

Vegetation of Coastal Marshes near Juneau, Alaska

Abstract

The purpose of this study was to demonstrate the relationship of physiography to the organization of southeast Alaskan coastal marsh vegetation. Distributions of species and vegetation units were analyzed in relation to marsh landform types in four Juneau-area coastal marshes. Eleven vegetation types were identified. Species composition of each vegetation type was not consistent within or among sampled marshes, but each vegetation type occurred consistently on a particular combination of landforms. These conditions seem to be the result of individualistic species behavior in habitats with inconstant, non-linear environmental gradients arising from site-specific combinations of physiographic processes. The marshes were compared and classified in terms of landforms and physiographic characteristics of associated vegetation types, that is, the habitat-vegetation complex. The complexes occurring in the Juneau area were tidal silt sedge and sedge-grass marsh; tidal sand *Salicornia* marsh; tide-influenced grass meadow; *Elymus arenarius* upper marsh border and drift line; prostrate and scrambling forbs and rhizomatous grasses of upper beaches and sand spits; coastal forb meadow on drift lines and above marsh borders; fresh sedge-forb marsh; and emergent forbs of marsh ponds. Classification in terms of habitat-vegetation complexes makes possible comparison of Juneau-area marshes with other marshes of different vegetation-type composition in southeast Alaska.

Introduction

Coastal marshes seem to be a relatively simple habitat (Bertness and Ellison 1987) with a common general hydrologic regime, the tides, creating a common set of physical parameters to which coastal marsh plants must adjust. Therefore, one could reasonably expect to identify some unifying characteristics of coastal marsh vegetation. Nevertheless, attempts to characterize marsh vegetation on the North American west coast (Macdonald and Barbour 1974; Macdonald 1977a,b; see Stone 1984 for additional references) make clear how much marshes differ from place to place. In Alaska the problem of identifying common characteristics is further complicated by gradients of physical parameters apparently oriented in different directions (e.g., seaward, landward, and transverse) (Batten *et al.* 1976), making it difficult with available analytical techniques to sort out the effects on plants of individual physical characteristics of coastal marsh habitats.

A physiographic approach (e.g., Miller and Egler 1950) avoids these problems by viewing species and vegetation in relation to types of coastal marsh landforms rather than to numerical values of physical parameters. Landforms integrate particular combinations of physical conditions (Hack and Goodlett 1960). Therefore, inferences (*sensu* Egler 1977) may be drawn about species and vegetation behavior in relation to physical characteristics of habitat even though gradients of individual

parameters may be non-linear, multi-directional and not progressive. Reconnaissance of coastal marsh vegetation near Juneau, Alaska, indicated both non-linear, non-progressive behavior of physical gradients and inconsistent relationship of plant species and vegetation types to identifiable physical gradients. The purpose of this study, which was part of a larger project (Stone 1984), was to demonstrate the influence of physiography on the organization of coastal marsh vegetation in this area by describing species distributions and vegetation patterns in relation to landform types.

Methods

Study Area

The four coastal marshes studied (Table 1) encompass the widest variety of combinations of marsh physiography and vegetation types readily accessible in the Juneau area but still predominantly influenced by natural processes. The sites are within 50 km of Juneau, Alaska (58°18'0"N, 134°25'0"W) (Figure 1), a recently glaciated area of mild climate (for its latitude), high rainfall (140 to 234 cm), and structurally weak bedrock of high relief. Like most other coastal marshes, these sites are subject to the physiographic/hydrologic influences of coastal storms, river flooding, and freshwater seepage. However, other physiographic influences are, in combination, unique to southeast Alaskan marshes. Large sediment loads and large summer discharges of glacial rivers produce a greater rate of sediment deposition and a greater degree of freshwater dilution than in other North American coastal marshes. High tides, floods, and

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TABLE 1. Physical characteristics of coastal marshes sampled in the Juneau area.

	Mendenhall River	Lemon/Switzer Creek	Eagle River	Gastineau Channel
distance (km) and direction from Juneau	12 NW	8.3 N	32 NW	6.4 S
area (ha)	415	65	140 ^a	0.4
marsh landscape	glacial river delta	creek delta over glacial valley fill	glacial river delta	wave-carved pocket in rock fill
surrounding landscape	valley walls	valley walls	sand spits	rockfill terrace
exposure to sea	sheltered by peninsulas	sheltered by peninsula and valley wall	exposed on 3 sides	exposed on 1 side
substrate	silt	silt	sand, silt ^a	thin sand, gravel and silt over rock fill
sediment source	glacial meltwater	tidewater	glacial meltwater	tidewater
tidewater salinity ^b	brackish	brackish	saline, brackish ^a	brackish

^atwo marshes

^bafter Federal Water Pollution Control Administration (1966)

storms bring in drift logs, and cold air drainage off the icefields in winter generates particularly violent (to 300 km/hr) dry wind storms. The tide range is unusually large (≈ 6.3 m), and tidal influence reaches far inland in flat areas.

Data Collection

Neither established benchmarks nor tidal data recording stations were near enough to the marshes for use as valid reference points. Therefore, relative elevation was used to define landforms. Sampling transects, made in June and August, 1981, were of two kinds: measured (by hand-held compass, hand level, stadia rod, and pacing) and estimated (by marking sample locations on USGS 15-minute topographic maps and eye estimate of plot size). Positions and lengths of transect lines were chosen to cross all physiographic site types in a marsh. Physiographic site types were identified in the field by visually recognizable surface form, by breaks in slope, and by changes in degree and direction of slope (Small 1970, p. 6). Where a single transect could not be laid out to cross all types, additional transects were made. Sampling was extended beyond marsh borders in three of the four marshes. Measured sample plot size was 6 x 6 ft (1.8 x 1.8 m), an area consistent with the ground area sampled at points on estimated transects.

In each physiographic category encountered along the transect, one sample plot was placed in each homogeneous patch of vegetation. Thus, the

number of plots in each physiographic category at a given sample site depended on the number of vegetation types in the physiographic category and the number of times the category was crossed by the transect(s). Altogether 106 plots were sampled: 38 in the Eagle River sand marsh, 26 in the Eagle River silt marsh, 24 in the Gastineau Channel marsh, 15 in the Lemon Creek-Switzer Creek marsh, and three in the Mendenhall River marsh (upper part only was sampled). Totals for each physiographic category are given in Table 2. (The term "marsh," where unqualified, refers to sand and silt marshes together.)

For each sample plot, relative elevation, landform type (site categories of Table 2), and surface sediment texture (silt, sand, or gravel—determined by eye) were recorded. The identity of each vascular plant species present was also recorded, and species were listed as primary (meaning visually dominant) or secondary (not visually dominant). Plants not identifiable in the field were collected for identification, and a voucher specimen was taken of each vascular plant species found at the sample sites. Hultén (1968) was the nomenclatural authority.

Data Analysis

Four kinds of analysis were made from the data for each sample plot: physiographic classification of the site, physiographic classification of species (species distributions among the physiographic site

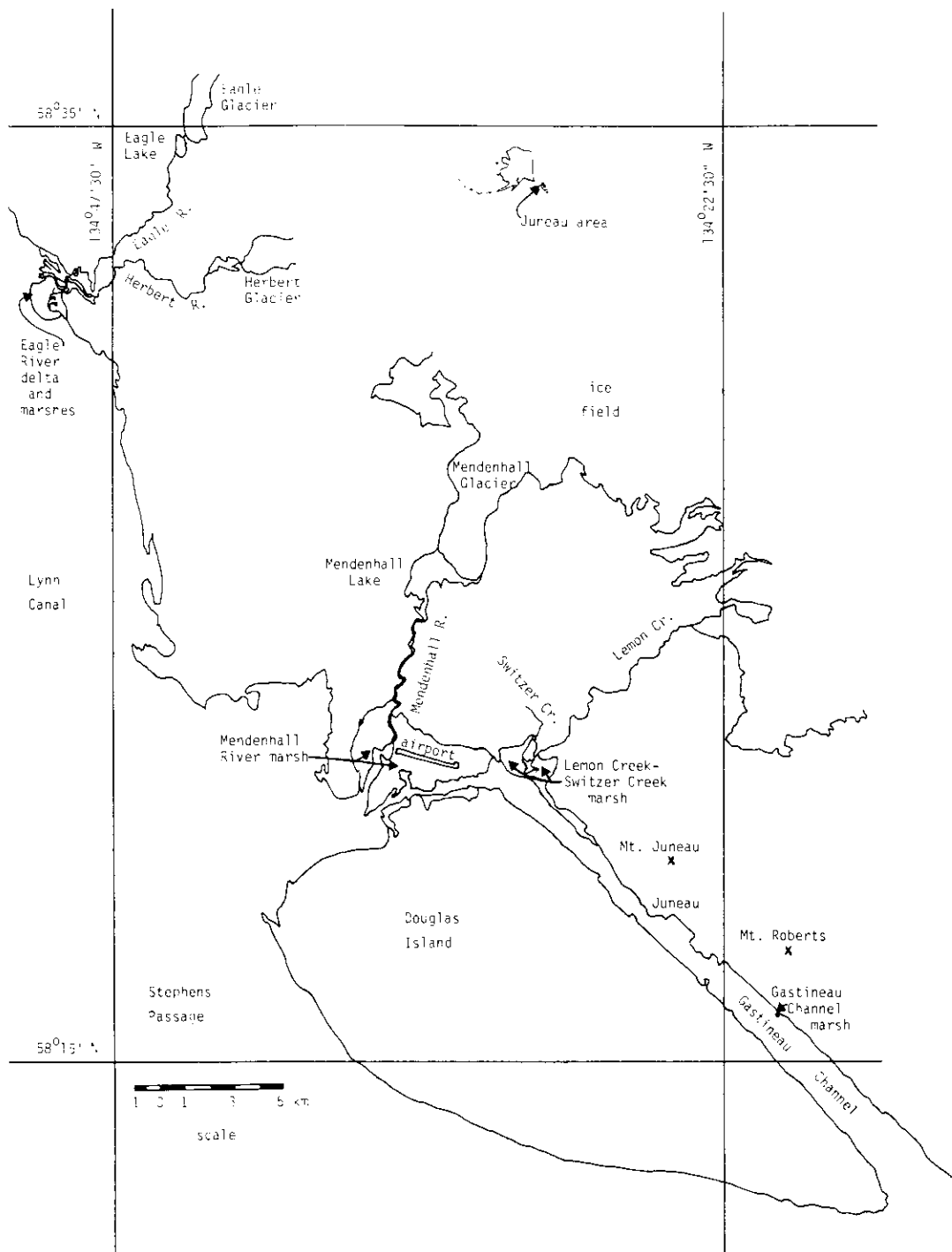


Figure 1. Juneau area, showing locations of sampled marshes. Glaciers and watercourses shown in positions as on source maps (USGS topographic series 1:63,360 Juneau A-1, B-1, B-2, B-3, and C-3, published 1948-1962, minor revisions 1966-1975). Inset: Location of Juneau area in Alaska.

TABLE 2. Landforms and physiographic categories of Juneau area coastal marshes.

Landform	Physiographic site category	Figure no. where illustrated	Number of sample points in category	Surface shape
marsh sites	lower marsh border	2c,d	6	straight or concave
	tidal marsh—sand	2c,d	26	straight (no levee)
	tidal marsh—silt	2b,c,d	27	concave with levee, straight without levee
	channel bank	2a,b	4	convex
	small channel	2a-c	2*	concave
	tide-influenced meadow	2d	1	straight
upper marsh border sites	upper marsh border	2a,c,d	14	concave
	drift line	2a-d	6	convex
beach and foreshore	beach	2a,d	3	straight or concave
slopes above marsh border	front spit slope	2a,d	2	straight
	back spit slope	2a,c,d	6	straight
	seepage slope	2b,c	2	straight
	fill slope	2c	2	straight
upland	spit top	2a,d	3	convex
extratidal wet sites	fresh marsh	2b	2	straight or concave
	marsh pond	2b	2	concave
Total sample points			106	

*combined in Table 5 with tidal silt marsh sites

categories of Table 2), vegetation-type classification of species, and physiographic classification of vegetation types. These analyses made it possible to elucidate the spatial arrangement of marsh landforms and the relationships of species and vegetation types to them (Zimmermann and Thom 1982).

The physiographic site types identified in the field were grouped in categories based on cross-sectional geometry in marsh elevation profiles (Small 1970). Cross-sectional form was combined with recorded qualitative field observations of moisture/tidal flooding regime and surface substrate composition to produce the physiographic site categories. Such landform analysis is standard procedure in geomorphology and physiographic ecology for definition and identification of physiographic features of habitat at the scale of the present study (Raup 1975, Semeniuk *et al.* 1989).

Classification of vegetation types of the 106 sample plots, based on species composition, was

done by the Braun-Blanquet method (Mueller-Dombois and Ellenberg 1974). The first segregation defined groups with no overlap in distinguishing species. Some of these groups contained locationally distinct subgroups and so were separated into two vegetation types. Vegetation types were named either for the primary species if there were only one or two, or for the physiognomic type (*sensu* Raup 1975, p. 159) (*e.g.*, grasses, forbs) of the several primary species.

Physiographic classifications of species and vegetation types were based on tabulations of species- and vegetation-type occurrences for each physiographic site type. A species or vegetation type was considered characteristic of a site category if it occurred in one third or more of all sites in a site category or only in that category, or if one fourth or more of the total sample sites for a species or vegetation type occurred in that site category (a procedure modified from Raup 1969).

Results and Discussion

Physiographic Classification of Sites

The six types of landforms of the Juneau-area coastal marshes and their subdivisions into physiographic site categories are shown in Table 2 and Figure 2. The shape, slope angle, position, and composition of these surfaces determine their hydrologic characteristics (Hack and Goodlett 1960), which are essential components of habitat in the sampled marshes. Concave surfaces collect water and so are flooded or saturated more frequently and/or longer than surfaces with other shapes. Convex surfaces shed water and thus are drier and flooded less often and for shorter periods than surfaces of other shapes. The straight surfaces have intermediate hydrologic conditions. The steeper slopes of levees and of landforms above marsh borders shed water faster than the imperceptibly sloping marsh and tide-influenced meadow surfaces.

Drift lines (Table 2, Figure 2) are created by logs left by storm tides. Sediment collects around the logs, slightly raising the ground surface above the surrounding landscape and thus increasing the drainage.

The differences in position and substrate composition of slopes in all site categories (Table 2, Figure 2) also produce different hydrologic conditions (Table 1) and thus are important components of habitat in the sampled marshes. Marsh sites occur at the lowest elevations and thus have the longest and most frequent tide coverage. Within these landforms, channel banks and lower marsh borders experience the highest current velocities as well as the longest tidal flooding periods. Tide-influenced meadows are flooded or partly flooded by the higher of the semi-diurnal mixed tides. Beaches and upper marsh borders are flooded by storm tides and higher spring tides. Because of their position facing the sea, beaches receive beating by waves, whereas marshes and upper marsh borders are more sheltered.

The position of the tidal inlet channel also affects hydrologic conditions in marshes. At sites where the channel opens directly into the ocean, entering tidewater is clear and undiluted by fresh water, and marsh floors have substrates coarser than silt (Table 1). These marshes are well drained and well aerated. At sites where the tidal channel opens into a river channel or the tidewater spreads over flats at a river mouth, the water flooding the

marshes is brackish, silty, tidally dammed river water. The floors of these marshes are silt (Table 1), less well drained and less well aerated than coarser substrated marshes.

Substrate composition, another basic component of habitat, influences the drainage characteristics of marshes, slopes above marsh borders, and uplands. Sand marshes are better drained than silt marshes. Sand spits are well-drained, whereas the bedrock (seepage and fill) slopes and hillsides of valley walls are impermeable under generally wet soils through which fresh water seeps into upper marsh borders, tide-influenced meadows, extratidal wet sites and upper parts of marshes (Figure 2).

The relationship of the upper marsh border to other site categories depends on the arrangement of landforms. The upper marsh border may occur at the upper edge of marsh (Figure 2a), within or above tide-influenced meadow (Figure 2d), or beside a tidal channel at the base of a spit. On gentle slopes above tidal marsh, the upper marsh border grades into or interfingers with the landforms of tide-influenced meadow and slopes above marsh borders. The variety of possible arrangements of landforms and the shape, slope angle, topographic position, and substrate composition of landforms determine the seaward-to-landward sequence of vegetation types (see "Habitat-Vegetation Complexes of Juneau-Area Coastal Marshes" below).

Physiographic Classification of Species

Based on their occurrence in the physiographic site types of Table 2, plant species can be grouped into five categories: tidal marsh species (on lower marsh borders, sand marshes, silt marshes, and channel banks), species of tide-influenced sites (on tide-influenced meadows, upper marsh borders, drift lines, and beaches), species of slopes above marsh borders (on spit slopes, seepage slopes, and fill slopes), upland species (on spit tops), and species of extratidal wet sites (in fresh marshes and marsh ponds) (Table 3). Within this classification species vary in their range of occurrence. On the coastal marsh and tide-influenced sites, 13 of the 14 primary species and two of the five secondary species were found on more than one site type. Above the upper marsh border, 21 of the 30 species occurred on more than one site type. This variability makes it difficult to use species distributions alone to identify common characteristics among coastal marshes of the Juneau area.

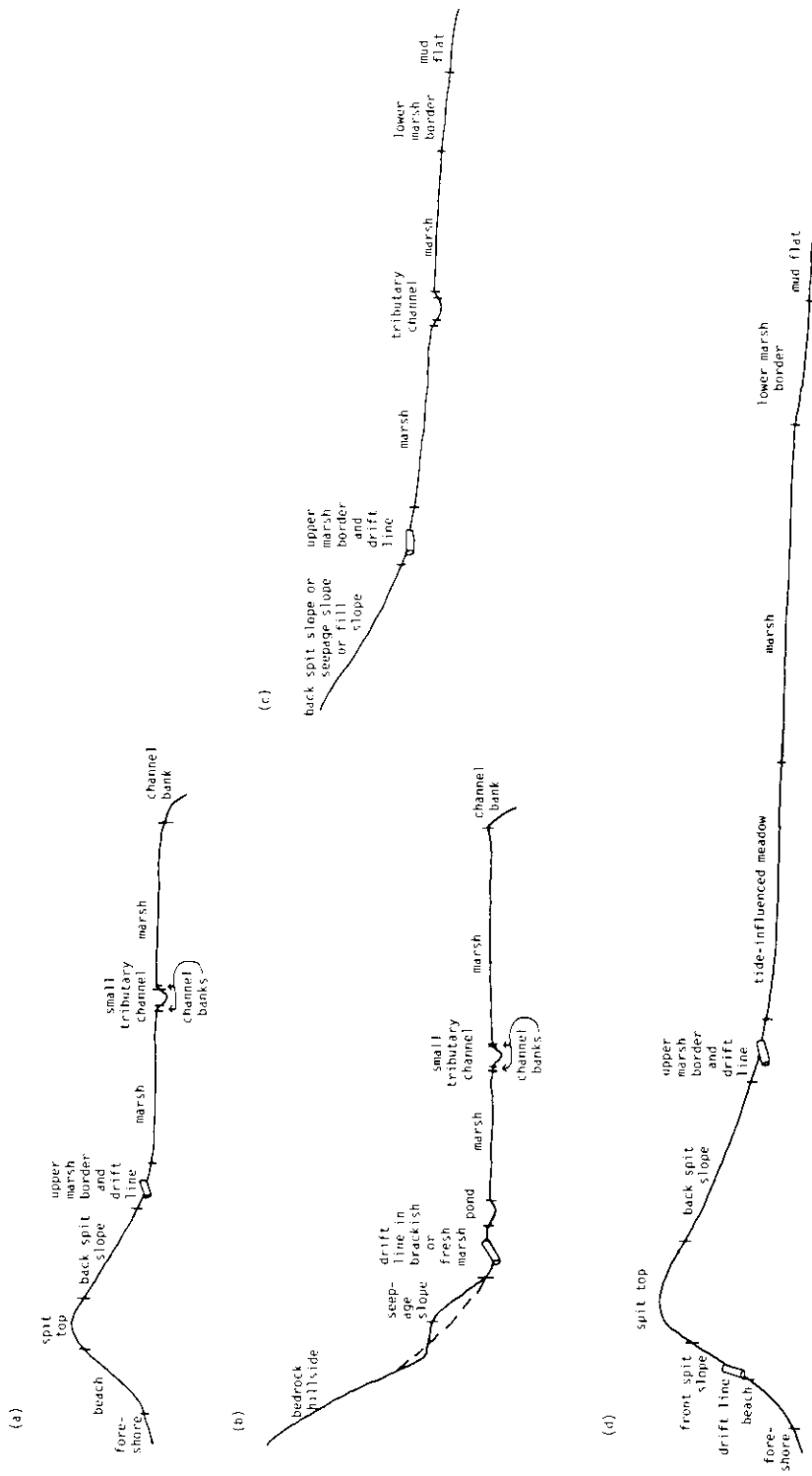


Figure 2. Generalized landforms of Juncos area coastal marshes illustrating the variety of combinations in the study area. (a) cross-section of marsh with natural levee (at channel bank) and ponds; (b) longitudinal profile of marsh without tide-influenced meadow; (c) longitudinal profile of marsh with tide-influenced meadow and ponds; (d) longitudinal profile of marsh with tide-influenced meadow and sand spit. Dashed line in (c) shows the former natural slope and solid line in the same area is the present cut-and-fill slope. Vertical scales exaggerated; horizontal scales not constant.

TABLE 3. Plant species occurrence by physiographic site category.

Plant species	marsh sites					upper marsh border sites	beach	slopes above marsh border				upland	extratidal wet sites		
	lower marsh border	sand marsh	silt marsh	channel bank	tide-influenced meadow	upper marsh border	drift line	beach	front spit slope	back spit slope	seepage slope	fill slope	spit top	fresh marsh	marsh pond
Tidal marsh species group															
<i>Puccinellia nutkaensis</i>	pri ^a	pri	pri	pri											
<i>Spergularia canadensis</i>	pri	sec	sec												
<i>Carex lyngbyae</i>	pri		pri	pri										pri	
<i>Triglochin maritimum</i>	pri	sec	sec												
<i>Fucus</i> sp.	pri	sec													
<i>Salicornia virginica</i>		pri													
<i>Plantago maritima</i>		pri	sec												
<i>Suaeda maritima</i>		sec													
<i>Glaux maritima</i>		s/p ^b	sec												
<i>Stellaria humifusa</i>		sec	sec	sec											
<i>Cochlearia officinalis</i>		sec													
<i>Atriplex gmelini</i>		sec	sec												
<i>Hordeum jubatum</i>		sec			pri										
<i>Eleocharis kamschatica</i>			sec												
<i>Potentilla pacifica</i>			p/s ^c			pri									
Tide-influenced species group															
<i>Festuca rubra</i>					pri			p/s	sec		pri	pri			
<i>Deschampsia caespitosa</i>					pri				s/p	sec	pri				
<i>Elymus arenarius</i>					pri	pri	pri	pri	pri	pri			pri		
<i>Honckeya peploides</i>						pri	pri	pri	pri				pri		
<i>Lathyrus maritimus</i>							pri	pri	pri	pri			pri		
Slopes-above-marsh-border species group															
<i>Achillea millefolium</i>						pri		pri	sec	pri	pri	pri			
<i>Hordeum brachyantherum</i>									sec	sec	sec				
<i>Angelica lucida</i>								pri	s/p	pri			pri		
<i>Mertensia maritima</i>									sec				pri		
<i>Lupinus nootkatensis</i>								pri	sec	sec			pri		
<i>Castilleja unalaschensis</i>									sec				pri		
<i>Heracleum lanatum</i>								pri	sec	pri			pri		
<i>Ligusticum scoticum</i>								pri	p/s	sec			pri		
<i>Conioselinum chinense</i>								pri	p/s				pri		
<i>Galium trifidum</i>									sec				sec	sec	
<i>Malus fusca</i>									sec				sec		
<i>Maianthemum dilatatum</i>									sec				sec		
<i>Sagina crassicaulis</i>									sec						
<i>Actaea rubra</i>									sec						
<i>Epilobium angustifolium</i>									pri						
<i>Oenanthe sarmentosa</i>										pri				pri	
<i>Melilotus alba</i>											pri				

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TABLE 3 (Continued). Plant species occurrence by physiographic site category.

Site Category	marsh sites					upper marsh border sites	beach	slopes above marsh border			upland	extratidal wet sites			
	lower marsh border	sand marsh	silt marsh	channel bank	tide-influenced meadow	upper marsh border	drift line	beach	front spit slope	back spit slope	seepage slope	fill slope	spit top	fresh marsh	marsh pond
Plant species															
Upland species group															
<i>Equisetum arvense</i>													sec		
<i>Carex macloviana</i>													sec		
<i>Fritillaria camchatcensis</i>													pri		
<i>Rubus arcticus</i>													sec		
<i>Trientalis europaea</i>													sec		
Extratidal wet site species group															
<i>Parnassia palustris</i>														sec	
<i>Caltha palustris</i>														sec	
<i>Potentilla palustris</i>														sec	
<i>Myrica gale</i>														sec	
<i>Cicuta douglasii</i>														sec	
<i>Chrysanthemum arcticum</i>														sec	
<i>Hippuris tetraphylla</i>															pri

"pri = visual aspect dominant, sec = all other species (see "Data Collection" in text)

^boccurs as sec more often than as pri

^coccurs as pri and sec with approximately equal frequency

Vegetation-Type Classification of Species

The eleven vegetation types identified from Braun-Blanquet analysis are named for their constant primary species or physiognomic types (Table 4). Their occurrences in the sampled marshes are shown in Figure 3.

Although each vegetation type is distinguished by a unique set of primary species, many species occur in more than one vegetation type (Table 4). In the coastal marsh and tide-influenced vegetation types, 12 of the 14 primary species and three of the five secondary species occur in more than one type. Above the upper marsh border, nine of the 28 species occur in more than one vegetation type (two of the 30 species referred to in the preceding section occurred too infrequently to be classified in the Braun-Blanquet analysis). Furthermore, the vegetation types vary in species composition within and among marshes. This variability is quite evident in the tables produced for the Braun-

Blanquet analysis (Table 13 in Stone 1984) and is generally related to microhabitat differences within vegetation types.

Physiographic Classification of Vegetation Types

Table 5 shows the association of vegetation types with the physiographic site categories of Table 2. Each vegetation type occurs consistently on one physiographic site category or a few to several topographically related categories, such as marsh, lower marsh border, and channel bank; tide-influenced meadow and certain slopes above marsh borders; or categories usually above tidal influence. Figure 3 shows the spatial relations among vegetation types at the study sites. Notice that each marsh has a unique combination of vegetation types occurring in a unique sequence along a gradient inland, which makes similarities among marshes difficult to identify.

TABLE 4. Plant species occurrence by vegetation type.

Plant species	Vegetation type ^a										
	cm				ti	aumb	ti	aumb			
	<i>Salicornia virginica</i>	<i>Puccinellia-Plantago</i>	<i>Puccinellia-Carex</i>	<i>Carex lyngbyaei</i>	<i>Elymus arenarius</i>	<i>Honekenya peploides</i>	<i>Elymus-Lathyrus</i>	coastal grass meadow	coastal forb meadow	fresh <i>Carex</i> marsh	<i>Hippuris tetraphylla</i>
<i>Salicornia virginica</i>	pri ^b										
<i>Puccinellia nutkaensis</i>		pri	pri								
<i>Plantago maritima</i>		pri	sec								
<i>Suaeda maritima</i>		sec									
<i>Claux maritima</i>		pri	sec	sec							
<i>Potentilla pacifica</i>		sec		p/s ^c	pri					pri	
<i>Spergularia canadensis</i>		pri	sec	sec							
<i>Triglochin maritimum</i>		sec	p/s	sec							
<i>Stellaria humifusa</i>		sec	sec	sec							
<i>Cochlearia officinalis</i>		sec	sec								
<i>Hordeum jubatum</i>		sec						pri			
<i>Fucus</i> sp.		pri									
<i>Atriplex gmelini</i>		sec	sec								
<i>Carex lyngbyaei</i>			pri	pri						pri	
<i>Elymus arenarius</i>					pri		pri		pri		
<i>Honekenya peploides</i>					pri	pri	pri				
<i>Lathyrus maritimus</i>							pri		pri		
<i>Mertensia maritima</i>							pri				
<i>Festuca rubra</i>								pri	pri		
<i>Hordeum brachyantherum</i>								sec			
<i>Deschampsia caespitosa</i>								pri		sec	
<i>Achillea millefolium</i>									pri		
<i>Lupinus nootkatensis</i>									pri		
<i>Heracleum lanatum</i>									pri		
<i>Angelica lucida</i>									pri		
<i>Ligusticum scoticum</i>									pri		
<i>Conioselinum chinense</i>									pri		
<i>Castilleja unalaschensis</i>									pri		
<i>Galium trifidum</i>									sec	sec	
<i>Epilobium angustifolium</i>									pri		
<i>Malus fusca</i>									sec		
<i>Oenanthe sarmentosa</i>									sec	sec	
<i>Actaea rubra</i>									sec		
<i>Polygonum viviparum</i>									sec		
<i>Maianthemum dilatatum</i>									sec		
<i>Fritillaria camchaticensis</i>									pri		
<i>Rubus arcticus</i>									sec		
<i>Sagina crassicaulis</i>									sec		
<i>Trientalis europaea</i>									sec		
<i>Carex macloviana</i>									sec		
<i>Parnassia palustris</i>										sec	

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TABLE 4 (Continued). Plant species occurrence by vegetation type.

Plant species	Vegetation type ^a										
	cm				ti	aumb	ti	aumb			
	<i>Salicornia virginica</i>	<i>Puccinellia-Plantago</i>	<i>Puccinellia-Carex</i>	<i>Carex lyngbyae</i>	<i>Elymus arenarius</i>	<i>Honckenya peploides</i>	<i>Elymus-Lathyrus</i>	coastal grass meadow	coastal forb meadow	fresh <i>Carex</i> marsh	<i>Hippuris tetraphylla</i>
<i>Myrica gale</i>										sec	
<i>Caltha palustris</i>										sec	
<i>Potentilla palustris</i>										sec	
<i>Cicuta douglasii</i>										sec	
<i>Chrysanthemum arcticum</i>										sec	
<i>Hippuris tetraphylla</i>											pri

^acm = coastal marsh vegetation type, ti = tide-influenced, aumb = above upper marsh border

^bpri = visual aspect dominant, sec = all other species (see "Data Collection" in text)

^coccurs as pri and sec with approximately equal frequency

Habitat-Vegetation Complexes of Juneau-Area Coastal Marshes

Given the marsh-to-marsh differences in vegetation-type composition and arrangement on a sea-to-inland gradient in the Juneau area (Figure 3), comparing the marshes in terms of community composition (the usual approach - e. g., Watson 1981) would seem inadequate. Raup's (1975, p. 130) concept of the habitat-vegetation complex could be used in this situation. Raup described the shoreline vegetation of lakes in the Athabasca-Great Slave Lake region in terms of "form types" and recognized 10 types that, because they occupied sites of different "moisture regime, substrate, or topographic position," were called "habitat-vegetation complexes." These complexes are combinations of physiographic site characteristics with a physiognomic characterization of the vegetation, e.g., "aquatic habitats with submerged and/or emergent plants" and "herbs and low or trailing shrubs on middle beaches of large lakes."

Raup (pers. comm.) originally intended his concept to be used only in certain situations where he has worked. I believe that it is also applicable to an understanding of southeast Alaskan coastal marsh vegetation patterns, because it frees us from

the restricted possibilities for comparison imposed by the use of communities, whose definition requires particular species compositions. It also allows meaningful comparisons of vegetation in groups of marshes with unique sets and spatial arrangements of vegetation types by providing a vegetational component (a physiognomic type) integrated with environmental parameters in physiography (as in Hack and Goodlett 1960).

Habitat-vegetation complexes for coastal marshes of the Juneau area can be derived by generalizing from the physiographic classification of vegetation types of Table 5. Each complex is distinguished by a unique physiographic site category (Table 2) or combination of categories occupied by a physiognomically distinct vegetation type (Table 4) or set of vegetation types as described below. Nine habitat-vegetation complexes are recognized here for Juneau-area coastal marsh systems. (The unique distinguishing feature of each complex is underlined.)

The habitat-vegetation complexes of the marshes and their immediate surroundings are:

- 1) tidal sedge and sedge-grass marshes on silt substrate;
- 2) tidal grass-forb marshes on substrate coarser than silt;

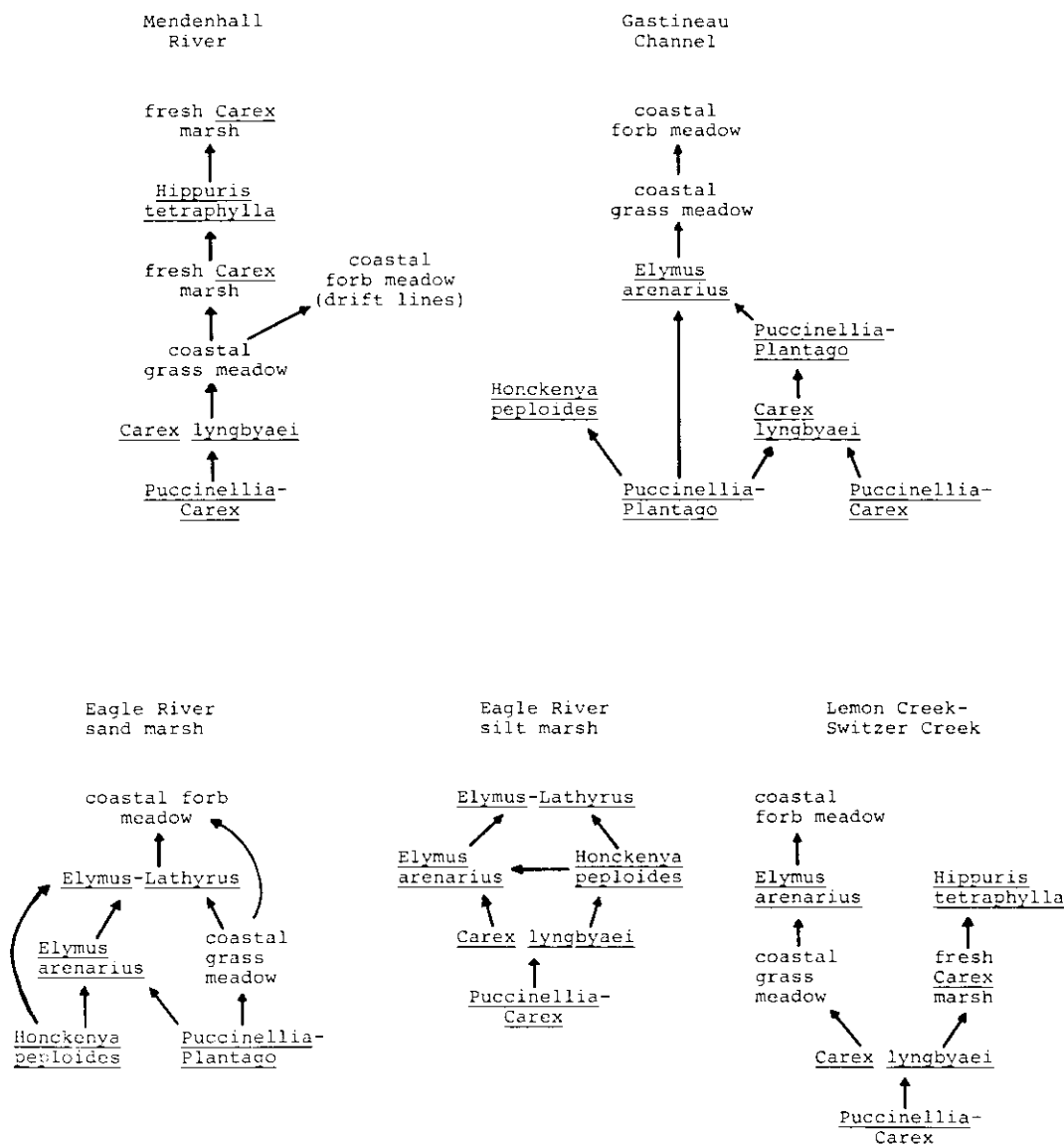


Figure 3. Spatial arrangement of vegetation types in Juneau-area coastal marshes. Arrows point inland.

- 3) succulent vegetation of tidal sand marshes;
- 4) gramineous vegetation of tide-influenced meadows;
- 5) Elymus arenarius vegetation type of upper marsh borders and drift lines;
- 6) prostrate and scrambling forb and rhizomatous grass vegetation of upper beaches and sand spits;
- 7) coastal forb meadow vegetation of sand spits, slopes above marsh borders, and drift lines;
- 8) sedge-forb vegetation of fresh marshes inland of usual tidal influence or recently elevated above tidal influence;
- 9) emergent vegetation of apparently brackish marsh ponds in tidal and recently tidal marshes.

Complexes 1 and 2 include small channels, channel banks, and lower marsh borders as marsh sites, because the vegetation of these sites is physiognomically similar within each complex on

TABLE 5. Physiographic classification of vegetation types (x = vegetation type characteristic of the indicated site categories).

Physiographic Category	marsh sites					upper marsh border sites	beach	slopes above marsh border			upland	extratidal wet sites			
	lower marsh border	sand marsh	silt marsh	channel bank	tide-influenced meadow	upper marsh border	drift line	beach	front spit slope	back spit slope	seepage slope	fill slope	spit top	fresh marsh	marsh pond
<i>Salicornia virginica</i>		x													
<i>Puccinellia-Plantago</i>	x	x													
<i>Puccinellia-Carex</i>	x		x	x											
<i>Carex lyngbyaei</i>			x												
coastal grass meadow					x					x		x			
<i>Elymus arenarius</i>						x	x								
<i>Honckenya peploides</i>								x							
<i>Elymus-Lathyrus</i>							x		x	x			x		
coastal forb meadow							x		x	x	x	x			
fresh <i>Carex</i> marsh														x	
<i>Hippuris tetraphylla</i>															x

these site categories. Complex 1 also combines two vegetation types, *Puccinellia-Carex* and Lyngbye sedge (*Carex lyngbyaei*) because their habitat behaves as a single unit. Complex 3 is included tentatively, since it is known from only one site. It is distinguished from complex 2 by its succulent vegetation type and its isolated occurrence. Complex 5 combines all site categories with the lyme grass (*Elymus arenarius*) vegetation type; complex 6 all site categories with the seabeach sandwort (*Honckenya peploides*) and *Elymus-Lathyrus* types. Complex 7 includes all the kinds of physiographic sites with coastal forb meadow vegetation. The other complexes are self-explanatory with reference to the list above and to Table 5.

Five habitat-vegetation complexes are associated with marshes; the others occur on landforms surrounding the marshes (Tables 2 and 5). The complexes are intended to describe the vegetation and landscape of the sampled marshes so as to identify their similarities; they are considered not necessarily definitive for a larger area.

The relationship of vegetation type to landform in the habitat-vegetation complex can be used to explain major aspects of the differences in species

and vegetation-type composition among the sampled marshes of the Juneau area. Because a particular vegetation type is associated with only one or a few kinds of landforms, it will be present in a marsh only if its associated landform(s) is(are) present. The spatial relationship of landforms in a marsh will determine the spatial relationship of vegetation types and thus account for the differences in the spatial sequence of vegetation types among marshes shown in Figure 3.

For example, where the substrate is coarser than silt, the *Puccinellia-Plantago* vegetation type occurs over the whole tidal sand marsh site category. This explains why *Puccinellia-Plantago* is the only marsh vegetation type in the Eagle River sand marsh. Where the marsh floor is silt, there are two marsh vegetation types: *Puccinellia-Carex* always occurs below *Carex lyngbyaei* in elevation. Three marshes in the Juneau area have this sequence: Mendenhall River, Lemon Creek, and Eagle River silt marsh. The Gastineau Channel marsh has both the *Puccinellia-Carex* to *Carex lyngbyaei* sequence and the *Puccinellia-Plantago* vegetation type, because it has a small area covered with silt surrounded by a sand and gravel surface (Table 1).

Immediately above the marsh, there are four possible vegetation types: coastal grass meadow, *Elymus arenarius*, fresh *Carex* marsh, and *Honckenya peploides*, depending on landform configuration. Where the slope beyond tidal marsh is flat or gradually rising, it creates a tide-influenced meadow landform suitable for coastal grass meadow (Figure 2d). Mendenhall River, Lemon Creek, and Eagle River sand marsh have this configuration (Figure 3). Where the edge of tidal marsh reaches to a steep slope, the sequence is from a marsh vegetation type to a narrow *Elymus arenarius* upper marsh border (Figure 2c), as in Gastineau Channel marsh, Eagle River silt marsh, and along the sides of Lemon Creek and Eagle River sand marshes.

The landward slope of the tidal marsh at Mendenhall River and Lemon Creek-Switzer Creek is down instead of up (Figure 2b), so that fresh seepage water is ponded at the base of the valley sides, creating a habitat for fresh *Carex* marsh vegetation. The progression of vegetation types is from brackish-and-wet *Carex* tidal silt marsh to fresh-or-less-brackish-and-wet fresh *Carex* marsh and ends in ponds with mare's tail (*Hippuris tetraphylla*) as primary species (Figure 3). Tide-influenced coastal grass meadow can occur between the two types of *Carex* marsh.

The fourth sequence, marsh-to-*Honckenya peploides*, is less common than the marsh-to-*Elymus arenarius* sequence. It occurs in some parts of the Gastineau Channel marsh and Eagle River silt marsh, where the *H. peploides* vegetation type replaces the *Elymus arenarius* vegetation type as the upper marsh border (Figure 3).

Honckenya peploides is also an upper beach species on the outside of sand spits. It can occur there as the lowest elevation vegetation type just below *Elymus arenarius*. Whether the sequence is *H. peploides* - *E. arenarius* or *H. peploides* - *Elymus-Lathyrus* depends on the elevation of the lowest *E. arenarius* on the outside of the spit. *E. arenarius* can tolerate beating from waves, but beach pea (*Lathyrus maritimus*) cannot, so if *E. arenarius* is growing in the zone of storm waves, *Lathyrus* will be absent (Eagle River sand and silt marshes in Figure 3).

In the sampled coastal marshes around Juneau, the most common vegetation-type sequences from marsh to higher ground are: marsh - *Elymus arenarius* - (*Elymus-Lathyrus*) - coastal forb meadow; and marsh - coastal grass meadow - *Elymus arenarius* - (*Elymus-Lathyrus*) - coastal forb

meadow. *Elymus-Lathyrus* where present is often a narrow band between *Elymus arenarius* and coastal forb meadow on steep slopes above marshes. Since both *Elymus* and *Lathyrus* occur also as primary species in coastal forb meadow (Table 4), the progression *Elymus arenarius* - *Elymus-Lathyrus* - coastal forb meadow is apparently a consequence of differential reactions of species to the influence of tides and storms.

Habitat-Vegetation Complexes in Other Southeast Alaskan Coastal Marshes

The habitat-vegetation complex explains the differences in presence and arrangement of vegetation types in Juneau-area coastal marshes. If this concept is to be more generally useful, it must explain such differences elsewhere. Three other studies of southeast Alaskan coastal marsh vegetation reported in the literature (Stephens and Billings 1967, del Moral and Watson 1978, Watson 1981) contain enough habitat information to permit examination of the usefulness of the concept. Figure 4 shows the spatial relationships of the vegetation types in these studies. As in the Juneau area, no two marshes have the same vegetation-type composition or spatial arrangement of vegetation types. Because none of the studies was made on a completely physiographic basis, habitat-vegetation complexes cannot be defined, but they can be tentatively inferred from the published information combined with this author's field observations at two of the sites.

Stephens and Billings' (1967) description of the marsh at Kadashan Bay is most like the Juneau area marshes, with a sequence of *Carex* marsh - coastal grass meadow - upper marsh border. (The tufted hairgrass (*Deschampsia caespitosa*) community at Kadashan is inferred to be analogous to coastal grass meadow since *D. caespitosa* is a primary species of this vegetation type at Mendenhall River.)

Watson (1981) found five vegetation types in seven coastal marshes of the Sitka area (Figure 4). All marshes had different sequences of vegetation types along elevation gradients, but the types were consistently associated with particular substrates. Alkali grass (*Puccinellia nutkaensis*) was the assemblage at lowest elevations in all but one marsh. It occurred on silt and gravel. Because it has almost the same species composition as the *Puccinellia-Plantago* assemblage of the Juneau area and because *Carex lyngbyaei* is absent, it would appear

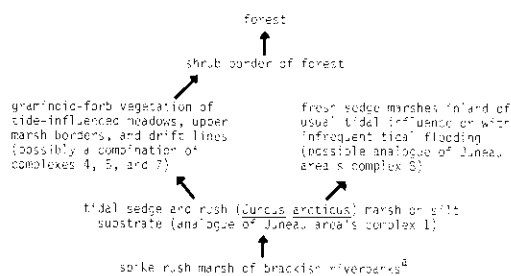
tolerance. It must be related to differences among marshes in distribution of silt and of silt overlying gravel. Because these differences result from physiographic processes, the relationship of vegetation types and substrate supports the concept of the habitat-vegetation complex as useful in understanding southeast Alaskan coastal marsh vegetation.

The Gastineau Channel vegetation diagram in Figure 3 indicates a way in which sequences such as Watson found at Halleck Island, Kizuchia Creek, and Starrigavan River might have come to be recorded. It is possible in the Gastineau Channel marsh to run a transect from the lowest elevation *Puccinellia-Plantago* through *Carex lyngbyaei*, another patch of *Puccinellia-Plantago*, into *Elymus arenarius* upper marsh border. The marsh floor along such a transect changes from sand, gravel, and cobbles, to silt to sand, gravel, and cobbles, to broken rock fill. Field observations in northern and central southeast Alaska indicate that this kind of substrate variability is usual in coastal marshes of this region. Therefore, a sequence of changes in substrate and/or elevation or landform and repetitions of these changes could be responsible for the repetitions of vegetation types along Watson's transects.

The sequence of vegetation types on the Stikine Flats (del Moral and Watson 1978, Sparks *et al.* 1977) is more complicated (Figure 4), because a larger area was sampled (4.5 km² vs. the 150 ha of the largest completely transected Juneau-area marsh) with four shrub and forest vegetation types in addition to marsh vegetation. Three communities of the Stikine Flats (*Calamagrostis nutkaten-sis*, *Potentilla-Festuca*, and *Carex mackenziei*) appear to be analogues of the Juneau area's coastal grass and forb meadow vegetation types in species composition and geographic/physiographic position (Table 1 and p. 4 in Sparks *et al.* 1977). Like these two vegetation types in the Juneau area, the three Stikine communities are described (p. 4) as "heterogeneous" and intergrading, with no strong dominants. Thus, in terms of habitat-vegetation complexes, the vegetation sequence at the Stikine Flats might be written as shown in Figure 5. A generalized arrangement of habitat-vegetation complexes for all coastal marshes studied so far in southeast Alaska is given in Figure 6.

Conclusion

Coastal marshes vegetation types and their habitat characteristics can be generalized into habitat-vegetation complexes, which allow us to make



^a... observed also near Haines, Alaska (Stone, unpublished data, 1983, 1987)

Figure 5. Spatial arrangement of possible habitat-vegetation complexes on the Stikine Flats, southeast Alaska (inferred from Sparks *et al.* (1977)). Arrows point inland.

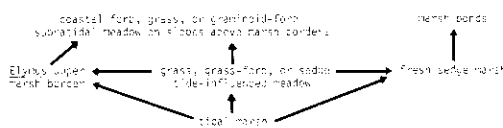


Figure 6. Generalized spatial arrangement of habitat-vegetation complexes in southeast Alaskan coastal marshes. Arrows point inland.

ecological comparisons of marshes with different sets of vegetation types. For southeast Alaska, the comparison is tentative outside the Juneau area because complete physiographic information is not available. Nevertheless, coastal marshes studied so far in southeast Alaska have a recognizable general arrangement of habitat-vegetation complexes. Even within the Juneau area this pattern varies because of the individualistic behavior of plant species and the differences in landform type and arrangement at different sites, and because of historical differences among marshes.

Acknowledgments

The author is indebted to H. M. Raup, W.W. Chilcote, and R. F. Parsons for advice and encouragement, to E. A. Adam for field and financial assistance, to staff of the Botany Department, La Trobe University, to W. J. Woelkerling for comments on an earlier draft, and to Alaskan friends too numerous to mention for logistical support. The comments and enthusiasm of several reviewers and K. V. Kardong are much appreciated.

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Received 1 August 1992

Accepted for publication 1 June 1993