river were counted as separate marshes, because they are not physically joined and our field studies show that they often sustain remarkably different assemblages of plant species. Thus, large marsh complexes such as those in Wells and Scarborough are represented in the data set as several discrete marshes. Tests for quality control showed that the accuracy of the planimeter and the consistency of the operator were both well above the resolution of the maps. The resulting data provided the basis for statistical analyses of size-frequency, distribution, and total abundance of salt marshes in Maine.

Selection of Study Sites

Many salt marshes in Maine have been used for agricultural purposes intermittently since colonial times. Dikes were constructed in marshes to exclude tides and to promote production of forage crops. These constructions, which are now in various stages of decay, are still easily recognizable in many Maine marshes (Smith and Bridges, 1982; Smith and others, this volume). Ditches constructed to control mosquito populations by draining pooled water from the marsh surface are also common in salt marshes of Maine. These attempts to alter marsh hydrology had varying success. The extent to which they continue to affect the modern vegetation is unknown.

To avoid such anthropogenic complications, we restricted our work to marshes with little or no history of human disturbance. It is noteworthy that in Maine there are at least a few marshes that have never been diked or ditched. Such examples of natural salt marshes are essentially nonexistent in southern New England. Our 18 study sites (Fig. 1) were salt marshes markedly different from one another in size, slope, tidal amplitude, proximity to open water, and other factors, some of which are summarized in Table 1.

Vegetation Analysis

In each marsh we established from 2 to 6 transects, each oriented perpendicular to the water's edge from bare mud to the upland border. The number of transects in each marsh was determined by its areal extent and its width from bare mud to upland. Topography along each transect was surveyed with a theodolite. We recorded the occurrence and abundance of all vascular plant species in 1-m^2 plots placed at regularly spaced intervals along each transect. Species abundance was recorded as one of the following cover classes: r (1%), + (5%), 10%, 20%, ..., 100%. Taxonomic nomenclature follows Gleason and Cronquist (1963).

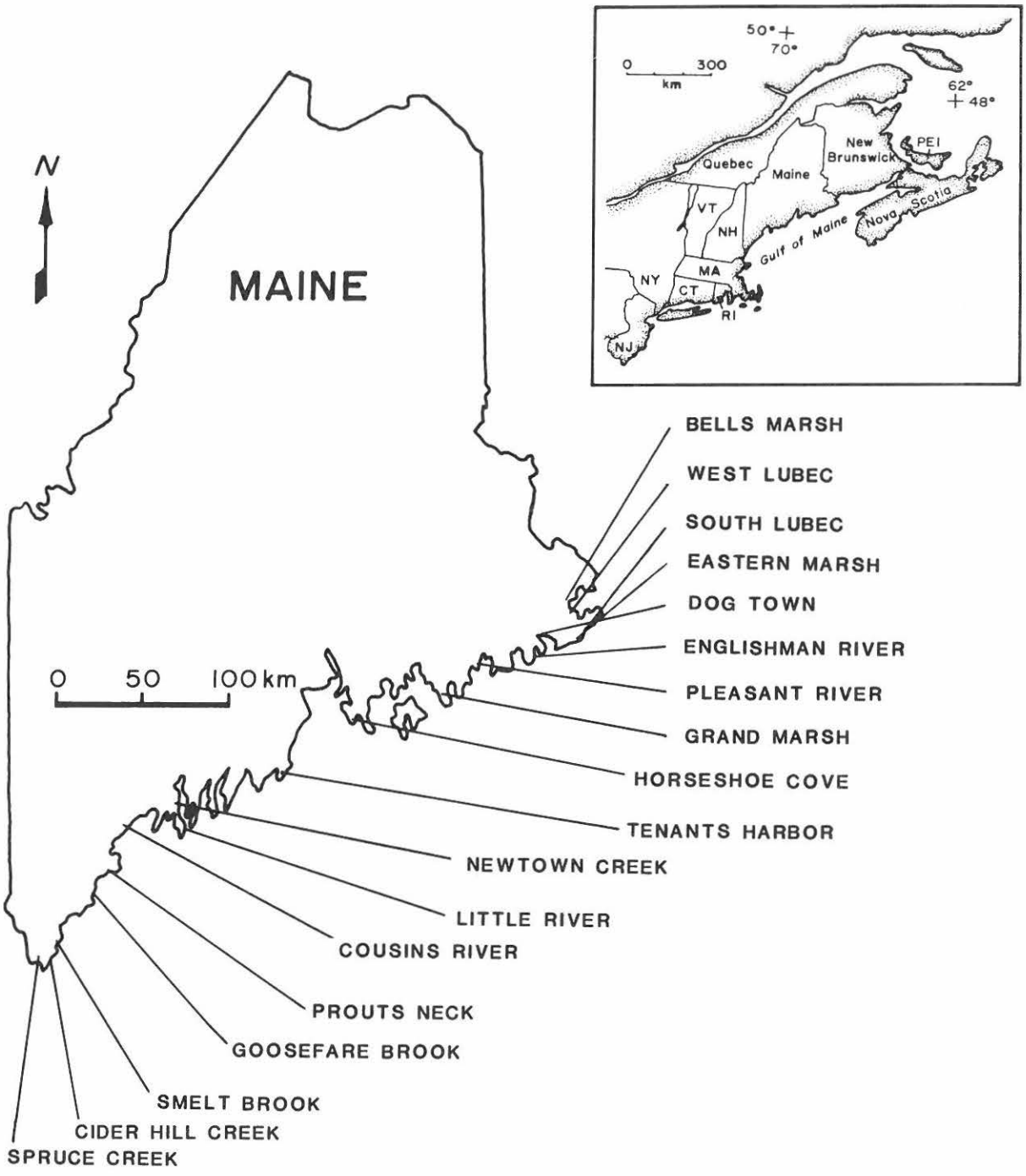

Figure 1. Locations of salt marshes included in this study (from Jacobson and Jacobson, 1989).

RESULTS AND DISCUSSION

Extent, Distribution, and Abundance

Salt marshes cover almost 1100 km, or approximately 20% of Maine's 5970-km coastline (Jacobson and others, 1987). We counted 3017 separate marshes comprising a total area of almost 79 km^2; they range in size from 150 m^2 up to over 2 km^2, with a mean of 0.026 km^2. Approximately 90% of Maine's salt marshes have an area of less than 0.1 km^2 (Fig. 2); collectively these small marshes total 32 km^2, or more than 40% of the total salt marsh area in the State.

The distribution of salt marshes along Maine's convoluted coast is neither regular nor random. A map of the geographic

TABLE 1. LOCATIONS, SIZE, TOPOGRAPHIC FEATURES, AND TIDAL AMPLITUDE OF TIDAL MARSH STUDY SITES.

Study Site	Latitude	Longitude	Area (ha)	Vertical Range of Vegetation	Mean % Slope	Tidal Amplitude (m)
Spruce Creek	43°06'30"	70°43'45"	3	1.9	5.8	2.7
Smelt Brook	43°10'30"	70°44'00"	13	1.9	3.7	2.6
Ciderhill Creek	43°08'45"	70°41'15"	1	1.6	8.6	2.6
Goosefare Brook	43°29'45"	70°23'30"	45	1.4	1.5	2.7
Prouts Neck	43°33'00"	70°19'00"	97	N.D.	N.D.	2.7
Cousins River	43°48'15"	70°09'30"	9	2.0	3.9	2.7
Newtown Creek	43°50'00"	69°47'00"	86	1.7	2.4	2.5
Little River	43°47'00"	69°44'30"	101	1.5	1.1	2.7
Tenants Harbor	43°57'15"	69°12'45"	4	2.5	3.7	2.8
Horseshoe Cove	44°20'45"	68°56'00"	4	N.D.	N.D.	3.1
Grand Marsh	44°25'45"	68°00'30"	54	1.7	1.1	3.2
Pleasant River	44°25'45"	67°45'15"	1	2.4	4.1	3.4
Englishman River	44°37'45"	67°28'00"	28	0.9	0.5	3.7
Dogtown	44°37'45"	67°22'45"	1	2.8	9.6	4.0
Eastern Marsh	44°40'30"	67°14'30"	6	1.4	2.9	4.0
Bells Marsh	44°49'30"	67°09'00"	2	3.4	8.3	5.5
West Lubec	44°49'00"	67°04'00"	15	3.8	6.5	5.5
South Lubec	44°49'00"	66°59'30"	14	2.0	2.6	6.4

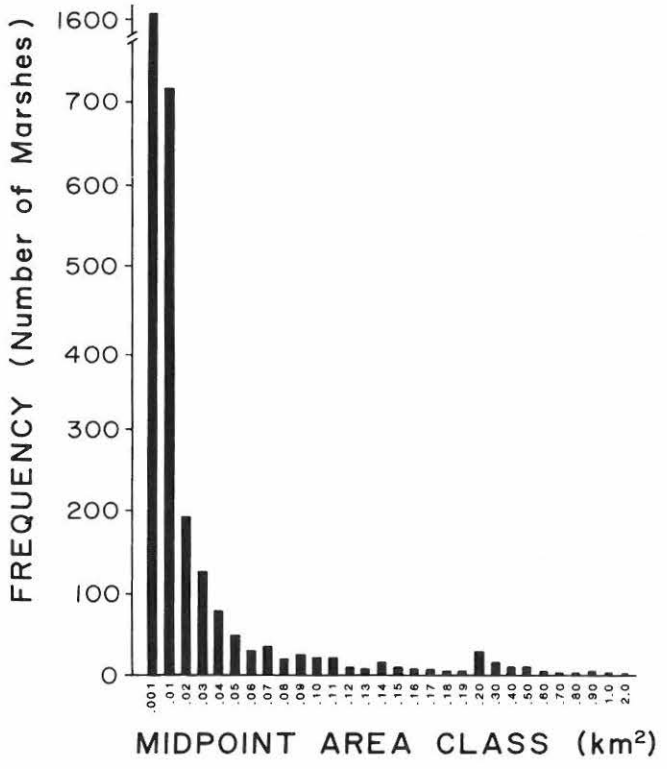

Figure 2. Area-frequency distribution of saltmarshes in Maine (from Jacobson and others, 1987).

distribution of total salt marsh area along the coast (Fig. 3) shows that more than two-thirds (68%) of the statewide total occurs southwest of Penobscot Bay, primarily in the Wells embayment (#3), Saco 8ay (#5), and the Kennebec River estuary (#8). In absolute numbers, more marshes occur northeast of Penobscot Bay than to the southwest. However, the mean area per marsh in the northeastern regions is only 0.02 km^2, or half that of marshes in the southwestern regions. Marshes in eastern Maine are concentrated in the Narraguagus (#18) and Pleasant River (#19) embayments, and to a lesser extent in the Machias (#22) and Cobscook Bay (#23) embayments (Fig. 3.).

The nonrandom distribution of salt marsh along the coast is clearly a result of substantial differences in gross coastal geomorphology caused by differences in the nature, location, and orientation of bedrock formations, and in the nature and availability of sediment (Kelley, 1987). In fact, the coast of Maine can be subdivided into four physiographic subsections (Fig. 4) (Maine State Planning Office, 1983).

Southwestern coastal Maine is characterized by arcuate bays, with beaches of fine sand behind which large salt marshes have developed. These marshes are supplied with fine sediments by erosion of the Presumpscot Formation (as defined by Bloom, 1963), which is primarily composed of marine silts and clays deposited in late-glacial time (Kelley, 1987). This subsection of the coast has approximately 300 salt marshes covering over 26 km^2, or approximately 0.39 km^2 for each linear km of coastline.

Over 1,000 salt marshes exist along the shoreline of the south-central section of the coast, which is characterized by indented embayments. In this region, a series of southward-trending bedrock peninsulas and islands protects marshes along tidal rivers and deep estuaries. Salt marshes are supplied with fine sediments by erosion of the Presumpscot Formation and deposits of glacial till (Kelley, 1987). Our results show that there are 0.31 km^2 of salt marsh per km of coastline in this area, and approximately 27.4 km^2 in sum.

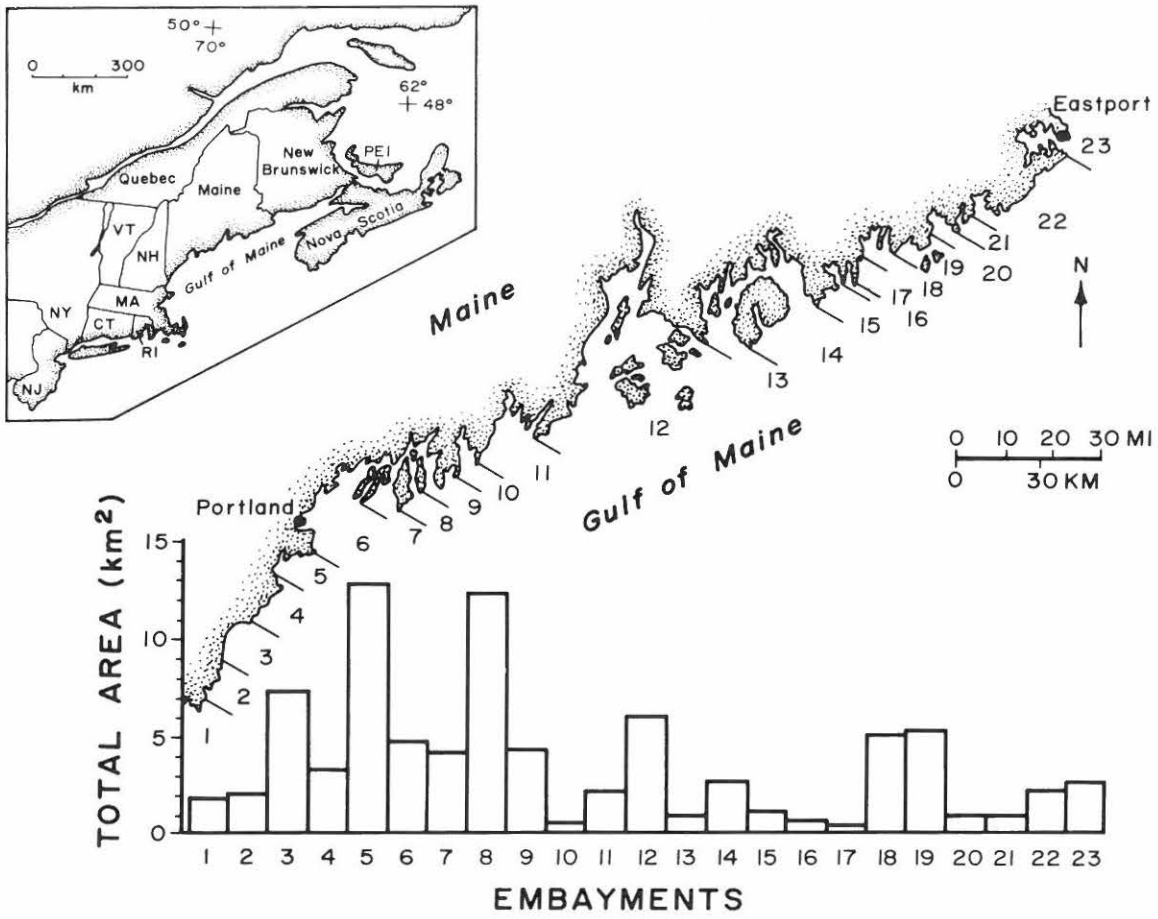

Figure 3. Geographic distribution of salt marshes within 23 coastal embayments (from Jacobson and others, 1987)

Thus, we find approximately 68% of Maine's total area of salt marsh in these two southern regions of the coast. These areas of arcuate bays and indented embayments have landforms that provide protection to intertidal marshes, as well as sources of fine sediments that are necessary for marsh formation.

The environments of the north-central and northeastern segments of the coast are considerably different, and this is demonstrated in the acreage of salt marsh east of Penobscot Bay. Sediment supply is limited in the island-bay complex of the north-central region. Except in a few protected harbors, its coastline of exposed granite ledge affords little opportunity for large salt marshes to become established. However, over 1,100 small salt marshes were recorded in this survey, almost 500 of which border Penobscot Bay. In the northeasternmost subsection, the "eastern cliff shoreline", the sea meets hard volcanic and plutonic rock cliffs that are in some places 30-50 m high. The 470 salt marshes that occur there are restricted primarily to occasional strips bordering rivers and bays. The concentration of salt marshes in each of these eastern subsections is only 0.12 km^2 per km of coastline, although the absolute number of marshes is slightly higher than that of the two southernmost subsections.

Vegetation

Simple phyto-sociological tables (Appendix) contain the data collected in this portion of the study; the tables are arranged in geographic order from southwest to northeast. The number of species per marsh ranges from 11 to 25, and only four species, *Spartina alterniflora, Spartina patens, Juncus gerardi*, Loisel. and *Atriplex patula* L., occur in every marsh we studied (Table 2). Another three, *Triglochin maritima* L., *Salicornia europea* L., and *Solidago sempervirens* L., occur in 16 of the 18 sites. The presence and abundance of the remaining species are highly variable. In some cases, species that normally inhabit either dry, disturbed upland soils or freshwater wetlands occur within a salt marsh, particularly near its upland edge. These plants are separated in Table 2 from those restricted solely to salt marsh habitats.

We find no geographic trend in species diversity, nor any significant correlation between number of species and marsh size (Table 1), as might be expected. We do note, however, that marshes with the highest number of plant species (Tenants Harbor, Newtown Creek, Eastern Marsh, West Lubec, Little River, and Englishman River) are in close proximity to either

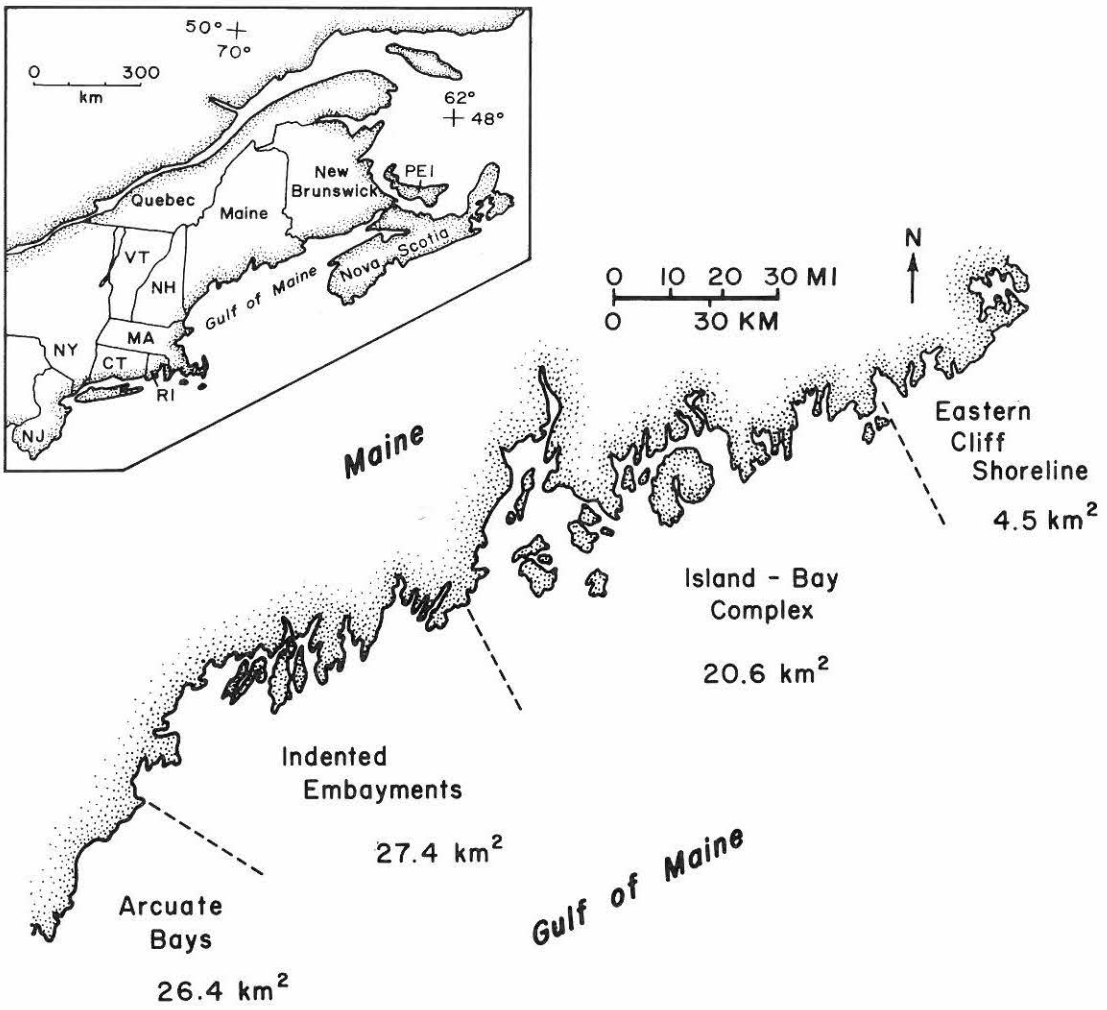

Figure 4. Total saltmarsh area within four physiographic subsections of the Maine coast (from Jacobson and others, 1987).

freshwater streams, or agricultural fields that might shed surface water, sediment, and seeds of upland plants.

With the possible exception of Tenants Harbor, marshes with high species diversity (excluding those species that are not normally restricted to salt marshes) tend to be developmentally "mature" to "old" in the development scheme outlined by Frey and Basan (1978). This may be because as a marsh matures its surface becomes more uneven, thereby increasing the diversity of microhabitats.

Zonation Patterns

Although the vegetation of each marsh occurs in distinct zoned patterns, we found that both the nature of the zones and their dominant species differ from site to site. Only one species, *Spartina alternifolia*, occurs primarily in monospecific stands. The other primary dominant species, *Spartina patens* and *Juncus gerardi*, sometimes occur alone, but more often grow in mixed stands with a few to many other plants (see the Appendix). Marshes located inland along tidal creeks often have species such as *Scirpus maritimus* L. and *Carex paleacea* Wahl. above, below, or within the *Spartina patens* and *Juncus gerardi zones.*

We have found eleven different sequences of zonation, only one of which occurs repeatedly in the 18 marshes (Fig. 5). This particular sequence, *Spartina alterniflora* to *Spartina patens* to *Juncus gerardi*, is the basic pattern from which almost all the marshes vary. Although the actual number and sequence of zones is highly variable, marshes that are relatively wider from bare mud to upland border tend to have more zones above the one dominated by *Juncus gerardi*.

Comparisons with Neighboring Regions

There is insufficient published information about the variability of salt marsh vegetation in southern New England and the Bay of Fundy region to allow rigorous comparisons of between-marsh variability in Maine with that of these neighbor-

TABLE 2. PLANT-SPECIES OCCURRENCE IN 18 SALTMARSHES IN MAINE. SPECIES ARE CATEGORIZED BY NATURAL HABITAT, LISTED IN ORDER OF FREQUENCY OF OCCURRENCE. SITES ARE LISTED IN GEOGRAPHIC ORDER FROM SOUTHWEST TO NORTHEAST.

(a: Goosefare Bk., b: Smelt Bk., c: Cider Hill Ck., d: Prouts Neck, f: Cousins R., g: Newtown Ck., h: Little R., i: Tenants Harbor, j: Horseshoe Cove, k: Grand Marsh, l: Pleasant R., m: Englishman R., n: Dogtown, o: Eastern Marsh, p: Bells Marsh, q: West Lubec, r: South Lubec.)

	SITES																	
SALTMARSH PLANTS	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r
(abundant)																		
Spartina alterniflora Loisel.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Spartina patens (Ait.) Muhl.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Juncus gerardi Loisel.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Atriplex patula L.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Triglochin maritima L.	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+
Salicornia europaea L.	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+		+
Solidago sempervirens L.	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	
(common)																		
Plantago maritima L.	+			+	+		+	+	+		+	+	+	+	+	+		+
Glaux maritima L.	+			+	+	+	+	+	+	+		+		+	+		+	+
Festuca rubra L.		+		+			+	+	+		+	+	+	+	+	+	+	
Carex paleacea Wahl.	+	+					+	+	+		+	+	+	+	+		+	+
Suaeda maritima (L.) Dum.	+		+		+		+	+	+	+	+				+	+	+	+
Agropyron repens (L.) Beauv.	+		+			+	+		+			+		+	+	+	+	+
Potentilla anserina L.	+	+	+	+		+	+	+	+			+	+				+	
Limonium Nashii Small	+		+	+	+	+		+	+		+				+		+	+
Spartina pectinata Link.		+		+		+	+	+	+		+		+	+			+	
Agrostis stolonifera L.							+	+	+		+	+		+	+	+	+	
Juncus filiformis L.		+		+				+	+		+		+			+	+	
Aster subulatus Michx.	+						+		+	+	+		+		+		+	
Hierochloe odorata (L.) Beauv.		+					+		+		+		+				+	
Scirpus maritimus L.		+					+		+				+		+		+	
Distichlis spicata (L.) Greene.					+		+	+	+			+						
Ruppia maritima L.											+		+		+			+
Eleocharis halophila Fern., Brack.		+											+		+		+	
Eleocharis parvula (R. + S.) Link.							+							+	+			
Puccinellia pumila (Vasey) Hitchc.													+		+			+
Spergularia canadensis (pers.) D. Don.			+					+							+			
(rare)																		
Solidago rugosa Mill.		+																
Cuscuta spp.									+									
Puccinellia maritima (Huds.) Parl.	+																	
Total saltmarsh species	16	16	12	14	11	12	20	19	23	9	17	15	19	15	22	13	20	14

	SITES																	
FRESHWATER WETLAND PLANTS	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r
Scirpus americanus Pers		+					+			+								
Typha angustifolia L.							+											
Phalaris arundinaceae L.										+								
Scirpus rubrotinctus Fern.																		+

	SITES																	
UPLAND PLANTS	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r
Convolvulus sepium L.		+		+			+		+				+					
Rosa rugosa Thunb.				+					+								+	
Hordeum jubatum L.												+			+	+		
Carex tenera Dewey.		+					+											
Elymus virginicus L.																+		
Poa trivialis L.												+						
Rhus toxicodendron L.				+														
Polygonum sagittatum L.																	+	
Total species	16	19	12	17	11	12	24	19	25	11	17	17	20	15	23	15	22	15

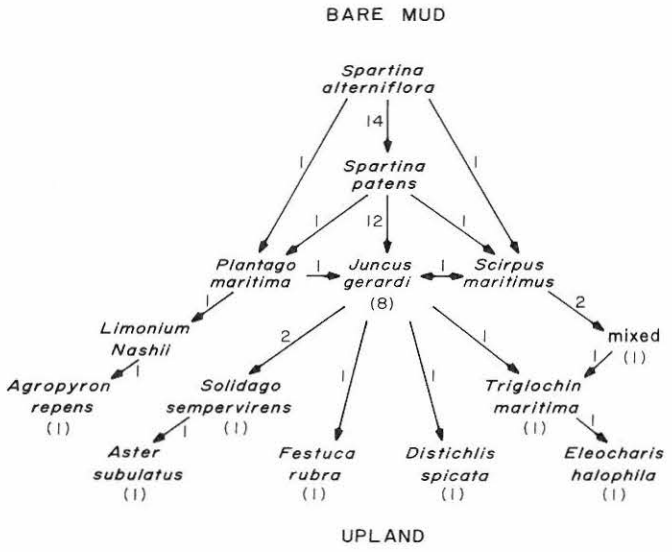

Figure 5. Variations in zonation patterns of salt marsh vegetation in coastal Maine. Numbers in parentheses refer to the number of study sites in which the uppermost zone is dominated by that species. Numbers by arrows refer to the number of sites in which that transition occurs. Arrows point from lower to higher elevation (from Jacobson and Jacobson 1989).

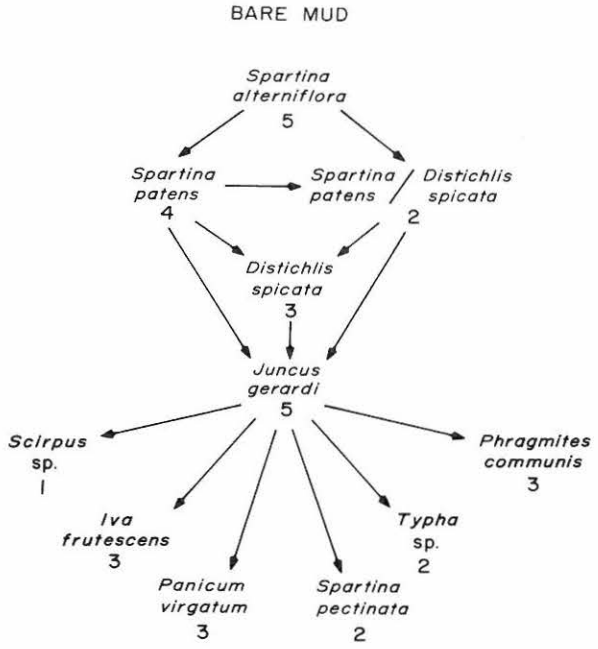

Figure 6. Variation in zonation patterns of salt marsh vegetation in southern New England as reported by Chapman (1940, 1960), Miller and Egler (1950), Niering and Warren (1980), Nixon (1982), and Bertness and Ellison (1987). Numbers refer to the number of records in the literature (from Jacobson and Jacobson, 1989).

ing regions. However, broad comparisons are helpful in providing perspective on characteristics such as variability.

In all three areas, the primary zones from bare mud to upland border are dominated by *Spartina alterniflora*, *Spartina patens*, and *Juncus gerardi*, in that order. In southern New England, however, a zone dominated by *Distichlis spicata* (L.) Greene., alone or in conjunction with *Spartina patens*, occurs commonly between the *Spartina patens* and *Juncus gerardi* zones, or sometimes replaces the *Spartina patens* zone altogether (Miller and Egler, 1950; Nixon and Oviatt, 1973; Niering and Warren, 1980) (Fig. 6.). In Maine *Distichlis spicata* occurs in only five of our 18 marshes, and dominates a zone in only one of these (Prouts Neck). This species is "comparatively rare" in the Bay of Fundy marshes, occasionally occurring in conjunction with *Limonium Nashii* Small (Thomas, 1983).

In southern New England, *Panicum virgatum* L. is a common dominant species occupying the zone upland of the *Juncus gerardi zone* (Miller and Egler, 1950) (Fig. 6). A zone dominated by *Iva frutescens* L. sometimes replaces or precedes the *Panicum* zone. *Phragmites communis* Trin. is another common dominant. None of these species occur at any of our study sites, nor are they mentioned in the literature for Bay of Fundy marshes.

The most common dominant above the *Juncus gerardi* zone in the Bay of Fundy region is *Juncus balticus* (Pielou and Routledge, 1976) (Fig. 7). This species is not recorded for southern New England nor was it found at any of our 18 study sites, although *Juncus filiformis* L. (a species that closely resembles *J. balticus*) was common at our study sites. In the Bay of Fundy region, the *Spartina patens* zone includes many associated species, probably because *Spartina patens* is close to the northern limit of its distribution there (Chapman, 1960). *Limonium Nashii* and *Puccinellia maritima* (Huds.) Parl. also play more significant roles in the Bay of Fundy region than they do in Maine.

In general, Maine's salt marshes appear to represent a continuum between the very different types found in southern New England and the Bay of Fundy region, with probably a majority of Maine's marshes being more similar to those of the Bay of Fundy region. These findings should not be surprising, given the greater similarity of local geology, water temperatures, tidal ranges, and climates between Maine and the Maritime Provinces of Canada. Our interpretation is that Maine's coastline provides a somewhat greater range of environmental settings than its neighboring regions and, as a result, it has greater site-to-site variability.

SUMMARY

Maine's coast is covered by a surprisingly large amount of salt marsh. More than 3000 separate marshes, most of which are small, collectively cover approximately 79 km^2 of coastal land. Roughly two-thirds of this total area of marsh lies southwest of Penobscot Bay in areas where the geologic setting provides both a source of appropriate fine-grained sediments and protection

from high-energy waves. Most salt marshes in eastern Maine form as small fringes along occasional protected stretches of rocky shore.

Our data show extensive variability in the vegetation of Maine's salt marshes. The number of species present is higher in marshes that are either developmentally mature, have freshwater input, or are adjacent to agricultural fields. There is considerable variation not only in the number of species, but also in the particular species that occur. Only four species, *Spartina alterniflora*, *Spartina patens*, *Juncus gerardi*, and *Atriplex patula* occur in all 18 marshes. Another three, *Triglochin maritima*, *Salicornia europea*, and *Solidago sempervirens*, occur in 16 out of 18 sites. Occurrence of the remaining species is highly variable. Zonation patterns are also highly site-specific and can in only the most general sense be characterized by the classic sequence: *Spartina alterniflora*, *Spartina patens*, and *Juncus gerardi*.

The tremendous variability in the size and vegetation of salt marshes in Maine is indicative of the high degree of variability in geologic setting, sediment supply, developmental history, and other environmental conditions along the coast. Maine is a geological and botanical transition zone between the vastly different marshes of southern New England and the Bay of Fundy region. In southern and eastern Maine, some marshes are similar to those of the adjacent regions, respectively, and many are unique to Maine.

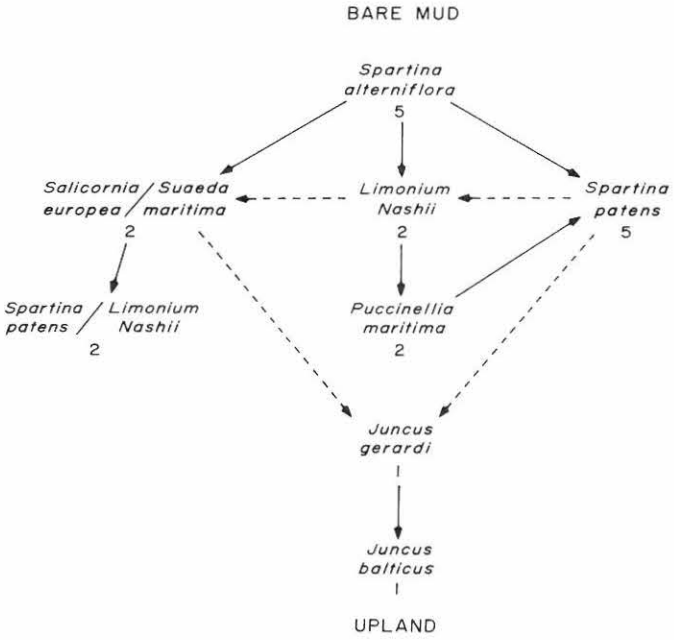

Figure 7. Variations in zonation patterns of salt marsh vegetation in the Bay of Fundy region as reported by Ganong (1903), Johnson (1925), Chapman (1937), Thomas (1983), and Gordon and others (1985). Numbers refer to the number of records in the literature. Dashed lines indicate "secondary succession" discussed by Chapman (1937) (from Jacobson and Jacobson, 1989).

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APPENDIX. REPRESENTATIVE VEGETATION TRANSECTS FROM EACH OF THE 18 STUDY SITES. THE SITES ARE ARRANGED IN GEOGRAPHIC ORDER FROM SOUTHWEST TO NORTHEAST.

SPRUCE CREEK	KITTERY, MAINE					transect 1 of 3											
	m from bare mud																
	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33
Spartina alterniflora	+	30	70	70	70	20	10	r									
Spartina patens						60	70	70	70	70	70	70	50				
Atriplex patula												r	r	r		r	
Juncus gerardi													20	80	80	90	50
Plantago maritima															10		+
Triglochin maritima															+	r	10
Solidago sempervirens															r		10
Puccinellia maritima															r		
Glaux maritima																+	r
Suaeda maritima																	r

SMELT BROOK	YORK, MAINE					transect 1 of 4											
	m from bare mud																
	1	4	7	10	13	16	19	22	25	28	31	34	37	40	43	46	49
Spartina alterniflora	60																
Scirpus maritimus		90	20														
Juncus gerardi			20	30	50	30	30	20	10	10	10	+					
Atriplex patula			r														
Solidago sempervirens			r		+							r	r		10		
Potentilla anserina				20	30	40	40	20	20	30	20	r		r	10		
Triglochin maritima				40	+	10	20	40	30	30	30	50	20	+	10		
Carex paleacea				+	r	r						+	+		10	60	40
Festuca rubra				r		r	r								+		
Salicornia europaea									+	+							
Spartina patens									r								
Plantago maritima												+					
Eleocharis halophila													10	20	20		
Juncus filiformis															10		
Hierochloe odorata															+		
Convolulus sepium															+		+

CIDER HILL CREEK	YORK, MAINE				transect 1 of 3				
	m from bare mud								
	1	3	5	7	9	11	13	15	17
Spartina alterniflora	99	r							
Spartina patens		90	90	50	r				
Juncus gerardi					90	90	90	80	80
Triglochin maritima					r				
Solidago sempervirens					r		+	10	10
Potentilla anserina						r	+	10	
Agropyron repens									+
Spartina pectinata									+

GOOSEFARE BROOK	SACO, MAINE							transect 2 of 4													
	m from bare mud																				
	1	4	7	10	13	16	19	22	25	28	31	34	37	40	43	46	49	52	55	58	61
Spartina alterniflora	80	10																			
Spartina patens		90	30	10	10	r	r	r	+	r	r									+	+
Juncus gerardi			40	40	40	30	30	30	30	20	20	40	20	30	60	20	20	20	30	30	20
Limonium Nashii			r	+	r	10	r	r	+	+	+	r	+	r	r						
Plantago maritima			r	10		+															
Triglochin maritima				+		r		+		10	+	+	+	10							
Glaux maritima								+				r									
Solidago sempervirens													r								

PROUTS NECK	SCARBOROUGH, MAINE					transect 2 of 3				
	m from bare mud									
	1	11	21	31	41	47	53	59	63	67
Spartina alterniflora	20	20	70	99	99	20	10	+		
Spartina patens						80	90	50	+	
Limonium Nashii						+	+			r
Plantago maritima						r				
Atriplex patula							r			
Juncus gerardi								50	99	10
Distichlis spicata										50
Glaus maritima										+
Suaeda maritima										r
Triglochin maritima										r

COUSINS RIVER	FREEPORT, MAINE					transect 2 of 3											
	m from bare mud																
	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33
Spartina alterniflora	30	70	90	80	80	40	20	r									
Spartina patens						30	70	80	60	r				r			
Juncus gerardi								r	20	80	80	80	80	20	20	40	30
Solidago sempervirens										r		10	r	20			
Glaux maritima											10	+	r	r	10	10	
Limonium Nashii											r	r		r	r		
Potentilla anserina														r	10	10	
Triglochin maritima														10			
Salicornia europaea												r					
Agrostis stolonifera																	10
Agropyron repens																	+

NEWTOWN CREEK	ARROWSIC, MAINE						transect 1 of 4											
	m from bare mud																	
	1	5	9	13	17	21	25	29	33	37	41	45	49	53	57	61	65	69
Spartima alterniflora	70	+	r															
Spartina patens		80	+															
Scirpus maritimus		+	20	20	20	20	20				+	+						
Potentilla anserina		+						+	10	40	r	+		r				
Atriplex patula		+																
Solidago sempervirens		+																
Glaux maritima			+	+	10	10	20	10		20	+	10				+		
Juncus gerardi						+	20	20	30	10	10	10						
Carex paleacea								10	20	30	+		+					
Triglochin maritima								r		+	20	20	20	20	20	20	10	
Plantago maritima											10	40	40	10	30	20	10	
Scirpus americanus											30			10	+			
Eleocharis parvula												+	+	10		+		
Suaeda maritima															+			
Agrostis stolonifera																r	10	
Aster subulatus																	+	20
Spartina pectinata																	+	20
Hierochloe odorata																		r
Festuca rubra																		+
Convolvulus sepium																		r

LITTLE RIVER	GEORGETOWN, MAINE						transect 1 of 4										
	m from bare mud																
	1	5	9	13	17	21	25	29	33	37	41	45	49	53	57	61	65	69
Spartina alterniflora	70	10	r					+									30	20
Spartina patens		20	+					10		20			20	80	30	70	+	
Glaux maritima		10	10	+	+		+		+		10		r					
Limonium Nashii		10	10	+	+				+		+							
Atriplex patula		+			r	r				r								
Salicornia europaea		+							r		r	+						
Suaeda maritima		+							r			r						
Spergularia canadensis		+																
Plantago maritima			70	50	20	+	50	50	30	20	30	+	30					
Juncus gerardi			+	20	50	90	30		30	40	20	40	20					
Festuca rubra			+			+							+		+	+	+	
Triglochin maritima					r			10	10		10							
Distichlis spicata					+													
Agrostis stolonifera						10	20	20	10	10	+		+		+			

TENANTS HARBOR	TENANTS HAROBOR						transect 1 of 3								
	m from bare mud														
	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29
Spartina alterniflora	10	20	40	30	60	60	+	r							
Salicornia europaea						r	+								
Spartina patens							70	40							
Atriplex patula							+	+							
Glaux maritima							+	+	+						
Juncus gerardi								50	50	20	20	20	10	20	
Plantago maritima								r							
Salidago sempervirens									20	60	60	60	20	+	
Festuca rubra										10	10	10	+	+	
Spartina pectinata												r	+	10	20
Aster subulatus													30	40	70
Agropyron repens													r		
Juncus filiformis													+		
Rosa rugosa															10

HORSESHOE COVE	BROOKSVILLE, MAINE						transect 2 of 3								
	m from bare mud														
	1	4	7	10	13	16	19	22	25	28	31	34	37	40	42
Spartina alterniflora	80	80	20	10	10	10	10								
Suaeda maritima		20	+	r	r										
Atriplex patula		r	+		+	+	10	r	r	r	r				
Salicornia europaea		r	+	+											
Spartina patens			80	90	99	99	90	99	99	50	50	50	50	50	50
Juncus gerardi										50	50	50	50	50	10
Glaux maritima										r					
Solidago sempervirens													r	r	r
aster sp.															20
Scirpus americanus															10

GRAND MARSH	GOULDSBORO, MAINE						transect 1 of 2															
	m from bare mud																					
	1	5	9	13	17	21	25	29	33	37	41	45	49	53	57	61	65	69	73	77	81	85
Spartina alterniflora	50	60	+	+	40	r	10	r	+				80	60	70	70	30	50	60	70	50	10
Atriplex patula	10		+	+	+	+		+		+	+	+										
Spartina patens			90	90	20	70	80	80	80	80	90	50										50
Limonium Nashii			10	10			+															
Plantago maritima				+																		
Festuca rubra							r		+													
Salicornia europaea							r		+													

GRAND MARSH	(transect continued from previous page)																	
	m from bare mud																	
	89	93	97	101	105	109	113	117	121	125	129	133	137	141	145	149	153	
Spartina alterniflora	10		70	10		60	20	10	20									
Atriplex patula	+	+		+			+	+		+	r							
Spartina patens	70	60		80			10	80	50	60	80	70	30	20				
Limonium Nashii	+	+		10														
Plantago maritima										+								
Festuca rubra		+		+										+				
Salicornia europaea							+											
Spartina pectinata										+	10						10	
Carex paleacea												10	30	50	20	10	20	
Solidago sempervirens												10	+			10		
Juncus gerardi															30	30	20	
Juncus filiformis																+	10	
Agrostis stolonifera																+		
Aster stolonifera																	10	
Hierochloe odorata																	+	

PLEASANT RIVER	HARRINGTON						transect 1 of 6												
	m from bare mud																		
	1	4	7	10	13	16	19	22	25	28	31	34	37	39	41	43	45	47	49
Spartina alterniflora	30	10	10	10	10	10	30	60	80	80	80	20	+	r					
Spartina patens												80	99	99	99	90			
Salicornia europaea													+	+	+	r	r		
Suaeda maritima													r	+	+				
Atriplex patula														+	10	+			r
Triglochin martima															r	+	r	+	+
Solidago sempervirens																10	+	+	+
Limonium Nashii																+	r		
Plantago maritima																	+		r
Juncus gerardi																	90	99	90
Potentilla anserina																	r	r	r
Glaux maritima																		+	+
Phalaris arundinacea																			10

ENGLISHMAN RIVER	ROQUE BLUFFS, MAINE							transect 2 of 2														
	m from bare mud																					
	1	6	11	16	21	26	31	36	41	46	51	56	61	66	71	76	81	86	91	96	101	106
Spartina alterniflora	90								60	+	10	50			10					20	10	
Spartina patens	+	10			70	80	70	80	+							90	80	90	90	50	50	90
Atriplex patula	+	10		+				+										+	r			
Puccinellia pumila	+																					
Juncus gerardi		50	90	90	+																	10
Solidago sempervirens		20	10																			r
Festuca rubra			r																			
Plantago maritima						+	+									+			+			
Ruppia maritima										99	90											

	m from bare mud															
	111	116	121	126	131	136	141	146	151	156	161	166	171	176	181	186
Spartinia alterniflora	+				20	10	10	+		+	+	+	50			
Spartina patens	80	90	80	70			80	+	50	60	20	90	+	40		
Atriplex patula	+	+	+				+									
Puccinellia pumila							r									
Solidago sempervirens			20	30										+		20
Festuca rubra												+		+		20
Plantago maritima		+		+			10									
Ruppia maritima					50	10	20	10	80	10						
Carex paleacea														40	+	
Potentilla anserina														+		
Scirpus maritimus														+		
Spartina pectinata														+		10
Triglochin maritima															40	+
Glaux maritima															r	
Juncus filiformis																10
Aster subulatus																10

DOGTOWN	MACHIASPORT, MAINE					transect 2 of 3							
	m from bare mud												
	1	3	5	7	9	11	13	15	17	19	21	23	25
Spartina alterniflora	60	70	60	70	20								
Atriplex patula					10	+							
Triglochin maritima					10						r		
Salicornia europaea					10								
Eleocharis parvula					+								
Solidago sempervirens					+				+		+		
Spartina patens						60							
Carex paleacea						20	10	10	+	+	10	20	10
Glaux maritima						+					+		
Juncus gerardi							70	80	80	80	50	30	
Festuca rubra								+	+	+			
Agrostis stolonifera										+		+	
Spartina pectinata											+	+	10

EASTERN MARSH BROOK	CUTLER, MAINE						transect 4 of 4							
	m from bare mud													
	1	3	5	7	9	11	13	15	17	19	21	23	25	27
Spartina alterniflora	50	20	30	10	10	30	10							
Suaeda maritima	+	20	r		+				+					
Salicornia europaea	+	10	r	+	+									
Spergularia canadensis	r	10		+										
Spartina patens		+	30	10	30	70	60	20						
Plantago maritima		r	+	10	+			10	r					
Atriplex patula		+							10	r	+			
Limonium Nashii			r	+	+									
Glaux maritima					+		+							
Festuca rubra					r				+	+	10	50	20	20
Carex paleacea							+	10		r	+	10	10	20
Puccinellia pumila							r							
Juncus gerardi								20	90	90	80	10		
Triglochin maritima								+						
Agropyron repens												10		20
Agrostis stolonifera												+	10	
Hordeum jubatum												+		
Aster subulatus														+

BELLS MARSH	EDMUNDS TWP, MAINE					transect 1 of 3						
	m from bare mud											
	1	3	5	7	9	11	13	15	17	19	21	23
Spartina alterniflora	90	99	99	99	60	+						
Spartina patens					10	99	80	80	+	+		
Atriplex patula					+	+						
Suaeda maritima					r							
Solidago sempervirens							20	20	40	60	40	40
Juncus gerardi								+	50	20	30	
Festuca rubra										+		20
Agropyron repens											+	+
Plantago maritima											+	10
Triglochin maritima											+	
Elymus virginicus												+

WEST LUBEC	WEST LUBEC, MAINE						transect 1 of 4													
	m from bare mud																			
	1	4	7	10	13	16	19	22	25	28	31	34	37	40	43	46	49	52	55	58	61
Spartina alterniflora	50	50	90	+																	
Spartina patens				90	100	90	10					+									
Suaeda maritima				+																	
Atriplex patula						+	+														
Juncus gerardi							50	60	40	40	40	30									
Solidago sempervirens							20	10	10	+	+	+									
Agropyron repens							+	+	20	20							+				
Festuca rubra								10	10	20	10	10		+		+	20	20	r		
Glaux maritima										+		+									
Agrostis stolonifera											+	20	10	10	10	+	10		20	+	+
Juncus filiformis											10					10	20	20	20	10	10
Aster subulatus											+	+					+	+			10
Triglochin maritima												+	30	+	10	10	+				
Potentilla anserina												r									
Carex paleacea													+	10	10	10	+	+	+	40	40
Eleocharis halophila													10	+	10						
Scirpus maritimus													+	20							
Spartina pectinata																	+	10	30		
Scirpus rubrotinctus																			10		20
Polygonum sagittatum																					r

SOUTH LUBEC	SOUTH LUBEC, MAINE						transect 1 of 3							
	m from bare mud													
	1	3	5	7	9	11	13	15	17	19	21	23	25	27
Spartina alterniflora	50	60	60	60	60	60	60	70	80	60	r			
Suaeda maritima	+													
Carex paleacea										20	40	10	+	
Juncus gerardi											20	20	50	20
Glaux maritima											+	20	30	+
Triglochin maritima												+	+	
Plantago maritima														30
Apriplex patula														+