

VEGETATION-ENVIRONMENT RELATIONSHIPS IN THE TIDAL MARSHES OF
THE FRASER RIVER DELTA, BRITISH COLUMBIA

by

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ABSTRACT

The literature on North American Pacific Coast tidal marshes north of Mexico is summarized.

Vegetation and environmental data from Fraser Delta tidal marshes at Ladner Marsh, Brunswick Point, and Boundary Bay were analyzed using principal components analysis and reciprocal averaging to investigate quantitative relationships between species performance and distribution, and selected environmental factors. These were: soil texture (percentage of sand, silt, and clay); soil concentration of nitrogen, potassium, calcium, magnesium, and sodium; and elevation (standardized by local tidal range). Ordinations were performed on both the vegetation and the environmental data sets. Different methods of data standardization (square root transformation, normalization, and correlation matrix) were tested for their usefulness in exposing ecological gradients.

Normalization and square root transformation of the data were found to be useful in vegetation ordination; the correlation matrix was not. Reciprocal averaging and principal components analysis gave results of equivalent quality with the vegetation data, but principal components analysis was generally superior to reciprocal averaging in the environmental ordinations.

The marshes of the study area separate conspicuously into

two types on both floristic and environmental criteria: a fresh-to-brackish type at Ladner Marsh and in northern and western Brunswick Point, and a saline type in southeastern Brunswick Point and at Boundary Bay. Within each area, four main species-environment sample groups were informally recognized, dominated respectively by: (1.) Carex lyngbyei and Agrostis alba; (2.) Agrostis alba and Scirpus maritimus; (3.) Scirpus americanus; (4.) Equisetum fluviatile, Scirpus validus, Agrostis alba, and Alisma plantago-aquatica; (5.) Atriplex patula; (6.) Carex lyngbyei and Distichlis spicata; (7.) Salicornia virginica and Triglochin maritimum; (8.) Spergularia canadensis. Patterns of performance and distribution of important tidal marsh species were shown to be related to levels of the measured environmental factors.

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1. INTRODUCTION

Tidal marsh ecosystems, belonging as they do neither entirely to the terrestrial environment nor to the marine, yet overlapping the frontiers of both, have long been a source of interest to ecologists -- even as man's ambition has led to the diking, draining, cultivating, or filling of coastal marshlands everywhere. Fortunately, the interactive relationships between industrial activities and natural ecosystems have been the object in recent years of some critical examination, with the result that it is now possible to appreciate marshlands as an economic resource, and ecological considerations are no longer ignored in economic and political decision making. There is hope, therefore, that remaining estuarine marshes will be valued as important living systems, rather than being treated as useless wastelands.

The tidal marshlands of the Fraser estuary, as local hunters and naturalists have long known, are principal nesting and feeding areas for migratory waterfowl;¹ recent research demonstrates their importance to the fisheries resource² as well. Not the least importance of these marshlands, however,

¹ Burgess 1970, Burton 1977, Campbell et al. 1972, Habitat Work Group 1978, Hoos & Packman 1974, Leach 1972, Vermeer & Levings 1977.

² Dorsey et al. 1978, Dunford 1975, Levy & Northcote 1981, Levy et al. 1979, Valiela & Kistritz 1980.

is their value as wilderness. Here are vast areas very near the city, teeming with birdlife and vibrant with floral splendor, in which the anxieties of a civilized existence seem to recede like the falling tide.

The present study is concerned with the elucidation of vegetation-environment relationships in the Fraser Delta. The objectives may be summarized as follows:

(1.) To describe and compare the vegetation of three Fraser Delta tidal marshes;

(2.) To relate performance and distribution of vascular plant species to measured environmental variables;

(3.) To assess the effects of different types of data standardization in exposing ecological gradients, using principal components analysis and reciprocal averaging.

It is hoped that any increased understanding of tidal marsh systems that may result from this study will be helpful to researchers and managers concerned with tidal marsh establishment and rehabilitation.

2. LITERATURE REVIEW: PACIFIC COAST TIDAL MARSHES

2.1 General Overview

The literature on tidal marsh ecosystems and their vegetation is voluminous, and cannot be dealt with here in its entirety. This review is therefore restricted geographically to the Pacific Coast of Canada and the United States. For comprehensive, global treatments of salt marsh, tidal marsh, and other coastal vegetation, the reader is referred to Chapman (1960, 1974, 1976, 1977) and Ranwell (1972).

The area being reviewed is mountainous for much of its extent, with a generally narrow continental shelf; the shoreline is usually steep-sloped and marked by rocky headlands. From Puget Sound north, the coast is deeply dissected into fiords and archipelagos, and has been subjected to rather recent glacial erosion and subsequent isostatic uplift (Mathews et al. 1970). Such conditions do not favour coastal marsh development, with the result that our marshes tend to be quite small, young (Macdonald & Barbour 1974, Jefferson 1974), and isolated -- commonly restricted to small bays, estuaries and river mouths (Macdonald 1977a).

The beach and salt marsh vegetation of the North American Pacific coast between Point Barrow, Alaska and Cabo San Lucas, Baja California was surveyed by Macdonald & Barbour (1974).

For the same area, Macdonald (1977a) summarized the knowledge to that date of salt marsh and mangal vegetation, and proposed a tentative phytogeographical classification of Pacific Coast salt marshes, based on regional floras, into five major groups: arctic, subarctic, temperate, dry mediterranean, and arid. These groups correspond roughly to: northern and western Alaska; southern and southeastern Alaska and the Queen Charlotte Islands; British Columbia, Washington, Oregon and northern California; southern California; and Baja California, respectively. A numerical analysis of data from theoretical sample sites (using "expected" species lists) broadly supported these groupings, but indicated a major break into northern and southern divisions at about 51 degrees north latitude. The scheme thus assigns Fraser Delta marshes to the southern group. (It would be interesting to redo the analysis now, using data from actual sample locations.)

Some directions in current marsh research are indicated in a compilation of abstracts¹ from papers delivered at the Sixth Biennial International Estuarine Research Conference, published in *Estuaries*, vol. 4, 1981.

In general, the published literature on tidal marsh vegetation in the review area is rather sparse. The marshes of California and Alaska are the best-documented. Marshes of

¹ especially Eilers 1981, Frenkel 1981, Mahall 1981, Mitchell 1981, Oliver & Reilly 1981, Onuf 1981, Wolf & Fucik 1981, Zedler 1981.

the Oregon, Washington, and British Columbia coasts are described mainly in unpublished theses and government reports (frequently quite obscure ones). In the remainder of this review, the literature is surveyed geographically: California, Oregon, Washington, Alaska, and British Columbia.

2.2 California

The first major published ecological investigation of tidal marsh vegetation in California seems to be that of Purer (1942), who studied twelve coastal salt marshes in San Diego County, in the southern part of the state. She described at length the ecology and anatomy of the nine principal vascular species in her study area.

The marshes of Newport Bay, also in southern California, were described by Stevenson (1954), Stevenson & Emery (1958), and Vogl (1966). Stevenson & Emery (1958) recognized five plant communities in the marsh proper -- the Spartinetum, the Salicornietum, the Suaedetum, the Monanthochloetum, and the Distichlidetum -- and related the community zonation to tidal immersion and soil factors. Vogl (1966) sampled quantitatively for frequency and cover, and found that the marsh could be separated into three zones: the lower zone dominated by Spartina foliosa, the middle one by Batis maritima and Salicornia virginica, and the upper one by Salicornia virginica and Monanthochloe littoralis. He found

that the zones did not have discrete boundaries, but that floristic composition gradually changed along environmental gradients, consistent with the continuum concept sensu Curtis & McIntosh (1951).

Zedler (1977) investigated the vegetation of the Tijuana Estuary salt marsh, at the southern end of the California coast, in relation to measured environmental factors over a one-metre elevation gradient. She found that dominance of vascular plants changed gradually with elevation; rigorous data analysis did not support the concept of intertidal zonation. She also studied species interactions and the role of competition in determining species distributions.

Further north, Cooper (1926) provided a brief early description of the marshes near Palo Alto in San Francisco Bay. Also in the Palo Alto area, Hinde (1954) identified three major vegetation associations, describing them and their dominant species (Salicornia ambigua, Distichlis spicata, and Spartina leiantha) in terms of their vertical distribution with respect to tide levels.

The salt marsh at Bodega Head, north of San Francisco, was described by Barbour et al. (1973), reporting on a study by Hamner (unpublished?), who sampled species cover along elevational transects.

In a series of three papers, Mahall & Park (1976a, b, c) described the ecotone between Spartina foliosa and Salicornia

virginica, corresponding to the level of mean high water, in two marshes with different topographical characteristics in northern San Francisco Bay. Their findings indicated: (1.) productivity of both species is low at the ecotone, with frequent open spaces, suggesting that the boundary results not from competition, but from poor environmental conditions there for both species; (2.) Salicornia occupies a habitat having considerably higher soil salinity than that of Spartina during the growing season; (3.) Spartina is less tolerant than Salicornia of rapid salinity changes, and much less tolerant of higher root medium salinities; (4.) soil aeration is not an important factor affecting the distributions of the two species about the ecotone; (5.) inhibition of growth resulting from tidal immersion may be an important factor checking the seaward advance of Salicornia.

Some recent Ph.D. dissertations in California have dealt with tidal marsh vegetation not from the point of view of community composition or ecological gradients, but rather in terms of energy budgets, chemistry, and nutrient cycling. Felton (1978) examined microclimatic conditions in a San Francisco Bay salt marsh in order to determine the detailed nature of the radiational and energy exchanges occurring in the marsh, and the extent to which vegetation differences can affect the marsh microclimate. Winfield (1980) studied three functional aspects of a salt marsh-estuarine ecosystem in the Tijuana Estuary: primary productivity of the salt marsh vascular plants, organic carbon cycle, and inorganic nitrogen

cycle. Newby (1980) investigated the levels of fifteen mineral nutrients and elements in tissues of Spartina foliosa and Salicornia virginica with respect to the species distributions in a marsh in Humboldt Bay. She found that phosphorus correlated best with percent cover of the two species, and that nitrogen, sodium, calcium, and iron correlated only weakly.

Macdonald (1977b) compiled a comprehensive and thorough summary of what was known to that date of the plant ecology of California coastal salt marshes.

2.3 Oregon

the earliest published study of tidal marsh vegetation in Oregon -- and probably anywhere on the Pacific Coast -- seems to be the paper by House (1914), who described the marshes of the Coos Bay region. The principal references, however, for Oregon tidal marsh vegetation are the unpublished Ph.D. dissertations of Jefferson (1975) and Eilers (1975).

Jefferson (1975) surveyed the vegetation of 19 Oregon tidal marshes with the objectives of determining and describing the marsh communities, determining successional relationships, and quantifying the relationships of salinity and tidal inundation to marsh species distributions.

She determined previous plant communities at selected

sites by examination of partially decomposed plant material in the soil, enabling the construction of detailed successional diagrams. She found that the inferred successional sequences corresponded closely with the existing zonation sequences. She obtained a time frame for marsh development by varve counting and radiocarbon dating (yielding dates of approximately 410 and 770 years for mature high marshes).

Jefferson's approach to the vegetation was phytosociological, and she presented association tables for six marsh types comprising 29 discrete communities. She felt that the characterization of vegetation in terms of communities rather than continua was warranted by the existence of environmental discontinuities which precluded any manifestation of continuous gradients, leading rather to the formation of homogeneous stands with distinct boundaries. (Nonetheless, her plots of species distributions along transects usually suggest species distributed independently of one another along continua.)

Eilers (1975) described the marshes at Nehalem Bay, in northern Oregon, by considering the continuous variation of vegetation along environmental gradients and by assessing community structure, together with an estimate of net primary productivity. He plotted species distributions along the elevational gradient for May, July, and September, using species dry weight as the index of plant performance. He identified communities, partly with the aid of a reference-

stand ordination procedure; these communities were found to correspond closely with major signature types recognized on colour and colour infra-red aerial photographs, permitting the construction of a phytosociological map of the marsh. Eilers found that plant species distributions, species diversity, community location, seasonal development, net aerial production, and amount of net aerial production exported were all closely related to elevation and associated tidal factors.

Vascular plant primary production in six marshes in Coos Bay, on the central coast, was investigated by Hoffnagle (1980), who calculated productivity values ranging from $400 \text{ g m}^{-2} \text{ year}^{-1}$ (in disturbed marshes) to $1200 \text{ g m}^{-2} \text{ year}^{-1}$ (in Scirpus validus marshes). He found April root standing crop values on the order of $20\,000 \text{ g m}^{-2}$.

Two recent studies have dealt with marsh establishment or restoration. McVay et al. (1980) seeded and transplanted Deschampsia cespitosa and Carex obnupta on sandy dredge material in an intertidal location in the Columbia River estuary, under different fertilization regimes and at different tidal heights. Mitchell (1982) studied salt marsh reestablishment following dike breaching in the Salmon River estuary.

2.4 Washington

The marshes of Grays Harbour, on Washington's Pacific Coast, were described by Messmer et al. (unpublished), using a classification system adapted from Jefferson (1975). They identified thirteen communities within seven marsh types, and presented graphs of species percent cover along an elevational gradient, indicating continuum-type distributions. (Rarely in the review area has a vegetation description system developed by one author been applied elsewhere by another, as was done here -- with the result that direct comparison of marshes described by different investigators is often difficult.)

The major published studies of Washington tidal marshes are those of Burg, Rosenberg & Tripp (1976), Disraeli & Fonda (1979), and Burg, Tripp & Rosenberg (1980).

Disraeli & Fonda (1979) examined a brackish marsh in Bellingham Bay, north of Puget Sound, using a gradient analysis approach. They recorded species cover, frequency, and biomass estimates; measured water table depth, salinity, and soil moisture; and determined soil texture. From elevation measurements and tidal data they calculated tidal submergence periods. Their results indicated that plant species distributions were related to all the environmental factors measured except salinity (which was quite low). They noted a critical tide level at 274 cm above mean lower low water. Below this level, the marsh had over 70 submergence

days per year, had sandy, poorly drained soils, and was dominated by Scirpus americanus; above 274 cm, the marsh had fewer than 50 submergence days per year, had siltier, better-drained soils, and was dominated by Carex lyngbyei. (Notwithstanding this apparent ecotone, their plot of species importance against elevation seems to indicate a continuum-type distribution of species.)

Burg, Rosenberg & Tripp (1976) and Burg, Tripp & Rosenberg (1980) studied the Nisqually marsh at the southern end of Puget Sound. They recorded species cover values and analyzed the data by means of a computer-programmed version of the polar ordination method of Bray & Curtis (1957). From field observation and ordination analysis, they recognized twelve plant associations, and prepared a detailed vegetation map of the delta showing the extent of each association. They obtained production estimates for eight of the associations.

2.5 Alaska

A general description of the Pacific Coast marshes of Alaska was provided by Crow (1977), who noted that out of hundreds of marshes in the region, few have been studied.

The earliest treatment of Alaskan tidal marshes seems to be that of Cooper (1931), who described the colonization of mudflats following recent glacial retreat at Glacier Bay.

Puccinellia pumila was the primary colonist, with Glaux maritima appearing at slightly higher elevations. Further up came a community dominated by Plantago maritima, Hordeum brachyantherum, and Triglochin maritimum. There was a meadow zone between the marsh proper and the forest, dominated by Elymus arenarius.

Hanson (1951) identified and described marsh communities and their zonation sequences at sites in Knik Arm and Kachemak Bay in south-central Alaska.

Another Kachemak Bay marsh was described by Crow & Koppen (1977), who identified and described nine "community complexes". Net aerial production was measured in each community complex, the highest being 661 g m^{-2} in the Elymus mollis - Potentilla anserina complex. Detritus removal was found to be close to 100%. A list of the diatom flora was included in the report. Crow (1968, 1971) described the vegetation of a large marsh complex in the delta of the Copper River, in south-central Alaska, which was uplifted almost 2 m by the earthquake of 1964. The raised marsh surface is no longer flooded by even the highest tides, and the soil is being desalinized, with a consequent invasion of what used to be lower marsh habitats by species characteristic of the higher marsh and upland zones.

Stephens & Billings (1967) reported a vegetation study of a tidal marsh on Chichagof Island in southeastern Alaska. Three major plant communities, quite discrete in appearance,

were subjectively identified, dominated (from lowest elevation to highest) by Carex lyngbyei, Deschampsia atropurpurea, and Elymus mollis. The soils of each community were described pedologically and chemically.

The only published study of an Alaskan Pacific Coast tidal marsh in which data are analyzed objectively is that of del Moral & Watson (1978), who investigated an island marsh in the delta of the Stikine River, in the southeastern part of the state. They identified eight marsh community types by an agglomerative clustering method; these groupings were supported by discriminant analysis using species as the discriminating variables. The community types (with one exception) were recognizable on aerial photographs and thus were mappable; boundaries drawn between them, however, were sometimes arbitrary because the types were often found to grade into one another imperceptibly. "While we treat the data as if they are derived from vegetation consisting of a series of discrete units," say the authors, "such is not always the case."

2.6 British Columbia

The earliest published literature source on British Columbia tidal marsh vegetation is apparently that of Calder & Taylor (1968), who provided a qualitative description of the salt marsh communities of the Queen Charlotte Islands. (To

date it seems that no other work has been published on the marshes of this floristically interesting archipelago.)

Pojar (1974), working in the Tofino area on the west coast of Vancouver Island, studied the reproductive biology of a salt marsh community in relation to community structure and function. The population structure of individual species was characterized by means of an aggregation index. Levels of interspecific association were calculated for different quadrat sizes and the results presented in the form of a constellation diagram. Polyploidy levels, flowering phenology, pollination and dispersal ecology, and various community parameters were determined, and the reproductive biology of each species was summarized.

During the 1970's, information on tidal marsh vegetation was collected in many locations by a variety of government agencies and private firms, and by several graduate students. Much of this information is summarized in a series of Environment Canada publications which inventory the environmental knowledge from all available sources for British Columbia coastal estuaries. These publications contain species lists, community descriptions, and maps, as available, for tidal marshes within the estuaries. The following estuaries have been surveyed so far in this series (more volumes are planned): Fraser (Hoos & Packman 1974), Squamish (Hoos & Vold 1975), Skeena (Hoos 1975), Cowichan and Chemainus (Bell & Kallman 1976a), Nanaimo (Bell & Kallman 1976b),

Kitimat (Bell & Kallman 1976c), Campbell (Bell & Thompson 1977), Courtenay (Morris et al. 1979), and Somass (Morris & Leaney 1980).

The Squamish Delta marsh has been better studied than most. Lim & Levings (1973) recognized and mapped ten vegetation types, identifying Carex lyngbyei as the most important species in both geographical extent and standing crop. Levings & Moody (1976) made production measurements in different areas of the marsh, finding high values for net above-ground production of Carex: up to 1323 g dry weight m^{-2} season $^{-1}$, with growth rates up to 22.9 g m^{-2} day $^{-1}$ in late June. A recently published management plan for the Squamish Estuary includes a detailed environmental summary (Habitat Work Group 1981).

The plant communities of 18 estuarine marshes on the east coast of Vancouver Island and one marsh on the mainland were described and mapped by Kennedy (1982), using aerial photograph interpretation and associated ground truthing. Kennedy found that at higher levels in both brackish and salt marshes, a floristic break occurred at Courtenay, with marshes north of Courtenay dominated more by brackish indicator species, and those south of Courtenay more by saline indicator species. This discontinuity she attributed to higher rainfall north of Courtenay. On the basis of community composition Kennedy classified the estuaries studied into eleven groups, which she believed resulted from the interaction of six

physical factors: time of maximum discharge, relationship between mean growing season discharge and size of delta, mean annual total precipitation, relative protection from wind and wave energy, direction and frequency of tidal inundation, and substrate particle size. She also determined standing crop and root reserves in monthly samples from eleven communities in five estuaries.

The largest tidal marsh system in B.C. is found in the delta of the Fraser River, and it is these marshes that are the most abundantly described. Some general reference works are: the ecological overview of the delta by Becker (1971), the comprehensive summary of published and unpublished sources on the estuarine environment by Hoos & Packman (1974), and the review of estuarine habitat in the context of a management plan by Habitat Work Group (1978).

Vegetation studies done in the Fraser Delta area are here grouped for convenience into two categories: those directed towards measurement of productivity, biomass distribution, or nutrient cycling; and those concerned with floristic, compositional, or synecological characterization.

In the first group, Yamanaka (1975) measured primary productivity in the marshes of the Fraser Delta foreshore between Point Grey and Crescent Beach, and mapped the zones of dominance of the major species. He estimated dry matter yields of up to $1819 \text{ g m}^{-2} \text{ year}^{-1}$, with an average yield of 490 g m^{-2} , or $4.9 \text{ tonnes ha}^{-1}$, per year. (This contrasts with

an average lower Fraser Valley hay crop of about 3.8 tonnes ha⁻¹ (Moody 1978).) Yamanaka found Carex lyngbyei to make the largest contribution to total standing crop (36%), with Scirpus americanus not far behind (32%).

Burton (1977), studying the food resource for wintering snow geese, sampled below-ground biomass of Scirpus americanus, a preferred food source, at various locations frequented by the geese. He then evaluated marsh areas for food producing capability on the basis of both rhizome density and crude protein level. He attempted to find a reliable method of estimating rhizome standing crop from objective above-ground parameters, but could not find significant correlations.

The Brunswick Point marsh was studied by Moody (1978), who was concerned with primary productivity, decomposition, and spatial and temporal distributions of the marsh vegetation. Moody harvested aerial biomass periodically through the growing season, and was able to relate growth rates, standing crops, shoot densities, reproductive shoot numbers and nitrogen contents for the major species to such variables as salinity, temperature, elevation, and time of year. Litter bag and laboratory studies indicated that soft, fleshy species such as Triglochin maritimum decomposed the fastest, and Carex lyngbyei decomposed the slowest. Transplantation experiments and historical and present observations suggested a successional sequence commencing with

Scirpus americanus and S. maritimus.

Ogwang (1979) investigated phytomass production and disposition in two brackish Fraser Delta marshes, at Iona Island and Brunswick Point, and also in a freshwater tidal marsh along the Pitt River (a tributary of the Fraser). He harvested aerial vegetation sequentially during the growing season, and extended the sampling over a three-year period. He related variations in peak standing crop between species, sites and years to such variables as climate, water regime, salinity, and substrate nutrient status. He found large differences between species in the timing of peak production, which were related to such factors as the presence or absence of overwintered shoots. He found that belowground phytomass comprised a high proportion (up to 85%) of total phytomass; the proportion varied among species. He identified the main disposition routes for the shoot phytomass as grazing (fairly unimportant), organic matter accumulation, and detritus export. He assayed the nutrient content of the emergent vegetation, and investigated aspects of nutrient leaching.

A series of reports by Kistritz and others has resulted from a program of studies on the Fraser Delta tidal marshes conducted by U.B.C.'s Westwater Research Centre. Kistritz (1978) reviewed the literature on ecological processes in tidal marshes, concentrating on primary production, the role of phytodetritus, estuarine food webs, marsh biogeochemistry, and nitrogen cycling. Kistritz & Yesaki (1979) and Kistritz,

Hall & Yesaki (1983) reported on a study of primary productivity, detritus flux, and nutrient cycling in a river marsh dominated by Carex lyngbyei. Monthly measurements of shoot growth, density, standing crop, root biomass, and tissue levels of carbon, nitrogen and phosphorus were made. Results indicated an annual net primary production estimate of 634 g ash-free dry weight (AFDW) per m²; net annual detritus production was estimated at 435 g AFDW m⁻², of which 62% was exported into the estuary, and the balance buried by sediment.

In the second category of studies, the earliest detailed floristic description of the Fraser Delta marshes is probably that of Burgess (1970), who studied the vegetation of the delta front tidal marshes from Iona Island to Brunswick Point, as part of a study of duck habitat and feeding ecology. Based on a line-intercept frequency sampling method, he described a lower and an upper marsh zone, floristically distinct, divided by a low cliff. He mapped the distributions of the principal marsh species and calculated seed production indices. He found the most important seed sources for ducks to be Carex lyngbyei, Scirpus validus and S. americanus.

Forbes (1972) conducted a vegetation survey of the foreshore marshes from Point Grey to Crescent Beach, providing subjective community descriptions, species abundance ratings and checklists, and vegetation maps (not very detailed). McLaren (1972) provided a similar treatment of the river marshes from Deas Island to Westham Island.

The salt marsh at Boundary Bay was the object of a study by Parsons (1975), who recognized and mapped six plant communities, relating the vegetation pattern to tide levels and soil conductivity. The Tsawwassen salt marsh was described by Hillaby & Barrett (1976), who assessed the degree of presence of each species in the marsh, but did not attempt to define or map communities.

The most detailed studies of vegetation and environmental relations in Fraser Delta marshes are those recently reported by Hutchinson (1982) and Bradfield & Porter (1982).

Hutchinson (1982) examined the brackish marshes along the delta foreshore of Lulu Island with the aim of relating vegetation composition to environmental parameters. Species composition of plots was determined by biomass measurement, and plots were grouped by a cluster analysis procedure, from which seven main clusters or vegetation types were recognized. These types were mapped, and their distributions related statistically to variation in elevation, salinity, and substrate texture. The lowest extent of marsh vegetation corresponded closely to the level of mean higher low water (MHLW). The level of mean lower high water (MLHW) appeared to separate a lower marsh, dominated by Scirpus americanus and Scirpus maritimus, from a higher marsh, dominated by Typha latifolia, Potentilla palustris, Distichlis spicata, and Agrostis exarata. Zones dominated by Carex lyngbyei and Triglochin maritimum occurred at about MLHW. The low cliff

described by Burgess (1970) was found to occur at about this level.

Bradfield & Porter (1982) investigated the vegetation structure of a river marsh under predominantly freshwater influence. Vegetation data consisting of cover class estimates were subjected to a cluster analysis procedure which permitted the recognition of seven subgroups, referred to as community types, within three main groups, corresponding to subjectively recognizable vegetation zones: a sedge zone in regularly flooded and drained areas, a grass-willow zone along the crests of levees, and a mixed forb zone in areas of poor drainage and high water table. For the seven community types, species mean percent cover and percent frequency were calculated and presented in tabular form, as were various diversity components, including total number of species found, species density or alpha diversity, beta diversity, and species evenness. The distributions of the community types were plotted along elevational transect profiles. In addition to being clustered, the plot data were subjected to ordination by means of principal components analysis (PCA) and reciprocal averaging (RA). Ordination results suggested relationships between trends in compositional variation and particular environmental gradients. The principal ordination axes appeared to be related to substrate drainage and to total period of inundation, suggesting that these two components of the hydrologic regime operate independently to control vegetation pattern. Elevation above chart datum was not found

to be a reliable predictor of vegetation.

3. THE STUDY AREA

3.1 Location

The Fraser Delta is located on the southeastern shore of the Strait of Georgia, in southwestern British Columbia, and extends from the city of Vancouver southwards to the United States border. Its geographic centre is at approximately $49^{\circ} 07' \text{ N}$ by $123^{\circ} 05' \text{ W}$; the locations sampled in this study are all within 12 km of that point (Fig. 1).

3.2 Formation and Development of the Fraser Delta

Southern Georgia Strait and the adjacent mainland lay buried beneath Pleistocene ice until about 13 000 years ago (Mathews et al. 1970). Post-glacial isostatic uplift was essentially complete by 8000 years before present, and the shoreline has remained close to its present level during the past 5500 years (ibid.)

The delta that exists today began to fan out from a gap in the highlands at what is now New Westminster about 8000 years ago, and now covers an area of about 380 square miles (980 km^2), including submerged portions, with an average thickness (in areas where sediment accumulation is complete) of probably about 380 feet (115 m) (Mathews & Shepard 1962).

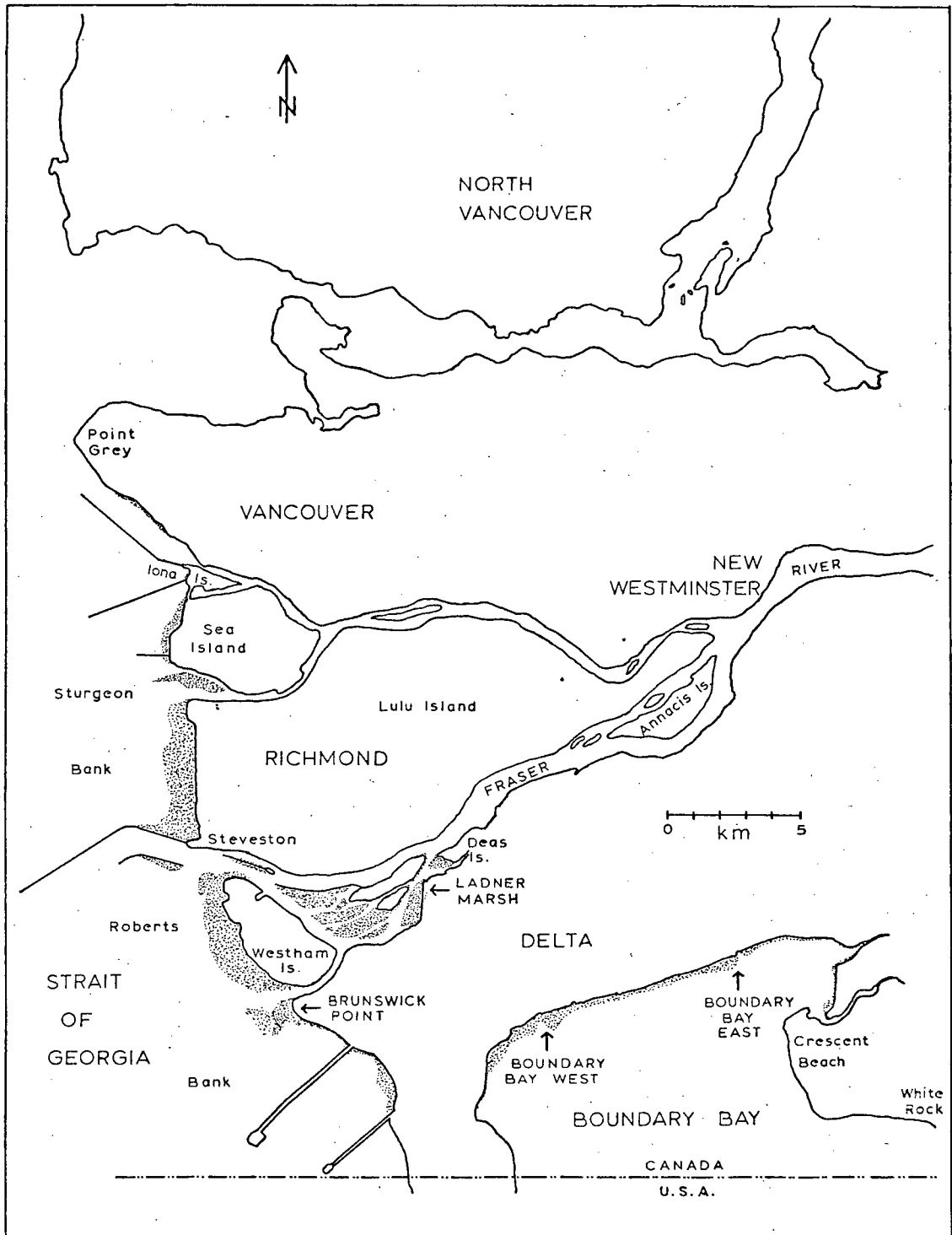


Figure 1 - Map of the study area

The active front of the delta extends some 23 km along its western perimeter, between Point Grey and Point Roberts; an inactive front about 13 km long faces southward between Point Roberts and Crescent Beach. Along the western delta front, a very gently inclined intertidal zone extends about 6 km from the dikes almost to the edge of the much steeper delta fore-slope. The equivalent zone along the southern delta front is about 4 km wide.

The Fraser River is currently depositing about 700×10^6 cubic feet ($20 \times 10^6 \text{ m}^3$) of loose silty sand and mud annually at the delta front, representing a load of about 21×10^6 tonnes (derived from Mathews & Shepard 1962 p. 1424). A zone of rapid advance occurs in the vicinity of the mouth of the main channel of the river; there are areas, however, where the delta front is retreating (Luternauer & Murray 1973). The measured rate of advance varies according to the depth below chart datum. A rate of 28 feet (8.5 m) per year at the 300 foot (91.4 m) contour over a 30-year period was determined by Mathews & Shepard (1962); the rate was much lower at shallower depths.

3.3 Extent of Tidal Marshes in the Fraser Delta

The existing tidal marshlands of the Fraser Delta are found mainly in three areas: in a broad belt, averaging about 1 km wide, along the western delta foreshore; in a wide,

braided portion of the river's main channel, close to its mouth; and in a rather narrow band, less than 1 km at its widest, along the north shore of Boundary Bay. Narrow fringes of marsh vegetation are found elsewhere along the main channel and its distributaries.

The mainly agricultural and residential delta lands are surrounded by protective dikes; the upper limit of marshland is generally the base of the dike. The lower limit seems to vary according to water salinity: Swinbanks (1979) determined the lower marsh limit at several locations from Westham Island around to Boundary Bay, and concluded that the lower limit of brackish marshes lies at least 1.0 to 1.5 m below that of salt marshes. Variations in tidal regime, however, may account for at least part of this difference.

From an examination of aerial photographs, Medley & Luternauer (1976) concluded that the marsh edge along the western delta front had been generally stable over the preceding 25 years, although there were some local advances and retreats. One area of apparently rapid growth is Brunswick Point, where an area of sand flats occupying about 90 ha first appeared on aerial photographs in 1948, and was densely vegetated with Scirpus americanus by 1969 (Moody 1978). At Boundary Bay, Kellerhals & Murray (1962) found evidence (in the form of a series of former beach ridges marked by driftwood) that the marsh is advancing over the tidal flats in the western part of the bay, but receding in

the eastern part, as indicated by an active erosional cliff about 0.7 m high. The rate of recession in this area was estimated to be at least 0.75 mi. (1.2 km) over the last 4350 years.

The total area of the delta tidal marshes has been estimated at 2683 ha, of which the western delta front marshes account for 1664 ha, the Main Arm river marshes 782 ha, and Boundary Bay 237 ha (Yamanaka 1975, Kistritz 1978). The marshes were more extensive before the arrival of Europeans; diking of the delta lands for flood control and reclamation, mainly during the 1890's, eliminated about 221 ha of saltmarsh and 629 ha of freshwater marsh (Romaine et al. 1976). Other activities continue to alter the marshlands. The construction, since the early 1900's, of several jetties, training walls and causeways, coupled with dredging of the river channels, has modified patterns of erosion, sedimentation, and salinity distribution. These activities have led to marsh growth in some areas, retreat in others, and changes in species composition. Some of the effects of training walls and jetties in the Fraser Estuary were described in detail by Levings (1980) and Tamburi & Hay (1978).

Much of the tidal marsh area of the Fraser Delta is now protected from development under some form of government reserve. Some areas, though, are directly threatened, for example by airport development. As indicated in section 3.2,

however, the delta itself is growing rapidly, so perhaps the long-term outlook for the marshes is one of continuing expansion.

3.4 Physical Environment of the Fraser Delta Tidal Marshes

3.4.1 Climate

Summers in the study area are mostly sunny, dry, and warm (seldom hot); winters are dull, rainy, and usually quite mild. Some major climatic variables are summarized in Table I.¹

The area lies within the Csb (mediterranean subhumid) climatic type in the classification system of Koeppen (1936). The mediterranean designation is a consequence of the pronounced summer drought; mean temperatures are considerably lower than in the mediterranean-climates of Europe (Hoos & Packman 1974).

¹ The data are from a station about 2 km east of the Brunswick Point marsh. Rose (1975) has pointed out, however, that there are microclimatic differences between coastal wetlands and the adjacent drylands, with the wetlands exhibiting a narrower range of temperatures both diurnally and seasonally. Daytime maxima are lower as a result of evaporation and transpiration, while night-time minima are higher because of the greater heat storage capacity of saturated soil.

Table I - Environmental data summary for the study area:
mean daily temperature, mean daily maximum temperature, mean
daily minimum temperature, mean total precipitation

	Jan.	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
T	2.3	4.2	5.7	8.6	11.8	14.6	16.4	16.1	13.5	9.6	5.9	4.3	9.4
Tmax	5.2	7.6	9.5	12.6	16.7	19.2	21.6	21.2	18.4	13.6	9.1	6.6	13.4
Tmin	-0.7	0.7	1.8	4.5	6.9	9.9	11.1	11.0	8.6	5.7	2.7	1.9	5.3
P	115	99	83	52	38	45	24	31	50	99	125	142	903

T = mean daily temperature (C)
Tmax = mean daily maximum temperature (C)
Tmin = mean daily minimum temperature (C)
P = mean total precipitation (mm)

(Data source: Environment Canada, Atmospheric Environment Service,
Vancouver, B.C.; records for Ladner Monitor Station.)

3.4.2 River and Marine Influences

The interacting and opposing influences of the Fraser River and Georgia Strait produce complex geographical, elevational, and seasonal variation in the salinity regime of different areas in the delta; this variation is the principal contributor to the very different character of the marshes in different localities.

The Fraser River drains an area of about 233 000 km², within which about two-thirds of the precipitation falls in the form of snow (Ages & Woollard 1976). With the melting of the snow pack in spring and summer, the river's discharge rises rapidly during May with a pronounced peak, called the

freshet, in late May or June; discharge remains high through July and August, decreasing to a low in December. Mean daily discharges (1912-1956 average at Hope) vary between $600 \text{ m}^3\text{s}^{-1}$ in winter and $8800 \text{ m}^3\text{s}^{-1}$ in summer; the peak flow recorded was $15\,200 \text{ m}^3\text{s}^{-1}$ on May 31, 1948 (ibid.).

Upon entering Georgia Strait, the silty brown river water fans out in a highly visible plume over the clear marine water, spreading sometimes to the opposite side of the Strait, 30 km away (Tabata 1972); the plume seldom if ever enters Boundary Bay (Swinbanks 1979).

Since the fresh river water is less dense than sea water, it floats. A certain amount of mixing takes place at the interface between the outflowing river water and the sea water beneath, so that the fresh surface water gradually becomes more brackish; in compensation for the entrainment of sea water in the outward-flowing water mass at the surface, salt water below flows upstream. This process gives rise to the phenomenon known as the salinity wedge. The effect is pronounced: for example, in a fairly typical observation at Sand Heads in August, salinity to a depth of 3.1 m was measured as 0.0 parts per thousand (ppt); at 9 m depth, the salinity was 25 ppt. The wedge has been observed as far upstream as Annacis Island, 10-15 km upstream from Ladner Marsh, when river discharge is low (Ages & Woollard 1976).

Detailed salinity distributions in the Fraser Estuary were plotted by Ages (1979) from observations made in 1976 and

1977. The data indicate that surface waters in the lower river at least as far as Steveston were almost invariably fresh during the period mid-May to mid-August. Even as far out as Sand Heads, surface salinity seldom exceeded 0.0 ppt during this period. Beginning in August and September, slightly brackish waters occasionally penetrate the outer estuary at the surface; by December, the month of lowest discharge, salinities in the range of 0-4 ppt (still only mildly brackish) were being recorded at the surface as far upstream as the vicinity of Ladner Marsh.

Surface substrate and surface water salinities in the Brunswick Point area were determined by Levings & Coustalin (1975) and Swinbanks (1979), whose results indicated a mildly brackish environment (ca. 0-8 ppt salinity) in northern and western portions of the marsh, and a moderately brackish to mildly saline environment (ca. 12-20 ppt salinity) in the southern portion. Swinbanks found that surface substrate salinities corresponded very closely to surface water salinities at low tide on ebb.

On the Boundary Bay mudflats, salinity measurements taken at different times of the year in tidal pools at low tide by O'Connell (1975) and Swinbanks (1979) indicate that freshwater input from the Fraser River is minimal or nonexistent, even during freshet. In the area of my Boundary Bay West transect they determined salinity values ranging from 23 to 33 ppt (with one anomalous reading of 39 ppt); the highest readings

were obtained on warm days in June. Slightly lower values (20-24 ppt) were recorded along a transect 5 km further east, possibly reflecting the influence of the minor rivers emptying into Mud Bay.

3.4.3 Tides

The tides in the study area are described as "mixed, mainly semi-diurnal" (Ages & Woollard 1976, Canadian Hydrographic Service 1981), which means there are "two complete tidal oscillations daily with inequalities both in height and time reaching the greatest values when the declination of the moon has passed its minimum" (Canadian Hydrographic Service 1981).

In summer, when the days are long and warm, the lowest tides occur during the day -- a beneficial combination of circumstances for the marsh plants (and for botanists). In winter the lowest tides occur at night.

The detailed character of the tidal curve varies considerably from one sampling locality to another within the study area. Thus the tidal range for large tides is 4.4 m at Crescent Beach in Boundary Bay, with a mean water level of 2.3

m above chart datum;¹ at Sand Heads on the active edge of the delta the range is 4.8 m, and the mean water level is 2.9 m above chart datum (data source: Canadian Hydrographic Service 1981). Moreover, because of the strong summer peak in Fraser River discharge (Section 3.4.2), summer tide levels in the lower river are higher than the levels elsewhere at the same time, and are higher than winter tide levels in the same area. The effect is most pronounced on low tides. For example, June high water levels at Deas Island (near Ladner Marsh) are higher than winter highs by about 0.4 m; June lows are higher than winter lows by about 1.4 m (data from Canadian Hydrographic Service 1977). The summer elevation of tidal heights is less pronounced at Steveston, nearer the river mouth; at Boundary Bay it is not significant. Winter low water levels are at about the same level throughout the study area, more or less as a consequence of the definition of chart datum.

The considerable variation in tidal regime from one sampling location to another within the study area is inconvenient, since it precludes any direct comparison with respect to elevation of sample plots from different areas. (My solution to this problem is explained in Section 7.3.)

¹ Chart datum is defined in Canada as the plane of lowest normal tides (Canadian Hydrographic Service 1981). This is not the same as chart datum in the United States, where the level of mean lower low water is used (Tide Tables 1976). Thus American chart datum is a little higher than Canadian.

3.4.4 Sedimentation and Substrate

As indicated in Section 3.2, the Fraser River carries a very large load of sediment into the delta each year; most of this is suspended load (Ages & Woollard 1976). Up to 10% of the suspended load may be clay, and the rest is about equally sand and silt (Mathews & Shepard 1962). Most of this material reaches the delta during the freshet (Pretious, 1972). Presumably it is at this time of year that most of the sediment deposition in the river and delta-front marshes takes place, the dense marsh vegetation acting as a sediment trap as tidewaters rise over the marsh.

At Boundary Bay the sediment contribution from the Fraser River may be slight (Swinbanks 1979), but sediments are supplied by the smaller Serpentine and Nicomekl rivers, depositing silt and clay, and by erosion of the cliffs at Point Roberts and even of the marsh itself (Kellerhals & Murray 1969).

The differing sedimentological regimes within the study area give rise to differing rates of vertical marsh accretion. Because of erosion, it is necessary to distinguish between the net or long-term accretion rate and the short-term rate. Several centimetres of mud may be deposited locally in a single season, only to be subsequently eroded away. Burgess (1970) cited the knowledge of local residents that the surface of the Westham Island marsh had risen by 4 feet (1.2 m) in

under 35 years; i.e. about 3.5 cm year^{-1} . Moody (1978) quoted the same figure (perhaps derived from the same sources) for Brunswick Point. Presumably these rates represent short-term accumulation. Using the known rate of lateral delta-front advance and assuming a constant average slope, Burgess (1970) calculated a long-term sedimentation rate of 0.004 feet (1.2 mm) per year. This calculation would be an average for the entire foreshore zone from the dike to the edge of the delta front; within the relatively narrow strip of tidal marsh, however, the rate could well be higher.

At Boundary Bay, Kellerhals & Murray (1969) determined a short-term mean sedimentation rate of 5.0 mm year^{-1} , but they calculated a much lower long-term rate of $0.42 \text{ mm year}^{-1}$ over the last 4350 years.

Sediment accumulation within tidal marshes is thought to be enhanced significantly by the plants and animals there; biotic influences on sedimentation were reviewed by Frey & Basan (1978). Among the mechanisms they discussed were: the damping effect of vegetation on wind-generated waves; the impedance of current flow by vegetation, with resulting loss of current competence and settling out of suspended load; and the trapping by macroinvertebrates of suspended particulate matter, with subsequent deposition in the form of feces.

The alluvial sediments of the Fraser Delta tidal marshes range in texture from sands to clayey silts, with weak to nonexistent development of mineral horizons. The coarsest and

most highly sorted sediments are found at Boundary Bay, probably as a result of both reworking by winter storm waves, and the absence of a major source of suspended mud (Swinbanks 1979).

At the highest elevations, several centimetres of organic material may accumulate at the surface. The humus produced by decomposing marsh vegetation is sometimes augmented by local accumulations of driftwood and by washed-up rafts of eelgrass (mainly Zostera marina) from offshore.

Mineral sediments may incorporate a considerable amount of organic matter, consisting of decaying roots, rhizomes, shoot bases, and algal mats. In a waterlogged environment, reducing conditions prevail, and this material decomposes anaerobically, giving rise to coal-black sediments reeking of hydrogen sulphide.

In some areas the substrate displays a pronounced varve-like stratification: alternating narrow horizontal layers of mineral and organic material. As discussed by Kellerhals & Murray (1962) for Boundary Bay, this stratification results from the growth during summer and fall of filamentous green and blue-green algal mats on the marsh surface, followed by winter storms which bury the algal mats beneath a layer of sand. In spring and early summer the algae re-colonize the surface. Each varve thus represents an annual cycle of growth and deposition. Stratification observed in the marshes of the river mouth and delta foreshore, however, presumably reflects

the rather different annual cycle prevailing there, in which sedimentation peaks with the summer freshet.

3.5 Transect Locations and Site Descriptions

3.5.1 Selection of Locations

Sampling locations were selected at Ladner Marsh, Brunswick Point, and Boundary Bay, all in the Municipality of Delta, British Columbia (Fig. 1), with the objective of representing the wide range of vegetational and environmental variation in the delta marshes, from areas of mainly fresh-water influence in and near the Fraser River to areas of mainly salt-water influence on Boundary Bay and Georgia Strait.

3.5.2 Ladner Marsh

Ladner Marsh (Fig. 2) was sampled near the north end of Ferry Road. A single transect perpendicular to the river, Transect J, extends 45 m from a swampy thicket dominated by cottonwood, willows and red osier dogwood to the bare mud of a slough. The dominant species along the transect are Equisetum fluviatile, Agrostis alba, and Carex lyngbyei. Somewhat less

important are Scirpus validus, Typha latifolia, Eleocharis palustris, and Oenanthe sarmentosa. Lythrum salicaria and Sium suave are conspicuous by their showy inflorescences in the higher part of the marsh, and several minor species are also present. The bare mud at the lower edge of the marsh is being colonized by Equisetum fluviatile.



Figure 2 - Ladner Marsh, vicinity of Transect J.
Foreground: Lythrum salicaria, Carex lyngbyei. Background:
Populus trichocarpa. Right: Scirpus validus

3.5.3 Brunswick Point

Brunswick Point is a peninsular marshland bounded on the north by Canoe Pass, a minor distributary of the Fraser River, and on the west and south by Georgia Strait. Thus there is a gradient from predominantly fresh-water influence on the north side to brackish or marine influence on the south.

Transect D samples the high marsh vegetation on the north side of the point, where the community is mainly composed of Carex lyngbyei, Potentilla pacifica, Juncus balticus, Eleocharis palustris, Agrostis alba, and scattered clumps of Typha latifolia and Lythrum salicaria. Other species also present include Sium suave, Bidens cernua, and Juncus articulatus.

Transect A, the longest, runs 1420 m across the point from north to south. On the river side, bare mud is being colonized mainly by Scirpus americanus, and also by Eleocharis palustris; these are the principal species in the lowest fringe of this marsh area. Higher up (Fig. 3), Carex lyngbyei and Agrostis alba are the dominant species in an extensive community which also includes Triglochin maritimum, Sagittaria latifolia, Bidens cernua, Lilaeopsis occidentalis, Potentilla pacifica, and several other species. Ruppia maritima is common in channels. Towards the south end of this transect (Fig. 4), Scirpus maritimus becomes important. At the south end, the mudflats are being colonized by Scirpus americanus

and are covered by dense mats of filamentous algae. Floodwaters here are fairly fresh, sweeping around the point from the river.

Transect B runs perpendicular to the dike in an area of evidently marine influence on the south side of the point (Fig. 5). Nearest the dike the dominant species are Distichlis spicata and Atriplex patula. Further out is a community composed mainly of Distichlis spicata, Salicornia virginica, and Triglochin maritimum. At the lower end of the transect the marsh breaks up into clumps of Scirpus maritimus and Triglochin maritimum. The mud is covered with an algal mat and is being colonized by Spergularia canadensis. Further out on the tidal flat, well beyond the edge of the marsh proper, Scirpus americanus and S. maritimus are colonizing the mud.

A fourth transect, Transect C, is located in the same general area as Transect B, but runs at an acute angle to the dike, from the area of salt-water influence towards the area of fresh-water influence. The flora varies accordingly, from halophyte communities similar to those described for Transect B to a Scirpus maritimus - Scirpus americanus - Triglochin maritimum community resembling that in the southern part of transect A.

From the air, the Brunswick Point marsh (Fig. 6) displays a prominent pattern of circular blotches, which correspond to dense stands of mainly Carex lyngbyei or Scirpus maritimus.

Presumably these stands are colonies that have spread out rhizomatously. Johannessen (1964) considered such circular colonies at the edge of a marsh to be evidence of rapid marsh expansion. At Brunswick Point, where circular features are conspicuous in the higher, older parts of the marsh, they may be relicts of a previous episode of rapid expansion.

3.5.4 Boundary Bay

The Boundary Bay marsh was sampled at two locations, here called Boundary Bay East and Boundary Bay West.

The Boundary Bay East study area is located near the foot of 112th Street, Delta, in an area where the predominantly marine influence is moderated by freshwater input from nearby streams (Fig. 7). Three transects, E, F, and G, extend south into the bay, more or less perpendicular to the dike. Here the highest part of the marsh, next to the dike, is characterized by large driftwood deposits. The principal species in the high marsh is usually Atriplex patula; also important are Carex lyngbyei, Salicornia virginica, Potentilla pacifica, Agrostis alba, and Puccinellia nuttalliana. Carex lyngbyei, with occasional dense patches of Juncus gerardii, often dominates the middle levels. At slightly lower elevations, Distichlis spicata, Plantago maritima, Triglochin maritimum, Glaux maritima, Spergularia canadensis, and Salicornia virginica form a characteristic species assemblage.



Figure 3 - Brunswick Point North, vicinity of
Transect A. Carex lyngbyei is dominant. Conspicuous
inflorescences: Lythrum salicaria (magenta); Sium suave
(white)



Figure 4 - Brunswick Point South, vicinity of
Transect A. Triglochin maritimum forms isolated clumps at
marsh edge; clumps coalesce into continuous stand (right
background)



Figure 5 - Brunswick Point South, Transect B. Scene in
late winter

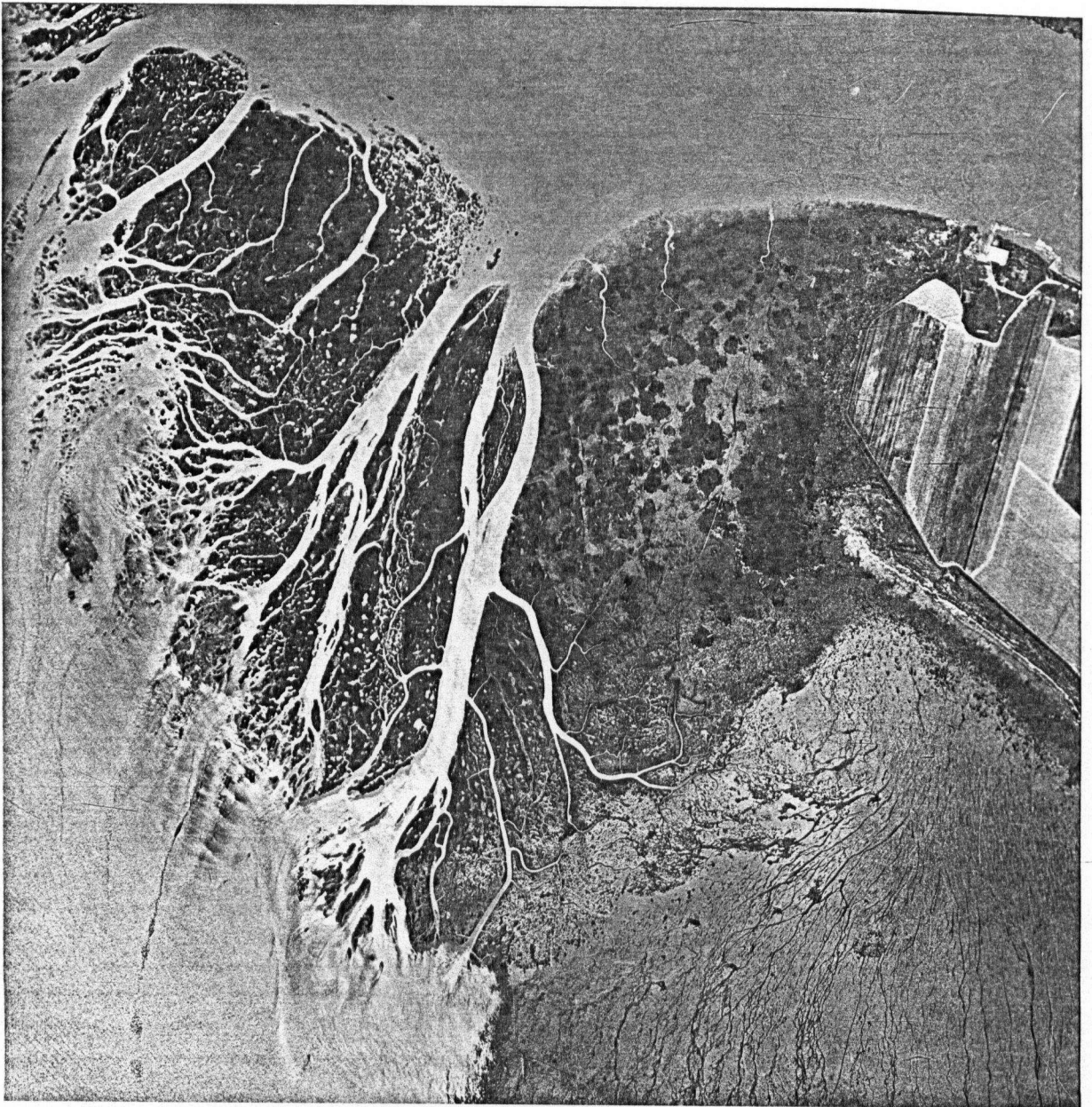


Figure 6 - Aerial photograph of Brunswick Point, showing circular patterning of marsh vegetation. Clumps are mainly Carex lyngbyei and Scirpus maritimus



Figure 7 - Boundary Bay East, Transect E. Mixed grasses in foreground; Carex lyngbyei (yellow-green) in mid-portion of transect; Salicornia virginica, Triglochin maritimum, Plantago maritima at far end of transect (dark green)

Several other species are also found. The mudflats here, as in other saline-influenced areas, are being colonized by Spergularia canadensis and are covered by algal mats. A summer diatom bloom colours the mud surface pinkish-brown (Fig. 8). Zostera americana and Ruppia maritima are plentiful in channel bottoms and water-filled depressions. As noted by Kellerhals & Murray (1962), the marsh in this area is eroding; I observed several centimetres of undercutting during one season of fieldwork.

The Boundary Bay West study area, at the foot of 72nd Street, Delta, is probably the most marine-influenced of the tidal marshes in this study. Salinities of 22 parts per thousand were determined for bay water sampled here at high tide in summer.

The higher marsh here, along Transect H (Figs. 9, 10), is characterized by old bleached driftwood, Atriplex patula, Salicornia virginica, Spergularia marina, and Grindelia integrifolia. At middle elevations, Salicornia virginica, Atriplex patula, and Distichlis spicata predominate; the Salicornia is densely infested with Cuscuta salina. The lowest part of the contiguous marsh is characterized by Plantago maritima, Salicornia virginica, Spergularia canadensis, and Triglochin maritimum. Colonizing the sandflats are clumps of Salicornia and Plantago.



Figure 8 - Boundary Bay East. *Triglochin maritimum* and *Salicornia virginica*, with patches of filamentous green and blue-green algae. Black reducing mud is covered by brownish diatom mat



Figure 9 - Boundary Bay West, vicinity of Transect H.
Atriplex patula dominates the driftwood zone in foreground.
Farther out, Salicornia virginica is infested by yellowish
Cuscuta salina



Figure 10 - Boundary Bay West. Grindelia integrifolia
flowers amid the driftwood

4. SOME FACTORS AFFECTING SPECIES DISTRIBUTIONS

4.1 Introduction

Chapman (1938), in a study of salt marshes, considered 10 environmental factors to be of major importance: tides, salinity, drainage, aeration, water table, rainfall, soil, evaporation, temperature, and biota. Obviously these are all to some degree interdependent in their influence.

Chapman's environmental categories seem applicable to tidal marshes in general. In the present study, I have collected data from four of them: biota, tides, salinity, and soil. Some of the other factors (i.e. drainage, aeration) can be inferred from these. The theoretical relevance of my environmental data to plant species distributions is discussed in the following four sections.

4.2 Tides

The unique phenomenon of tidal marsh habitats is, of course, the tides. Daylight flooding reduces photosynthesis by reducing the supply of carbon dioxide and, mainly because of suspended sediment, light. Tidal flooding during day or night may exclude oxygen from the rooting environment, affecting respiration. The flooding tide may bathe the marsh

plants in saline water and increase the salinity of the substrate; after the ebb tide, rainfall or seepage may reduce substrate salinity. Cool floodwaters may suddenly and sharply reduce the temperature of the marsh plants; the falling tide may then expose the vegetation to sharply increased temperatures. Evaporation on warm days after the tide has receded may substantially increase the salinity of surface pools and soil water. Evaporation of silt-laden water commonly leaves a fine coating of light-blocking mud on photosynthetic surfaces. The flow of water on flooding and ebbing tides subjects plant shoots to mechanical stress. Tidal activity affects sedimentation patterns, distributes propagules and carries away detritus.

At the highest elevations in the marsh, flooding is a brief and infrequent event, perhaps occurring for a few minutes once a month; at the lowest levels, flooding is daily and prolonged, sometimes lasting most of the day. Differences in frequency and duration of tidal flooding give rise to a very pronounced environmental gradient in the marsh, corresponding to a rather slight gradient in elevation.

A relation between tidal factors and the vertical zonation of intertidal organisms has been postulated since at least the early 1800's (Doty, 1957). A pioneering study of the relation of tidal marsh plant species distributions to tide levels was that of Johnson & York (1915). In a monographic treatment of a Long Island (N.Y.) salt marsh, they

considered the effects of tidal oscillation on transpiration, gas exchange, soil salinity, light supply, and other factors. In particular, they related the vertical distributions of marsh plant species to both the frequency and the duration of tidal flooding, and they summarized these parameters in the form of a ratio between total time exposed at a given elevation and total time submerged. They considered competitive interactions as well as autecological limits in explaining species distributions.

On the Atlantic coast, including the area of Johnson & York's study described above, successive semidiurnal tidal oscillations are nearly equal in range, but on the Pacific coast there is a marked inequality in the range of successive tides (Frey & Basan 1978). Thus neither the frequency of inundation or exposure, nor the cumulative duration of inundation or exposure, nor the duration of single episodes of inundation or exposure, changes smoothly along an elevation gradient. Rather, there are certain critical elevations, defined by levels in the tidal cycle, at which the values of these parameters jump abruptly. The result is a vertical series of several distinct exposure zones, each (one might predict) with its own characteristic biota, within the intertidal region. This concept of critical tide levels was first published by Doty (1946) in connection with the vertical distributions of marine algae in California. Doty identified the critical tide levels as: the lowest tide level, or low lower low water (LLLW); the mean level of the lower of the two

daily low tides, or mean lower low water (MLLW); the lowest level of the higher of the two daily low tides, or low higher low water (LHLW); the highest level of the two daily low tides, or high higher low water (HHLW); the lowest level of the two daily high tides, or low lower high water (LLHW); the lowest level of the higher of the two daily high tides, or low higher high water (LHHW); and the highest tide level, or high higher high water (HHHW).

Swinbanks (1979) pointed out that the curve of tidal heights varies according to at least four cycles of progressively increasing wavelength, having periodicities of 1 lunar day (24 h 50 min), 1 lunar month, 1 year, and 18.6 years. Each of these cycles gives rise to its own critical tide levels. Even the 18.6-year tidal cycle is significant, perturbing tide levels by about 0.5 m in the Fraser Delta area (hence the period over which tidal measurements have been recorded is of considerable significance).

The critical tide levels are universal, and can be used to cross-correlate very different types of tidal curves from geographically distant locations. Unfortunately, as Swinbanks noted, there are so many of them that any biotic zone boundary stands a good chance of coinciding rather closely with one.

I have described the critical tide level concept at some length because of its obvious appeal and likely significance in explaining the observed zonation of vascular plants within the intertidal marsh zone. However, the concept seems to me

to be of doubtful practical utility, at least in the context of my own study, for a variety of reasons, including the following: (1.) as stated, there are a great many critical tide levels, some of which are bunched closely together: which of several critical tide levels is a species responding to? (2.) the tide level data base is not everywhere adequate to the task, since observations over at least 18.6 years may be required; (3.) species autecological limits and requirements are not well enough understood, and what information exists has mostly been inferred empirically from field observation, making it useless for predicting correlations with field variables such as critical tide levels; (4.) interactions between tidal factors and other environmental variables (e.g. substrate texture, salinity) may be significant in determining species distributional limits; (5.) interactions between species probably influence their distributional limits.

Largely because of these reservations, I have not attempted to utilize the critical tide level concept in this study.

4.3 Salinity

In the Fraser Delta, with its strong gradient from fresh water to salt water habitats, the effect of salinity on tidal marsh plant species distributions is readily apparent.

Physiologically, an excess of NaCl in the growth medium can produce various toxic effects in higher plants, including protoplasmic swelling and changes in enzyme activity, leading to interference in respiration, disturbance of nitrogen assimilation, and abnormalities of protein metabolism (Larcher 1980). Uptake of essential nutrient ions may be reduced in the presence of NaCl (*ibid.*, Waisel 1972). Yet some species tolerate levels of NaCl that would kill most plants.

The adaptation of plant species to saline environments is expressed in the phenomenon of halophytism,¹ which is the subject of an extensive literature and is discussed only briefly here. For comprehensive reviews of the physiological ecology of halophytes, see the volumes by Waisel (1972) and Poljakoff-Mayber & Gale (1975); a wider-ranging symposium treatment of halophyte ecology is given in Reimold & Queen (1972). Useful, concise treatments of halophytism with respect specifically to salt marshes are found in Chapman (1974) and Ranwell (1972).

As Epstein (1969) pointed out, a plant, to function metabolically, must deal with its chemical environment in three ways: "It must selectively acquire essential nutrient elements from [the chemical environment], it must cope with

¹ I am using the term "halophytism" to mean adaptation to a saline environment, without implying the degree of adaptation, or whether the adaptation is facultative or obligate. The opposite term is "glycophytism", meaning adaptation to a freshwater environment.

elements present in excess, and it must acquire water." In a saline environment, then, a plant must overcome three main problems (Queen 1975): (1.) acquiring sufficient essential nutrients from a medium with an unfavorable ionic mix (high NaCl), (2.) maintaining its internal ionic balance and concentration within narrow limits despite the high concentration of NaCl in the external medium, (3.) acquiring water from an external solution with a high osmotic pressure (low water potential).

With regard to the first problem, Queen (1975) cited evidence that halophytes were better than glycophytes at discriminating between essential nutrient ions and their nonessential competitors (mainly Na^+ and Cl^-).

The second problem, that of regulating the internal ionic balance and concentration within tolerable limits, may be dealt with in three main ways: (a.) by internal segregation of excessive or toxic ions (mainly NaCl) within the vacuole; (b.) by external segregation of such ions, i.e. their removal from the plant; (c.) by succulence, i.e. dilution of salts by increasing cell volume.

Queen (1974, 1975) considered the evidence for method (a.), internal segregation, to be contradictory, but Flowers et al. (1977) reviewed the evidence and found it favorable, a view endorsed by Dainty (1979). As for method (b.), actually getting rid of excess salt, several mechanisms may be cited (Waisel 1972, Queen 1975): (i.) salt glands -- highly

selective excretors of Na^+ and Cl^- (in e.g. Glaux); (ii.) leaching from leaves (in e.g. Atriplex); (iii.) guttation; (iv.) shedding of salt-concentrated leaves or shoots (in e.g. Juncus gerardii, Atriplex, Salicornia); (v.) secretion by roots of salts translocated from shoots (in e.g. Salicornia); (vi.) accumulation of salts in salt hairs or bladders (in e.g. Atriplex). Method (c.), the succulence strategy, appears most conspicuously (in my study area) in Salicornia, in which it is a specific response to NaCl (Poljakoff-Mayber 1975, citing Russian sources).

The third problem, acquiring water from a saline medium, led early researchers to speculate that halophytes endured a water deficit, or "physiological drought". This idea is now discredited; halophytes are able to maintain a favorable water potential gradient by osmoregulation, accomplished in various ways (Gale 1975), including NaCl uptake.

Although a halophyte may reduce its internal water potential by taking in salt, the need to maintain a favorable gradient must be balanced against the need to keep the NaCl concentration below toxic levels. One might speculate, then, that halophyte enzymes are more tolerant of high NaCl concentrations than glycophyte enzymes. Queen (1974, 1975) considered the evidence contradictory for this, but Dainty (1979), citing Flowers et al. (1977), was quite definite: "there is no evidence that enzymes of halophytes are different, in their sensitivity to NaCl, from the enzymes of

other plants." Jefferies (1973) estimated the protoplasmic (not vacuolar) Na^+ concentration in Triglochin maritimum to be about 100 mM, which is fairly low. Various organic solutes, however, are found in halophyte protoplasm at about the right concentrations for osmoregulation; thus it seems likely that osmoregulation in halophyte cells involves the production of organic osmotica (Dainty 1979, Stewart et al. 1979, Jefferies et al. 1979). Some of these compounds may also serve somehow to protect salt-sensitive enzyme systems against high levels of NaCl (Stewart et al. 1979).

Much evidence now shows that very few if any salt-tolerant species are actually obligate halophytes (Flowers et al. 1977, Chapman 1977); most perform best at low or zero salinity. Barbour (1970) reviewed the literature and found that very few species appeared to be restricted to salinities above 5 ppt. Some common tidal marsh halophytes for which maximum growth has been found experimentally to occur at minimum or zero salinities are Juncus gerardii (Rozema 1976, 1979), Plantago maritima (Chapman 1977), and Triglochin maritimum (Pigott 1969). (An anecdotal observation from my own study area is that Triglochin maritimum plants appear to grow much larger in the less saline areas.) Other halophytes show optimal growth in brackish conditions: e.g. Atriplex patula, Puccinellia nuttalliana, Distichlis spicata, and Ruppia maritima (Flowers et al. 1977). Of genera found in my study area, only Salicornia may be an obligate halophyte, restricted to saline habitats (Ranwell 1972, Chapman 1974);

even for this genus, though, there is some evidence to the contrary (Flowers et al. 1977).

Although most halophytes perform best in fresh water conditions in the laboratory, few are found in fresh water habitats in nature. Presumably the various halophytic adaptations to a high-NaCl environment have a significant energy cost, no doubt contributing to the poor competitive ability of halophytes in glycophytic environments.

4.4 Substrate Nutrient Regime

In tidal marshes, as elsewhere, the chemistry of the rooting medium may be expected to play a major role in determining the distribution of plant species. Aside from carbon, hydrogen, and oxygen, six elements, called macronutrients, are required in some abundance by higher plants: nitrogen, phosphorus, potassium, sulphur, calcium, and magnesium. Seven other elements, including chlorine, are required in trace amounts. The availability of these nutrient elements is strongly influenced by environmental factors operating in tidal marsh habitats: the salt content of the floodwaters enriches the rooting medium in several ionic species, especially toxic sodium; and the high water table, with periodic flooding, excludes oxygen from the interstitial solution, giving rise to reducing conditions. In addition, there may be chemical gradients from the high marsh to the low

marsh resulting from the gradients in frequency and duration of flooding.

The macronutrient cations Ca^{++} , Mg^{++} , and K^+ are generally made available to terrestrial plants by the weathering of clay minerals (Etherington 1975). Potassium is the nutrient cation required by plants in greatest quantity, yet its concentration in soil solution is often very low (Epstein 1969). In salt marshes, however, the macronutrient cations, including K^+ , are supplied in high concentrations by the saline tidal floodwaters (Table II). The fresh water of the Fraser River is nutrient-poor by comparison.

Table II - Typical concentrations (mg L^{-1}) of macronutrient cations plus Na^+ and Cl^- in soil solution, seawater, and Fraser River water

Ion species	Soil solution ¹	Seawater ²	Lower Fraser River ³	
			Jan.	June
Ca^{++}	136-560	400	18	15
Mg^{++}	46-168	1 300	44	3.6
K^+	27-39	400	9	1.4
Na^+	23-667	11 000	222	2.0
Cl^-	39-710	20 000	373	3.9

¹ Fried & Broeshart 1967. Ranges are from acidic soils to calcareous soils.

² Pigott 1969 and Larcher 1980.

³ Benedict, Hall & Koch 1973.

Much the commonest ions in seawater are Na^+ and Cl^-

(Table II), which are not only toxic in their own right to most plants (Section 4.3), but also reduce the uptake of essential ions, particularly K^+ and Ca^{++} (Waisel 1972, Larcher 1980). Halophytes obtain what they need from the soil in spite of high NaCl concentrations. The halophyte Triglochin maritimum has been shown to respond to an increase in the external sodium level by actively increasing its potassium uptake (Parnham 1971), presumably for osmoregulation.

Several studies have pointed to nitrogen as the limiting nutrient for tidal marsh halophytes (Pigott 1969; Stewart et al. 1972, 1973; Valiela & Teal 1974). Nitrogen metabolism may be closely related to salt tolerance; certain nitrogen-containing compounds, presumably osmoregulatory solutes, are present at high levels in many halophytes, particularly when grown in saline conditions (Stewart et al. 1979). Reported studies on nutrient limitation in tidal marshes seem all to have dealt with salt marshes; in freshwater marshes there is no salinity stress to be dealt with, and the nitrogen requirement may therefore be less.

An important source of nitrogen in tidal marshes is fixation of atmospheric nitrogen by blue-green algae and bacteria (Green & Edmisten 1974, Jones 1974, Patriquin & Keddy 1978). Nitrogen-fixing blue-green algae are abundant on the mud surface; nitrogen-fixing bacteria are found within the anaerobic muds and also in association with the root systems of many tidal marsh vascular plant taxa (Patriquin & Keddy

1978), at least 22 of which are present in the marshes of the Fraser Delta. To put matters in proportion, the level of root nitrogenase activity found by Patriquin & Keddy was one to three orders of magnitude greater in the legume Lathyrus palustris than in any of the other marsh species they studied. On the other hand, Green & Edmisten (1974), who sampled water, surface mud, green plant shoots, and dead shoots in a Gulf of Mexico Spartina marsh, found total nitrogen fixation rates of up to 1550 kg of nitrogen per hectare in one month, which is an order of magnitude greater than the fixation rate for commercial soybean or alfalfa crops.

The nutrient status of tidal marsh soils is greatly influenced by the effects of waterlogging. The high water table effectively excludes oxygen from the marsh sediments. This permits populations of anaerobic microorganisms to build up, leading to the development of chemically reducing conditions. In such an environment, iron is present in its toxic ferrous form, and sulphur is present as sulphide, bisulphide, or hydrogen sulphide, all highly toxic. Nitrogen is found as ammonia or ammonium ion, forms which are unavailable to many species.

A gradient in soil oxygen status from the high marsh, where the rooting medium may be essentially aerobic, to the lowest marsh, where only a thin surface layer is aerobic, presumably affects species distributions. Many marsh species are capable of anaerobic metabolism when under oxygen stress

(Armstrong 1975); many can assimilate nitrogen in either the nitrate or the ammonium form. A common strategy of wetland plants is the transport of oxygen via aerenchymatous tissue from the shoots to the roots, whence it diffuses into the rhizosphere (ibid.); thus toxic reduced ions approaching in the soil solution may be oxidized before they reach the plant. Some marsh species, e.g. Juncus spp., show xeromorphic adaptations, which presumably function not for water conservation as such, but rather to reduce the rate of water flow towards the roots, thus increasing the time available for oxidation of potential toxins in the rhizosphere (ibid.).

The availability of soil nutrients to plants is affected considerably by the soil pH, since ionic equilibria shift with changing pH. Soil microflora also are affected by pH differences, with possible consequences for higher plants (Etherington 1975). Most vascular plants have broad pH optima in the range between weak acidity and weak alkalinity (Larcher 1980). The pH of saline soils is usually more or less neutral but may be affected by leaching, temperature, and ion concentration (Waisel 1972).

4.5 Substrate Texture

Moody (1978) reported that the habitats of Scirpus americanus and Scirpus maritimus, the two major colonizing species in the brackish Brunswick Point marshes, were

differentiated by substrate texture: S. americanus colonizes on sandy substrates, and S. maritimus in silty areas. Once established on a sandy substrate, S. americanus may be replaced by S. maritimus in apparent response to increasing silt deposition.

Substrate texture probably affects species distributions in several ways. Coarse-grained soils are more permeable, so that the water table will fluctuate more, perhaps rising to the surface on a flooding tide; this does not happen in the less permeable fine-grained sediments (Clarke & Hannon 1969). Being more permeable, however, the coarse-grained soils are better drained and aerated, so that oxidizing conditions may dominate.

A more porous soil is more subject to the effects of leaching by precipitation or groundwater; thus salinity may fluctuate more. Presumably, with the overall greater fluctuation between atmospheric and aquatic conditions in a coarse-grained soil, other factors such as temperature and pH may also fluctuate more.

Cation exchange capacity increases with increasing fine-particle content; thus substrate texture may influence nutrient availability for marsh vegetation.

As pointed out by Jefferies (1972), the matrix potential of fine-textured soils may significantly reduce the external water potential. Thus even though the osmotic potentials of

sandy and clayey soils may be similar, the water potentials may be quite different.

5. SAMPLING METHODS AND DATA COLLECTION

5.1 Vegetation

Areas of marshland were selected which appeared to exhibit some vegetational or environmental dissimilarities to one another, and within these areas transects were laid out in the direction of evident or assumed environmental gradients (high elevation to low elevation; fresh water to salt water). Metre-square quadrats were placed subjectively at intervals along the transects in a manner intended to sample the full range of observed variation. Each quadrat location was marked with a wooden stake.

Within each quadrat, all vascular plant species were subjectively assigned coverage code values corresponding to aerial coverage classes of <1%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, and 96-100%. Data were recorded for a total of 64 species in 103 quadrats.

Plant specimens were collected for species identification and eventual deposition in the University of British Columbia Herbarium.

5.2 Soil

At each plot one or more small spadefuls of mineral sediment (roughly 500 g) were collected from the upper 15 cm for later physical and chemical analysis. Where a distinct organic horizon had accumulated, a sample of this material was collected as well.

Vegetation and soil sampling were carried out during the summer of 1978.

5.3 Levelling Survey

To obtain quadrat elevations and map locations, a levelling survey was performed in the winter following the sampling season. Aerial vegetation by this time had died down and visibility was thus greatly improved. By means of a Kern DKM2 theodolite, the horizontal coordinates of the quadrats were obtained and the quadrat elevations were determined to an accuracy of approximately plus or minus one centimetre.

The relative elevations thus obtained were later converted to elevations above local chart datum, using one of two methods: (1.) At Boundary Bay, engineering survey monuments of known geodetic elevation were found nearby. The quadrat levels were tied to the levels of these benchmarks, and their geodetic elevations converted to heights above chart

datum at White Rock. (2.) At Ladner Marsh and Brunswick Point, observations were made of the times at which the water level rose above arbitrary benchmarks on successive days. By extrapolation from hourly tide level records,¹ the heights of the benchmarks above chart datum at Steveston (for Brunswick Point) and Deas Island (for Ladner Marsh) were determined.

¹ Supplied for Ladner Marsh by Environment Canada, Water Resources Branch, Inland Waters Directorate, Pacific and Yukon Region, Vancouver, B.C., and for Brunswick Point by Institute of Ocean Sciences, Sidney, B.C.

6. SOIL ANALYSIS

Soil samples were oven-dried at 100 C for 24 hours, then crumbled with a rolling pin. Coarse plant material was separated from mineral sediments by hand-picking or with a sieve. Some samples had very little mineral material remaining after roots and rhizomes were removed. For this reason and also for reasons of economy, some samples were only partially analyzed.

The following analyses were performed:

- Particle size analysis, i.e. determination of percent by weight of sand, silt, and clay, using the Bouyoucos hydrometer method (Day 1965).
- pH determination on 1:1 soil:water extract, using a Radiometer pH Meter 29 with a Radiometer combined glass/reference electrode.
- Electrical conductivity determination on soil saturation paste, using a Radiometer type CDM2e conductivity meter with a Radiometer CDC 104 conductivity cell.
- Total nitrogen determination, by acid digestion and colorimetric analysis, using a Technicon AutoAnalyzer II.
- Determination of Ca^{++} , K^{+} , Mg^{++} , and Na^{+} in 1:1 soil:water extract, using a Perkin-Elmer 306 atomic absorption spectrophotometer.

Except as indicated, the procedures followed were as outlined in Lavkulich (1978).

7. DATA ANALYSIS

7.1 Ordination Methods

The term "ordination" is used in ecology to denote techniques in which given entities, such as vegetation releves, "are ordered according to one or several of their properties in such a manner that their arrangement will reveal some useful information about their relationships" (Orloci 1978b). The ordination methods used in this study fall into the category which Whittaker (1967) called "indirect gradient analysis", in which samples are arranged along axes generated by vegetational variation.

Principal components analysis, first developed for interpretation of results of psychological tests, was introduced to ecology by Goodall (1954). The method reduces the redundancy in species-dimensional vegetation space by summarizing the variation on the original vegetation axes, corresponding to species, on a smaller number of ordination axes. In geometric terms, it fits lines or planes to a cloud of points, representing individuals (e.g. sample plots), whose coordinates in n-dimensional space are the scores for each of the n attributes (e.g. species). The first ordination axis then corresponds to the direction of maximum variance in the point cloud; each subsequent axis is aligned in the direction of greatest remaining variance. Geometrically, then, the axes

are orthogonal. However, since certain statistical criteria, especially the assumption of multivariate normality, are not met by ecological data (Beals 1973), the axes are not biologically independent. An ecological gradient may thus not be represented linearly by PCA; this has given rise to a great deal of activity by mathematically-inclined ecologists to discover a better method.

A possible replacement for PCA in ecological ordination is reciprocal averaging. Like PCA, this method was used earlier in the social sciences; the earliest English-language applications of this method in ecology were those by Hatheway (1971) and Hill (1973). As described by Hill, the procedure is one of successive reciprocal re-calibrations of species and stand scores, in which both are defined and redefined in terms of each other. The method is thus related to Whittaker's direct gradient analysis and to the weighted averages technique of the Wisconsin school (Whittaker 1978). Computationally, RA is similar to PCA; its chief distinction is that it yields simultaneous paired species and stand ordinations, "neither of which has logical pre-eminence" (Hill 1973).

The PCA and RA programs employed in this study were developed by Dr. G.E. Bradfield from descriptions in Orloci (1978a).

7.2 Treatment of the Vegetation Data

Recognition of plot groups: Initially, the cover data values for 64 species in 103 quadrats were organized in a floristic table (Table III). This procedure was facilitated by the use of a tabular sorting program written by Dr. G.E. Bradfield of the University of British Columbia Botany Department.

It became evident that the plots fell rather neatly into two floristically distinct main groups. The first group comprises the plots from western and northern Brunswick Point and from Ladner Marsh (transects A, D, and J), and was designated the "freshwater" group; the second group includes all the Boundary Bay plots plus the plots from southeastern Brunswick Point (transects B, C, E, F, G, and H), and was designated the "saltwater" group.

PCA on unstandardized data: As previously noted, the complete species cover value data set displayed a marked discontinuity in species distributions, indicating a high level of between-habitat or beta diversity. Since PCA has been shown to produce highly distorted ordinations from data with high beta diversity (Swan 1970; Whittaker & Gauch 1973, 1978), the data set was split into the more homogeneous "freshwater" and "saltwater" subsets, identified previously, for most ordination procedures. Results of PCA ordinations on these freshwater and saltwater cover data sets are shown in

Table III - Floristic table: 64 species in 103 sample plots. Group at left, mainly fresh-water influenced; group at right, mainly salt-water influenced

AAJJJJJJJJJJAAAAAADDADDDAAAAAADAABCCBEEHHBEEGGHHHHFFBCCEGGGGGFBHHHCGBBBCCEFBEGHHBCCG
596971523486811222278257461411122211213112203321788136785278236911534334565498957411112456419876231121
08012 2467367595 1348 092 0 10 01

EQUISETUM FLUVIATILE 22233222
ALISMA PLANTAGO-AQUATICA 22221 1
SCIRPUS VALIDUS 44+211
AGROSTIS ALBA 1 +45532 121555223211+11+33555451+ ++1 1+ + + 5 6 6
CAREX LYNGBYEI 2 3 35 4465+46266231562+ 13 13 2 5
ELEOCHARIS PALUSTRIS +1++ 1+ 1 +11++ +111113+3 1 3
SAGITTARIA LATIFOLIA 121 111 " 1+++ + 1+22 + 12+ 12
SCIRPUS AMERICANUS 23 " + 5 3. 32 122 11522164 2+1++ + 2
SCIRPUS MARITIMUS 14++ 2 11522+ 2 2 + 42 1 + + 1 23 + 21
RUPPIA MARITIMA 11 1+ ++
CHARA BRAUNII 62
JUNCUS BALTICUS 5 ++5
POTENTILLA PACIFICA 2 1 2 2 + 3 +
TYPHA LATIFOLIA 2 22 2 2 2 6
LYTHRUM SALICARIA + 2 3 3
SIUM SUAVE " 111 2 " " 11
BIDENS CERNUA 1 "1"++ 1 + " + 1 " +2 11
COTULA CORONOPHOLIA " 13 +2
TRIGLOCHIN MARITIMUM + 12+ 1 2 1 1 1
SALICORNIA VIRGINICA +35+1222212214111 +22+ "2223 3" +2 1 5 + " 52 3
DISTICHLIS SPICATA +1233+12+12233261221+232412+-421" ++ +
SPERGULARIA CANADENSIS +3+2113+ 6342 626552 + + "26525526
ATRIPLEX PATULA 1+ + + +13 +3 33 +1+33422 1+ + +132
PLANTAGO MARITIMA + + " 422+ 21 4+ + 3 3 222 4 23 66
SPERGULARIA MARINA 122 2 12 +22 232 +
CUSCUTA SALINA + +2
PUCCINELLIA NUTTALLIANA + + 22 1 2
GRINDELIA INTEGRIFOLIA 1 +1 2 + +
GLAUX MARITIMA " 2 1 1
LILAEA SCILLOIDES +++ 3. 1 1 1
HORDEUM BRACHYANTHERUM + +
JUNCUS GERARDII 21 1+ 5
SPA13 1 + +
OENANTHE SARMENTOSA +2
JUNCUS ARTICULATUS 1
LILAEOPSIS OCCIDENTALIS 1 ++ 1
AGROPYRON REPENS 1
CALTHA ASARIFOLIA 1 1 1
LIMOSELLA AQUATICA + + + +
CALLITRICHE SP. + + + +
SPC2
SPG10
ACHILLEA MILLEFOLIUM + +
HYGROHYPNUM LURIDUM 1
LEPTODICTYUM RIPARIUM +
ASTER EATONII 1 1
SONCHUS ARVENSIS 2
MYOSOTIS LAXA +
LATHYRUS SP. +
TRIFOLIUM OLIGANTHUM
JUNCUS BUFONIS
MENTHA ARVENSIS 1
DESCHAMPSIA CESPITOSA
ELYMUS GLAUCUS
ELYMUS MOLLIS 2
FESTUCA ARUNDINACEA
PUCCINELLIA NUTKAENSIS 1 2
SPC3
SPD1
SPE1
POLYGONUM AVICULARE 2
SPU1A 1 +
MIMULUS GUTTATUS
SPU4A 2

Legend: " = solitary individual, negligible cover; + = several individuals, < 1% cover; 1 = 1-5% cover; 2 = 6-25% cover; 3 = 26-50% cover; 4 = 51-75% cover; 5 = 76-95% cover; 6 = 96-100% cover

Nomenclature is according to Hitchcock et al. 1969. See Appendix A for species names with authorities.

Figs. 11 and 12. (Unless otherwise stated, all PCA ordinations are performed using a variance-covariance resemblance matrix.)

A PCA ordination on the complete cover data set was performed, but results proved unsatisfactory, because many of the 103 plots were overprinted on one another.

Data standardizations: The usefulness of an ordination method in exposing ecological gradients may be considerably affected by the data standardization or transformation employed; hence different standardizations and transformations were tested on the data in order to evaluate their effects. These are described in the remainder of this section.

Square root transformation: It was noted that the high weightings on the principal component axes were given to high-cover species, leading to the suspicion that the information supplied in lower cover values was being more or less ignored by PCA. Accordingly, a means was sought to even out somewhat the disparity between high and low cover values. Thus the percent cover values, ranging from 0 to 100, were transformed to their square roots, ranging from 0 to 10. Results of PCA ordinations on the square root transformed freshwater and saltwater cover data matrices are given in Figs. 13 and 14. Results of the PCA ordination on the square root transformed complete cover data matrix are shown in Fig. 15.

Normalization: The lowest portions of the marsh, where

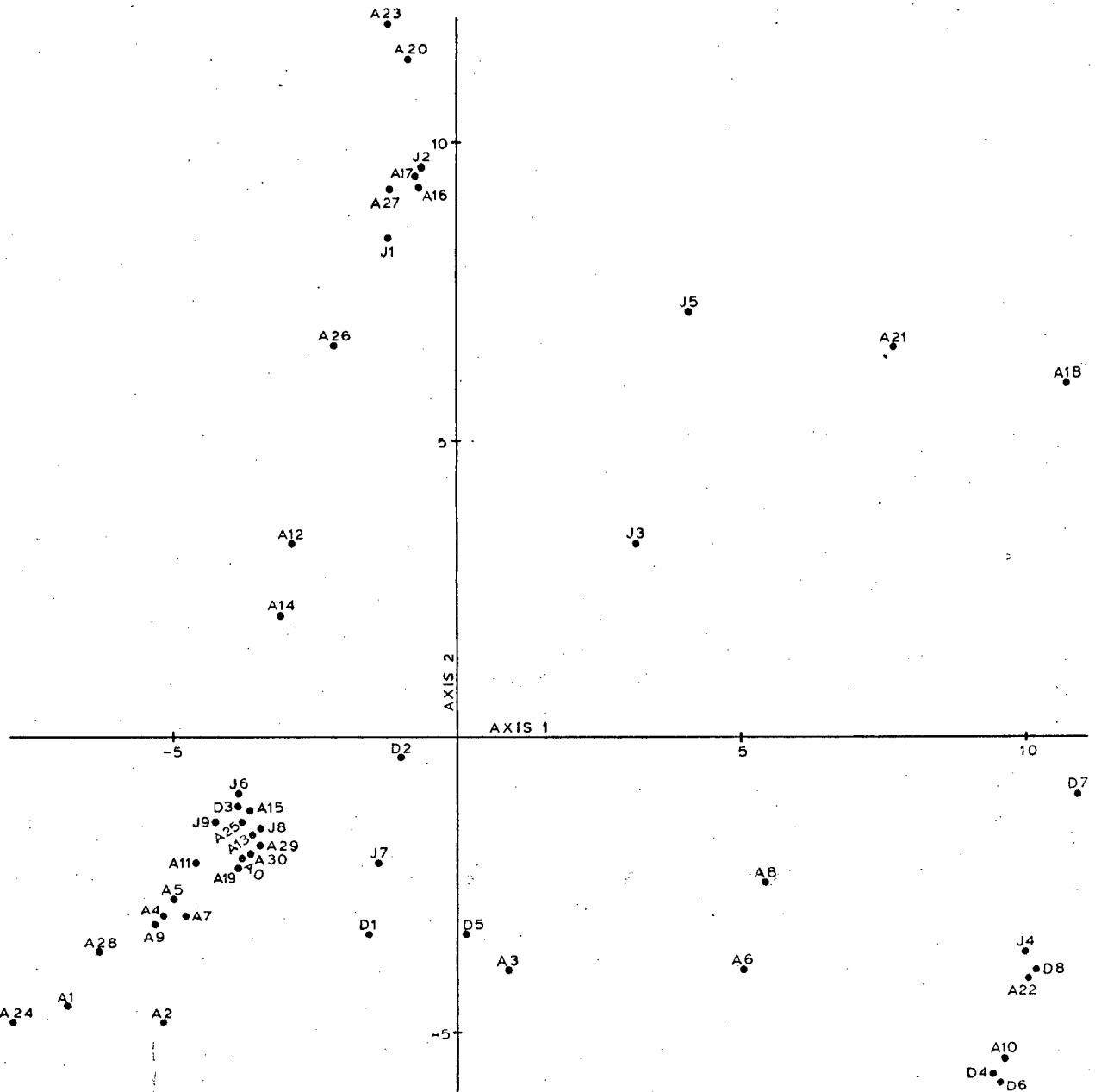


Figure 11 - PCA ordination of samples using species cover data from freshwater plot group

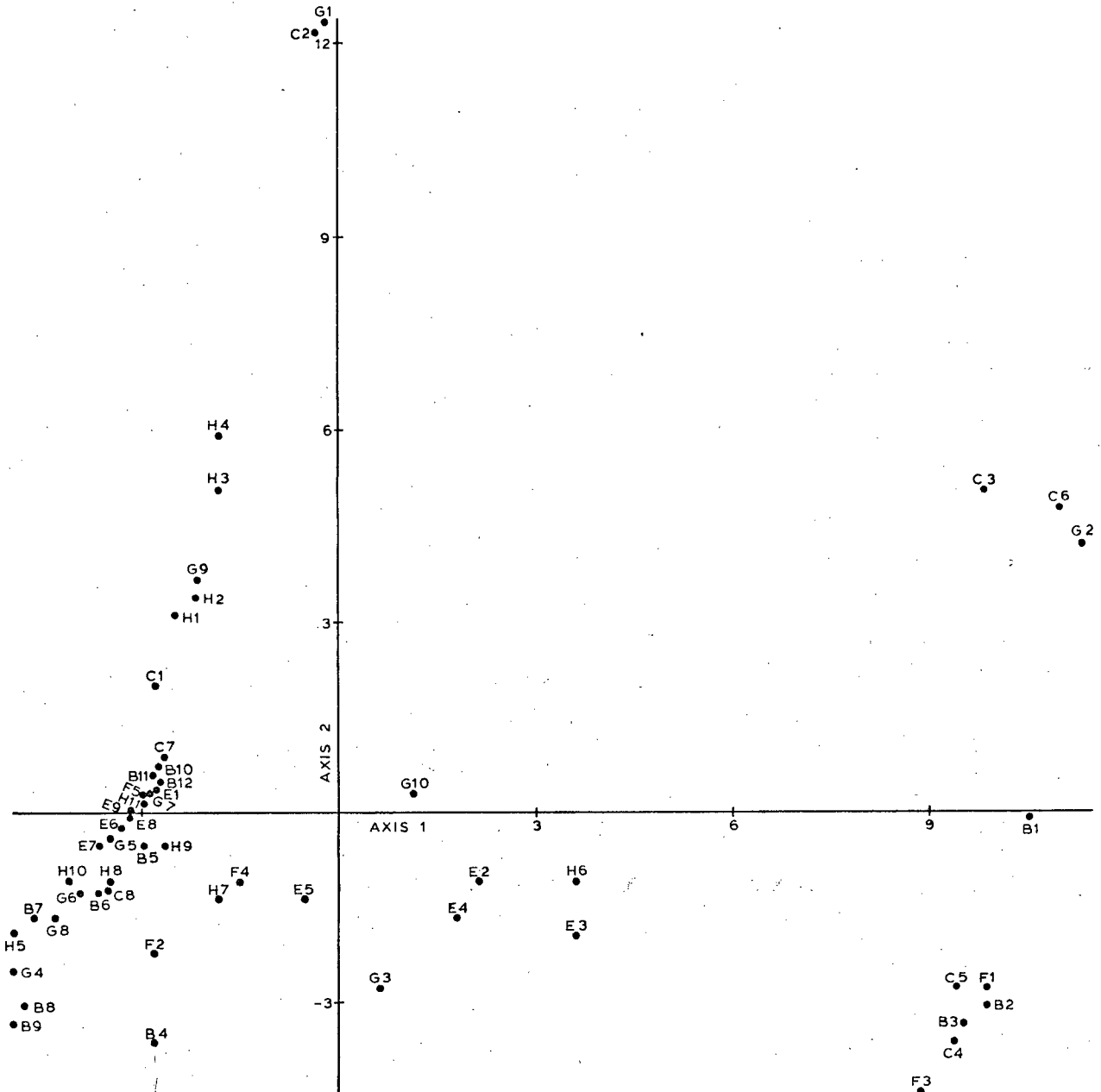


Figure 12 - PCA ordination of samples using species cover data from saltwater plot group

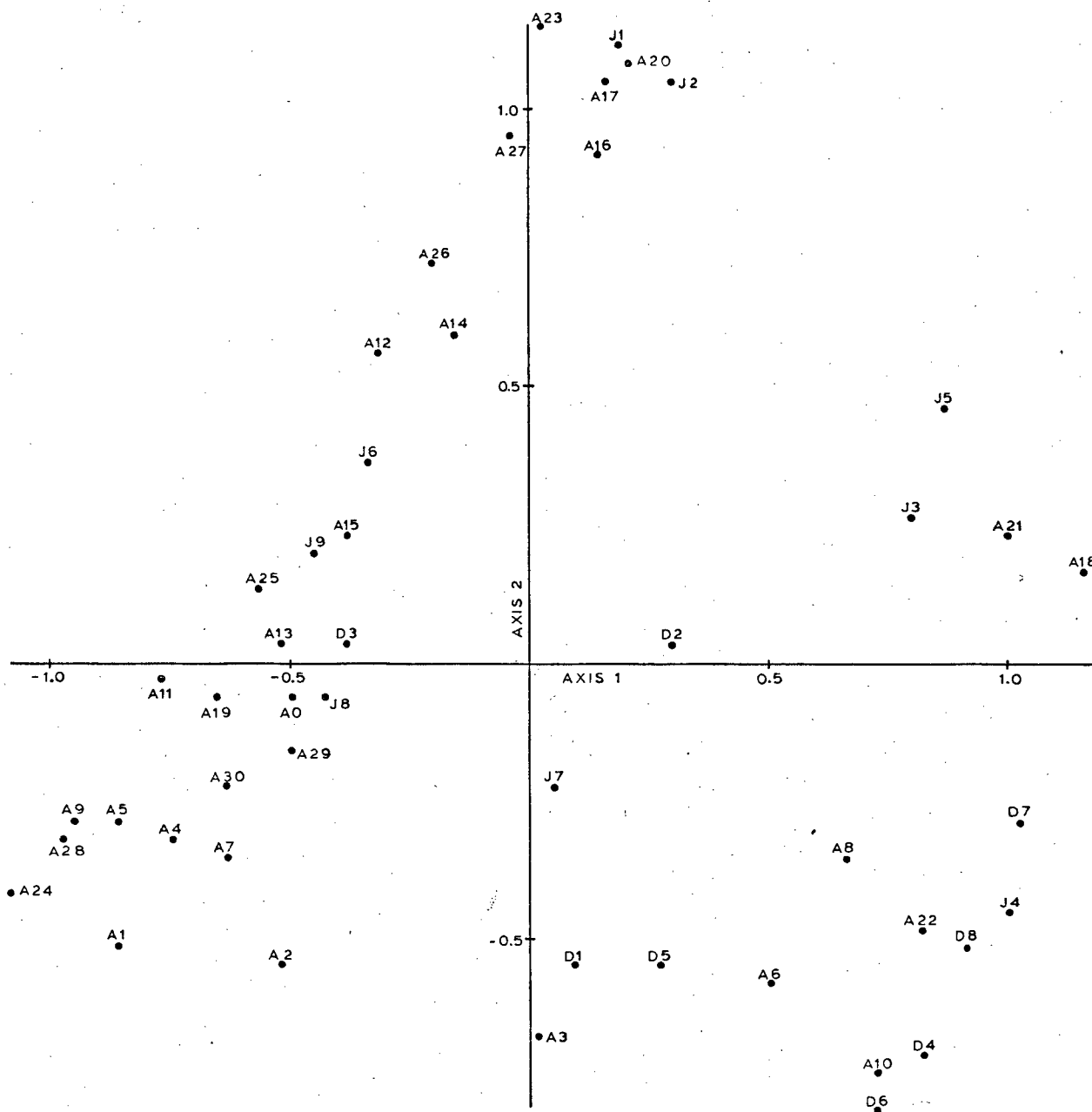


Figure 13 - PCA ordination of samples using square roots of species cover data from freshwater plot group

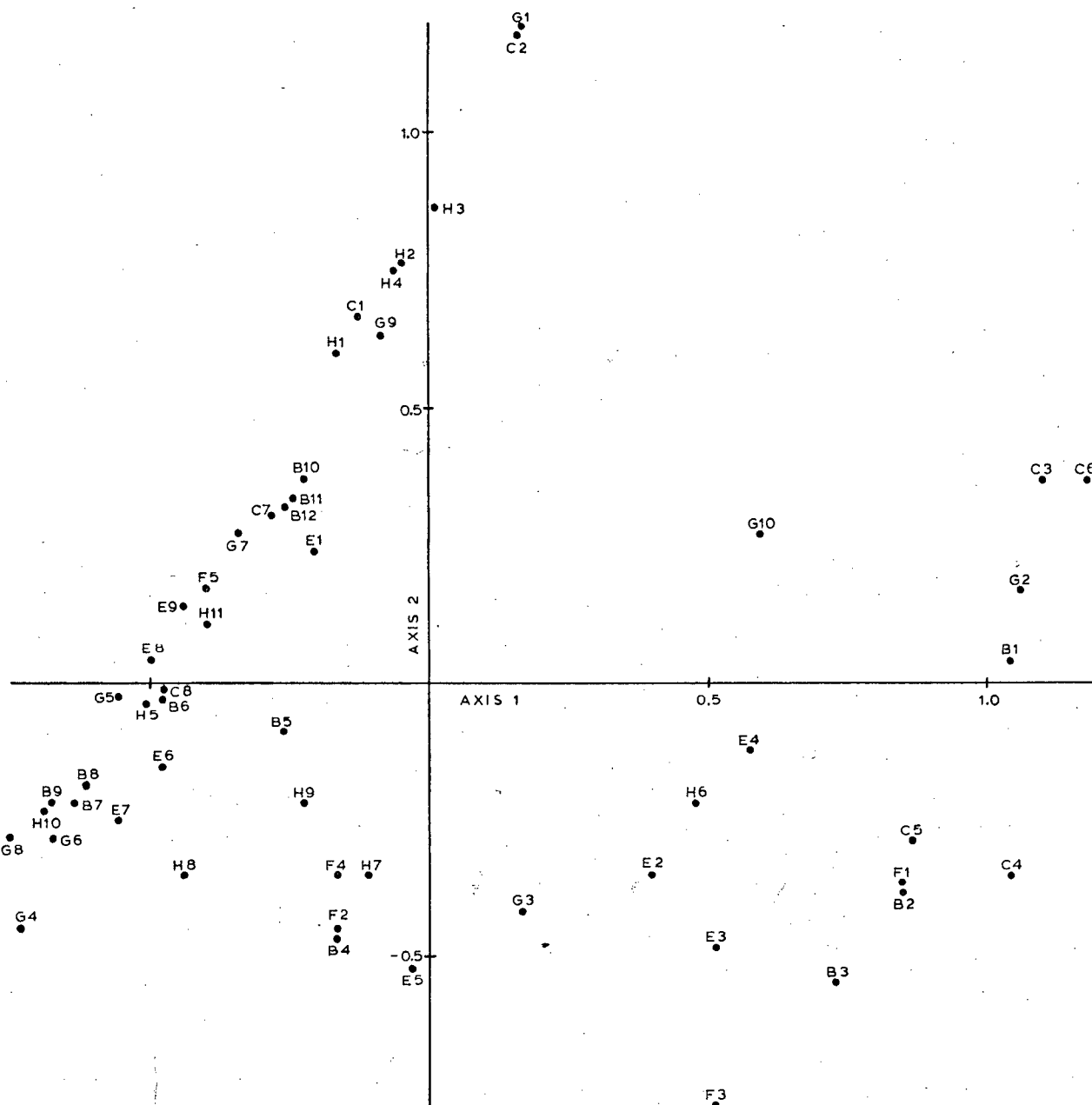


Figure 14 - PCA ordination of samples using square roots of species cover data from saltwater plot group

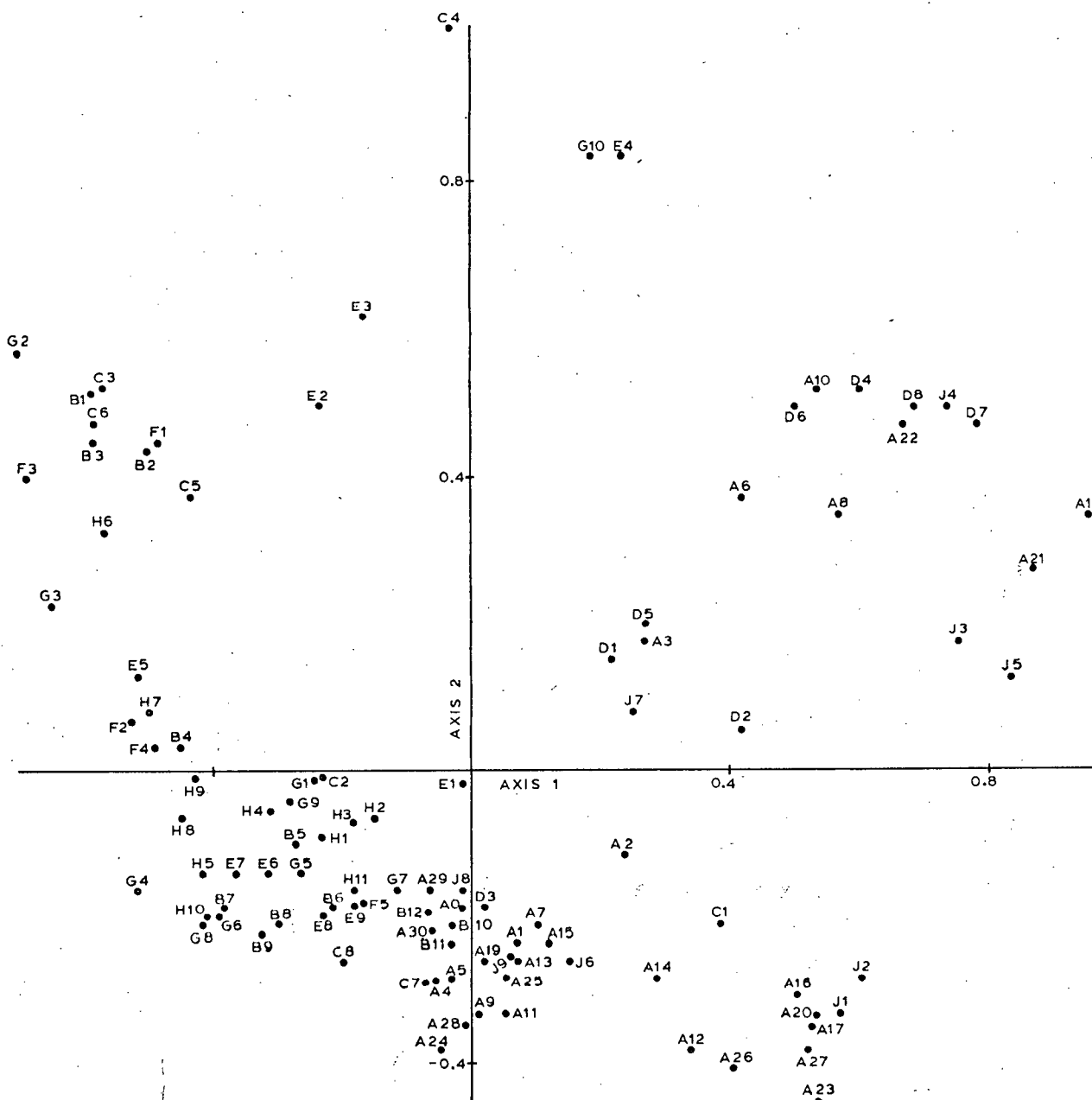


Figure 15 - PCA ordination of samples using square roots of species cover data from all plots (freshwater group, Transects A, D, J; saltwater group, Transects B, C, E, F, G, H)

flooding effects are most severe, present a hostile environment for plant growth. Plant performance is poor in such marginal habitats, and cover values are correspondingly low. Relevés from such areas were lumped near the origin on the PCA scatter diagrams, rather than being grouped with stands of similar species composition but higher cover values. A means was therefore sought which would give equality to stands with low total cover.

Normalization of the data accomplished this objective. Each element in a quadrat vector (i.e. each species cover value in the quadrat) was divided by the length of the quadrat vector (i.e. the square root of the sum of the squared cover values in the quadrat). The consequence of this standardization is as if the plants in a sparsely-vegetated quadrat were to extend themselves to cover all the bare areas, without changing the proportion of total cover represented by each species in the quadrat. Results of PCA ordinations on the normalized freshwater and saltwater cover data matrices are shown in Figs. 16 and 17.

Correlation matrix: The variance-covariance resemblance matrix used in the preceding examples caused PCA to ignore rare, low-cover species. In contrast, a resemblance matrix generated by the product-moment correlation coefficient gives stronger weighting to rare species. It was felt that rare species might potentially contribute useful information to an ordination, so the data were analyzed using a resemblance

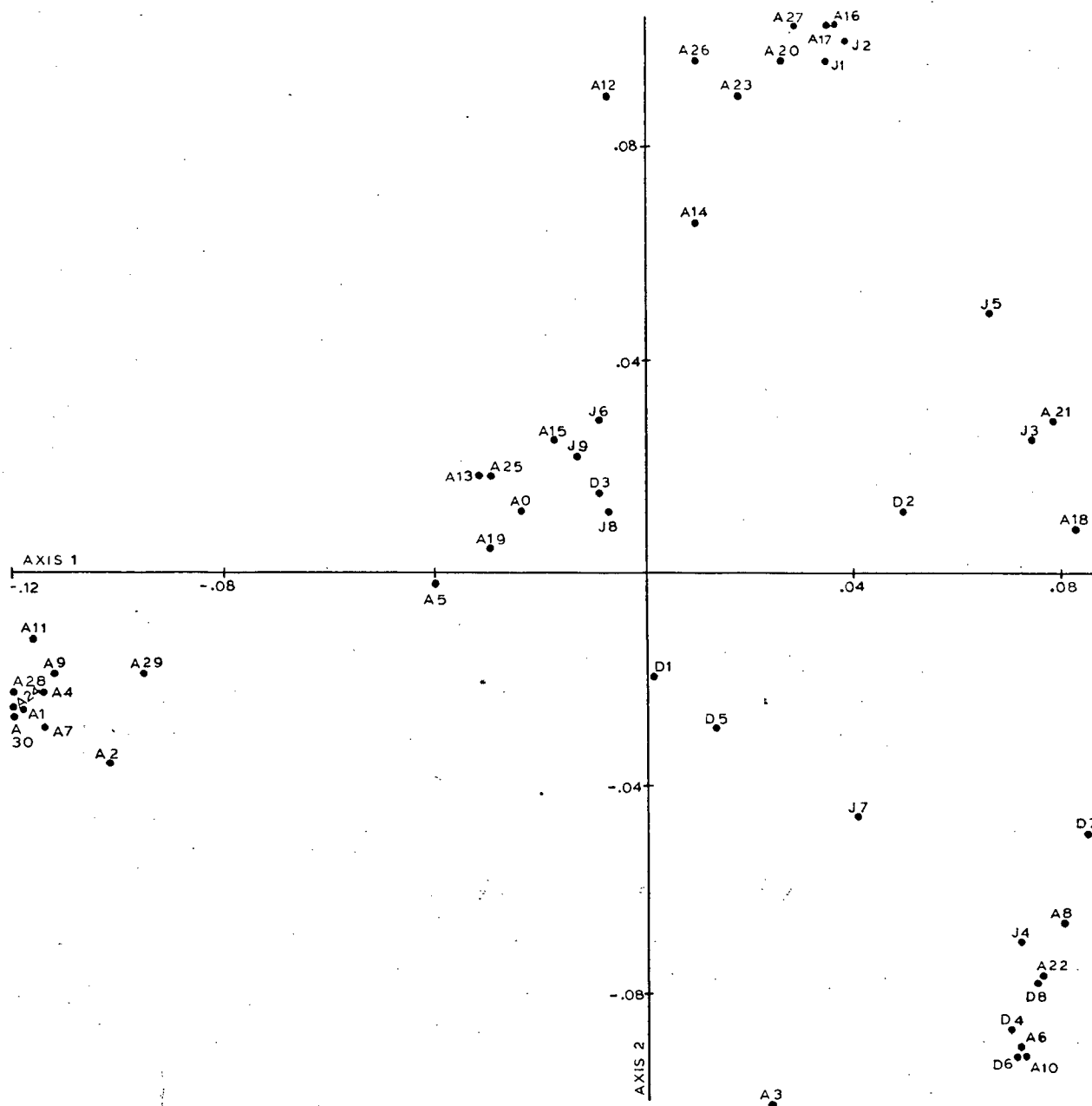


Figure 16 - PCA ordination of samples using normalized species cover data from freshwater plot group

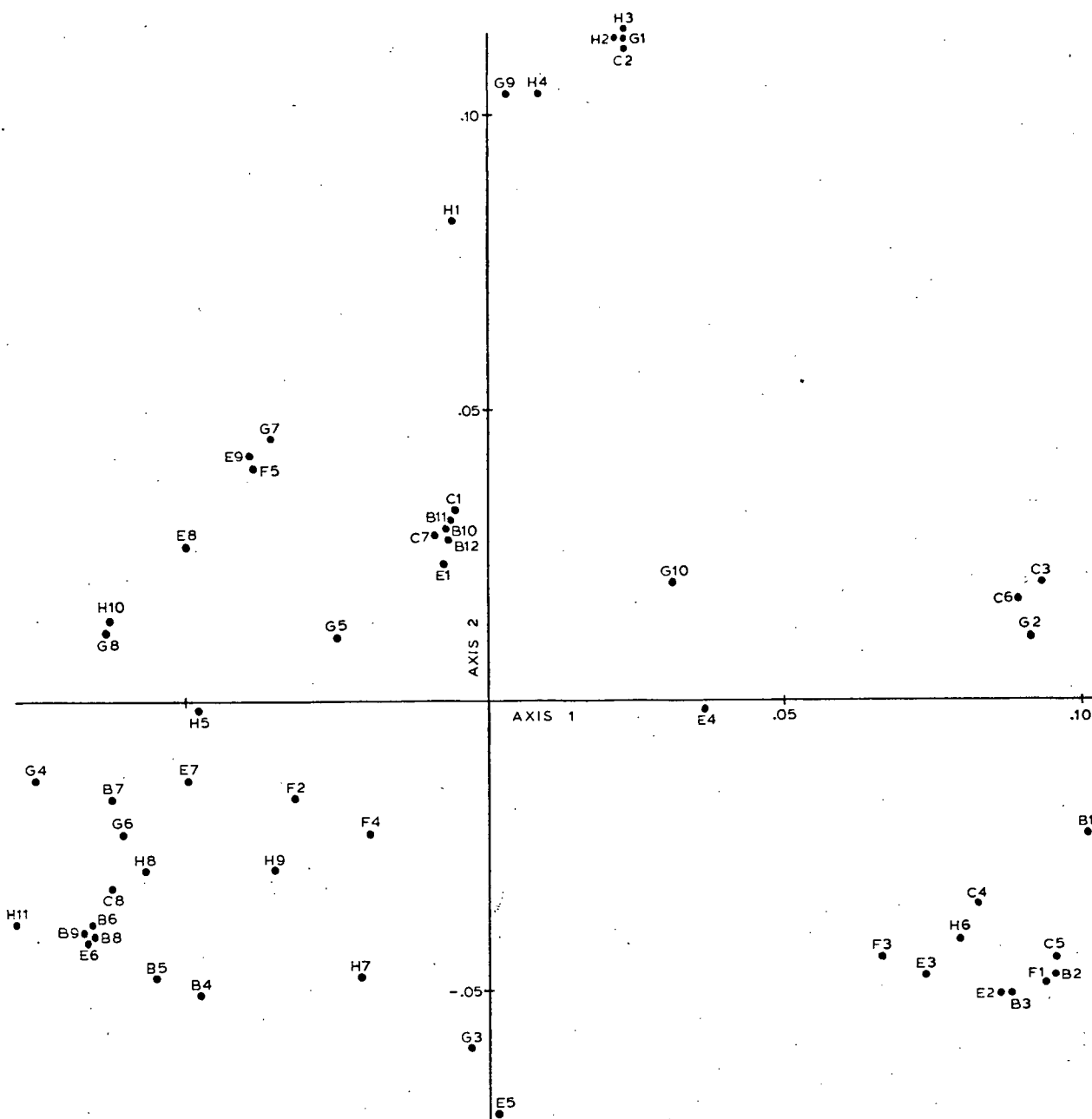


Figure 17 - PCA ordination of samples using normalized species cover data from saltwater plot group

matrix of correlation coefficients. The resulting ordinations (not shown) featured a very dense cluster of plots near the origin, with a few outliers around the edges.

Reciprocal averaging: This method may be regarded as a standardized version of PCA (Noy-Meir 1970, Hill 1973), so it is considered here as a standardization. It differs from PCA mainly in that it produces simultaneous species and stand ordinations.

Initial results of RA ordinations on freshwater and saltwater cover data matrices showed an extreme sensitivity to certain data anomalies. Typically, one or a few quadrats (and species) would appear as outliers at one edge of the scatter diagrams, with the other quadrats (and species) crowded along the opposite edge of the diagrams. By removing these outlying quadrats from the data matrices, greatly improved ordination results were obtained (Fig. 18).

7.3 Treatment of the Environmental Data

Standardization of elevation data: Elevation as such has nothing to do with the performance or distribution of species; rather it is a variable which conveniently estimates and summarizes the levels of influence of the factors which actually act on the organism. In the tidal marshes, elevation is mainly an index of the degree to which a plant is directly

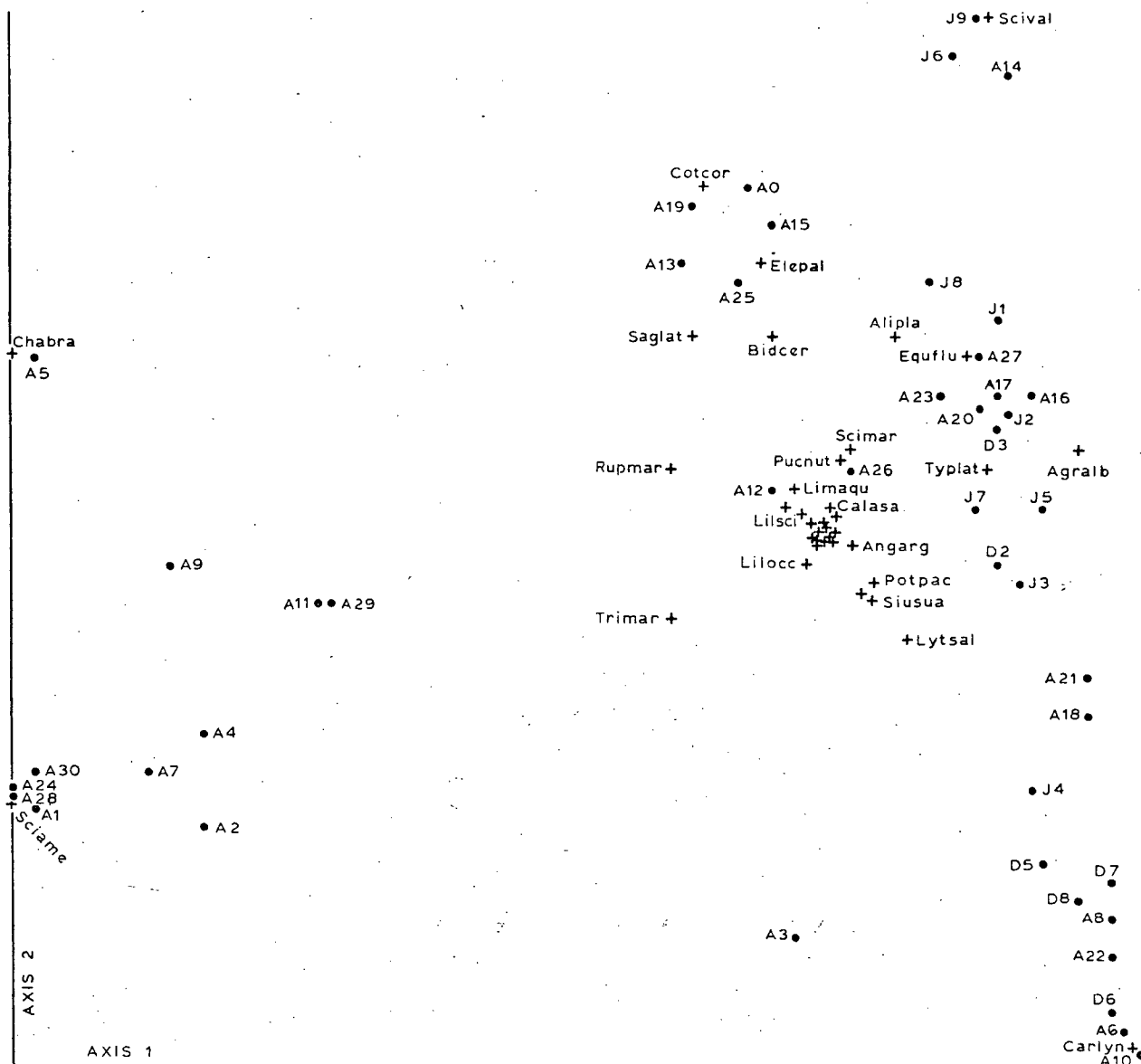


Figure 18 - RA ordination of species and samples using species cover data from freshwater plot group

or indirectly influenced by the level of the nearby water body. Unfortunately, water level fluctuations due to the tidal cycle and to variations in river flow do not follow the same pattern throughout the study area (Section 3.4.3). The result is that absolute elevation is not likely to be a very good predictor of plant performance when comparing data from different areas.

To resolve this problem, I standardized the elevation data according to local variations in tidal range. Thus the elevations above chart datum were divided by the tidal range for large tides at convenient tidal monitoring stations: Deas Island¹ for the Ladner Marsh plots, Steveston² for the northern and western Brunswick Point plots, Tsawwassen³ for the southeastern Brunswick Point plots, and Crescent Beach⁴ for the Boundary Bay plots. The standardized elevations are expressed in percentage units, and may range in theory from 0 (chart datum) to 100 (the highest local water level). The standardization procedure, however, depends for its reliability on the judiciousness of certain decisions -- such

¹ Data obtained from printout of 1978 hourly water levels at Deas Island Tunnel, supplied by Environment Canada, Water Resources Branch, Inland Waters Directorate, Pacific and Yukon Region, Vancouver, B.C.

² Data obtained from printout of 1978 hourly water levels at Steveston, supplied by Institute of Ocean Sciences, Sidney, B.C.

³ Data obtained from Canadian Hydrographic Service 1977, p. 18.

⁴ *ibid.*

as which tidal monitoring station to use as a reference, and over what time period to determine the tidal range. Thus the values obtained should be regarded as approximations.

Ordination: Eight soil variables and a site elevation variable were selected for ordination. The soil variables were: percentage by weight of sand, silt, clay, and nitrogen; and concentration in parts per million (ppm, or mg kg^{-1}) of potassium, calcium, magnesium, and sodium. The elevation variable was the standardized elevation above chart datum described above.

Initially, all plots for which any data values were missing were removed from the data set. The environmental data set thus differed in character from the vegetation data set, in which most of the values were zero (i.e. species not present). With species data, this is almost unavoidable, and tends to cause distorted ordinations, especially with PCA (Swan 1970; Whittaker & Gauch 1973, 1978). The environmental data ordinations, therefore, were free of at least this one source of confusion.

The environmental data set was split into "freshwater" and "saltwater" subsets on the same basis as for the vegetation data, and PCA and RA ordinations were performed on all three data sets. Since the variables were not all measured by the same units, a correlation matrix was used in the PCA. The PCA results are shown in Figs. 19, 20, and 21. The RA results were fairly similar, but were not as easy to

interpret and are not shown here.

Display of species cover values on environmental ordinations: A major assumption of this study was that plant species distributions and performance values could be shown to be related to the levels of selected environmental factors. To demonstrate such a relationship, cover class values for some important species were plotted on the environmental ordination diagrams. Results are shown for Agrostis alba, Scirpus americanus, and Carex lyngbyei on the freshwater ordination (Figs. 22, 23, 24), and for Salicornia virginica, Distichlis spicata, and Triglochin maritimum on the saltwater ordination (Figs. 25, 26, 27).

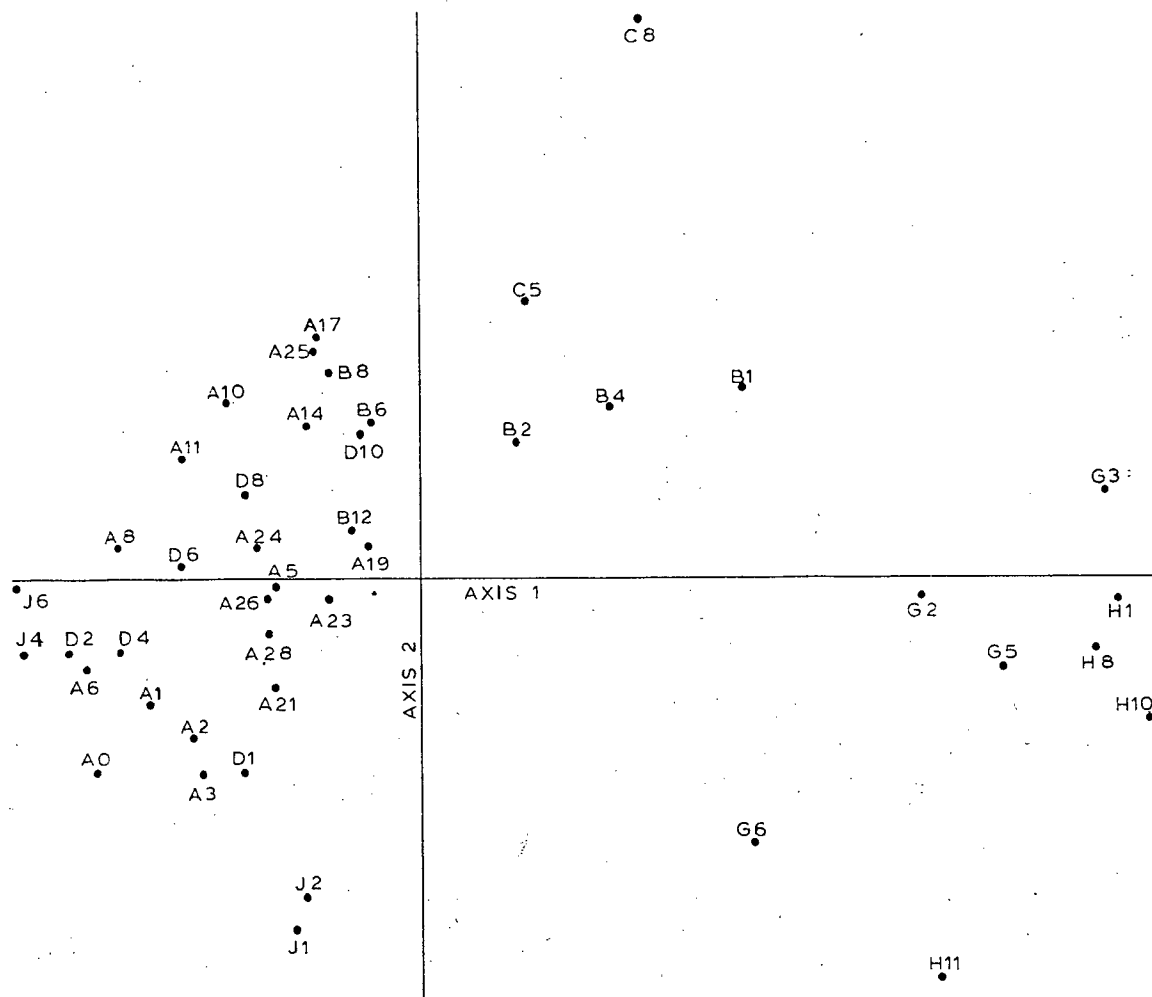


Figure 19 - PCA ordination of samples using environmental data from freshwater (Transects A, D, J) and saltwater (Transects C, G, H) plot groups

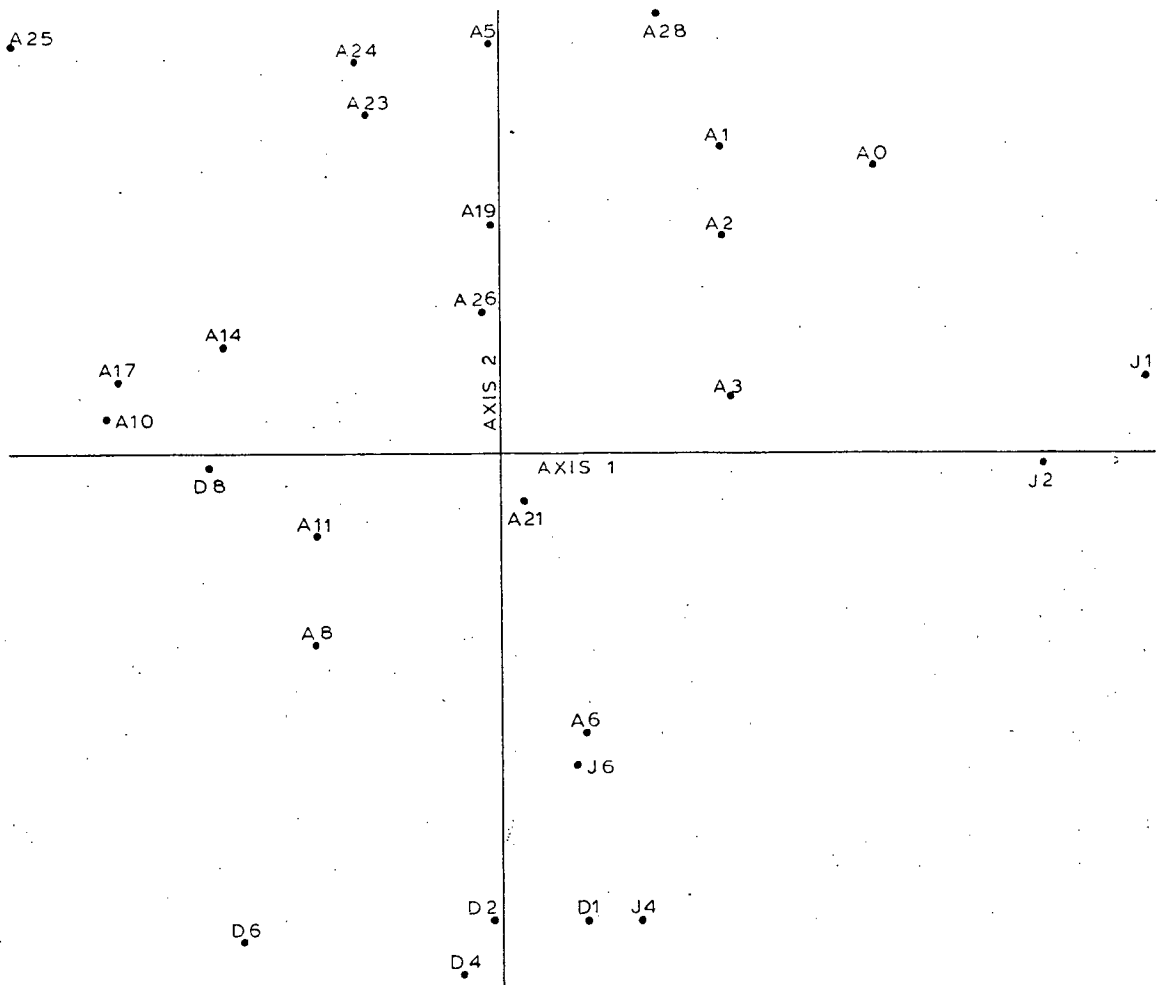


Figure 20 - PCA ordination of samples using environmental data from freshwater plots

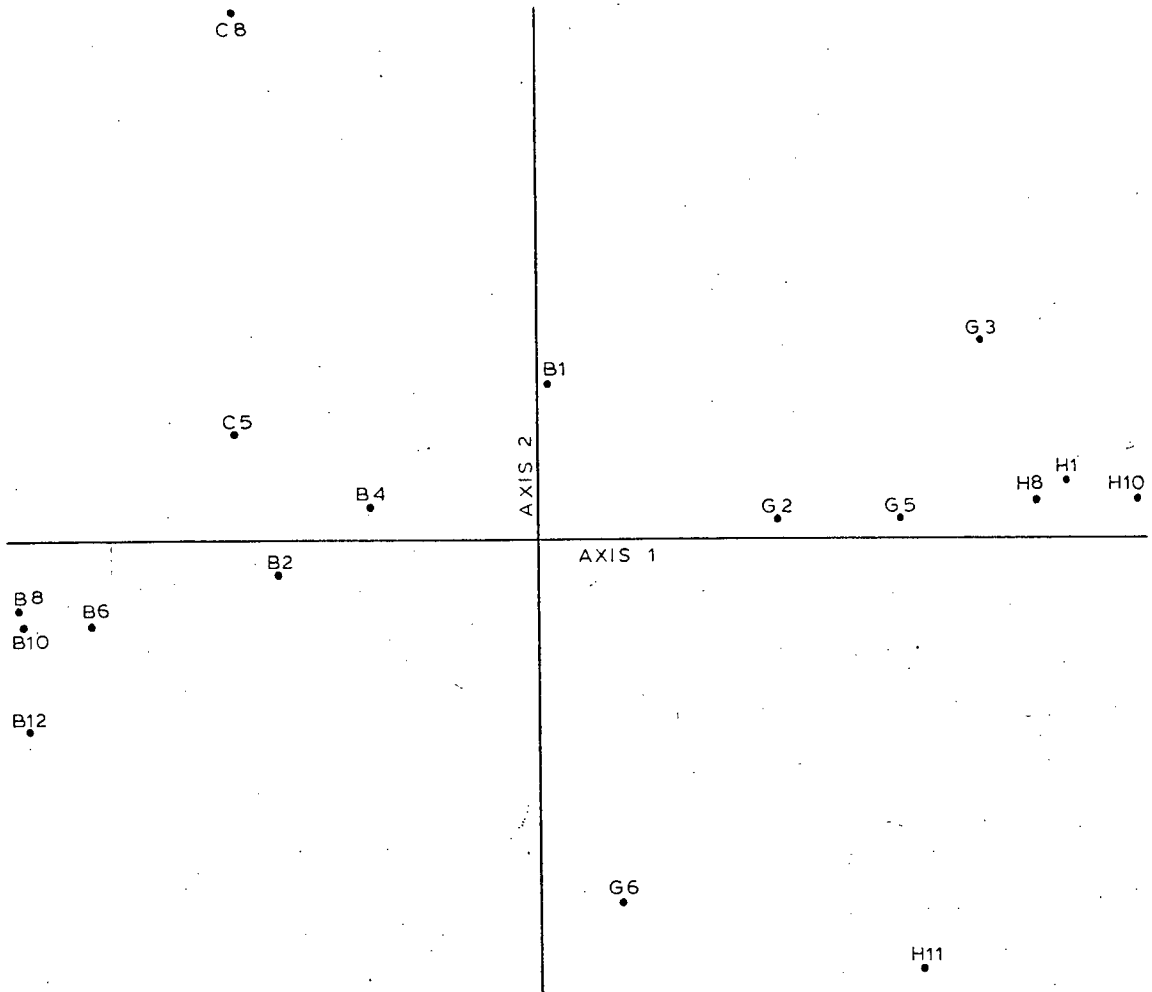


Figure 21 - PCA ordination of samples using environmental data from saltwater plots

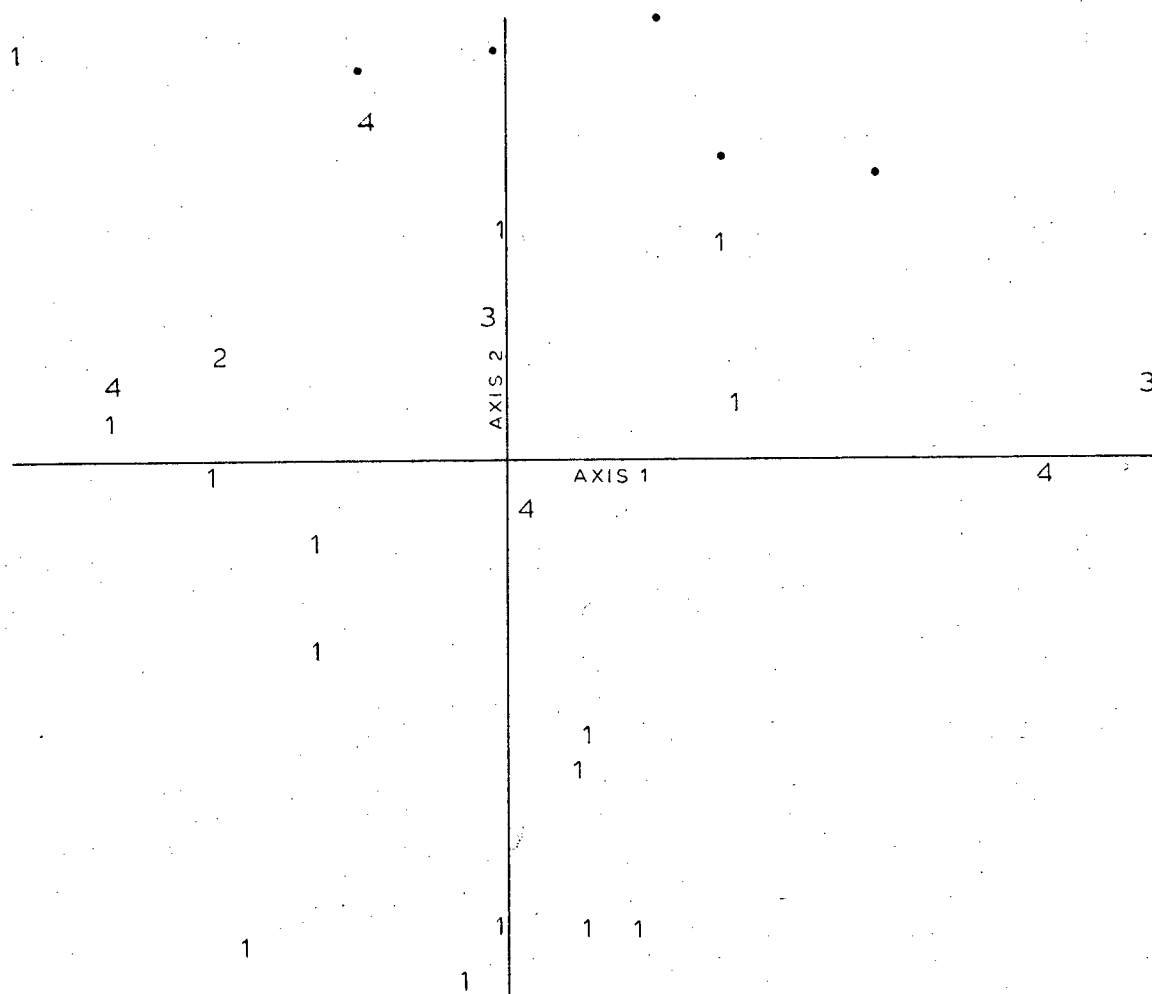


Figure 22 - Plot of cover class codes of Agrostis alba on the ordination of environmental data from freshwater plots.

1 = <25% cover; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%;

• = absent

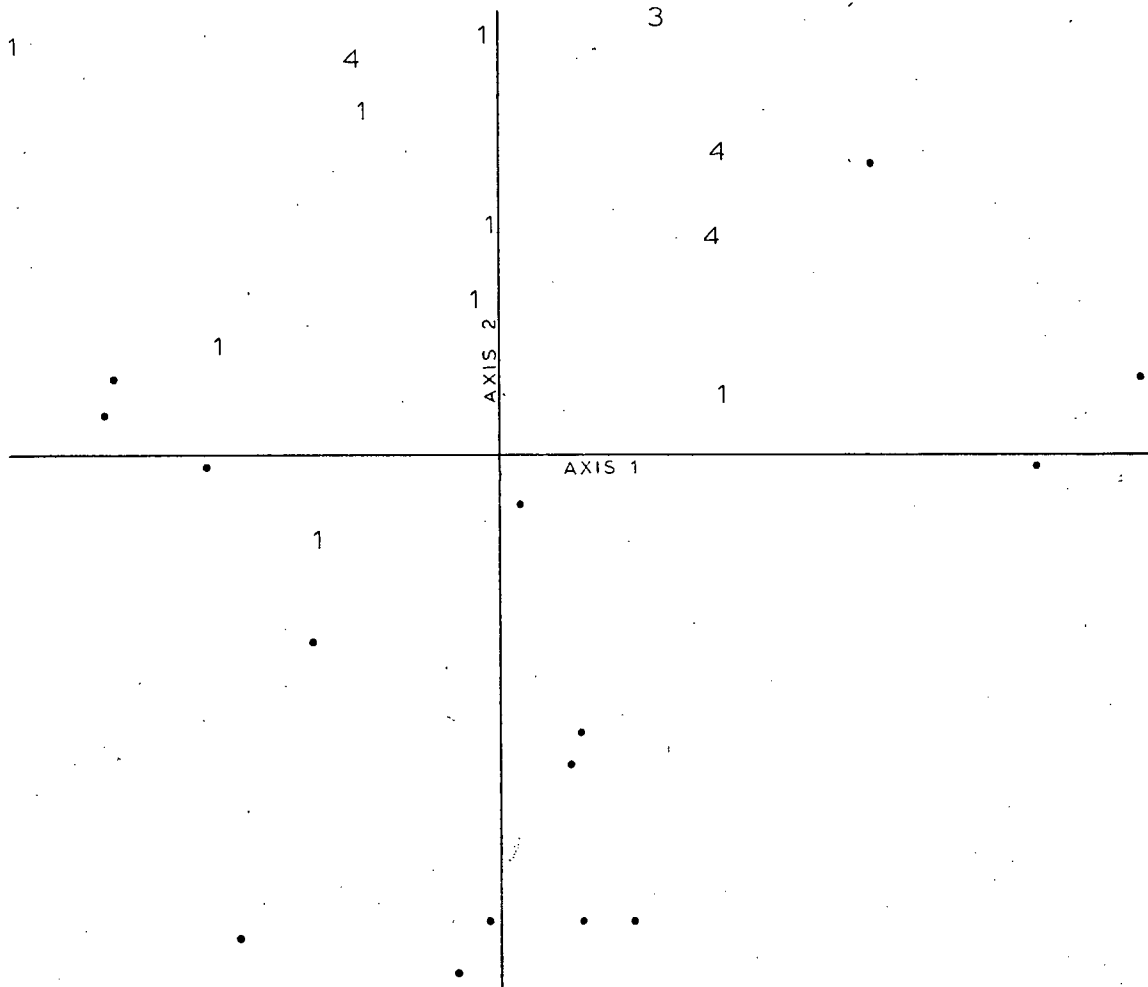


Figure 23 - Plot of cover class codes of Scirpus americanus on the ordination of environmental data from freshwater plots. 1 = <25% cover; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%; • = absent

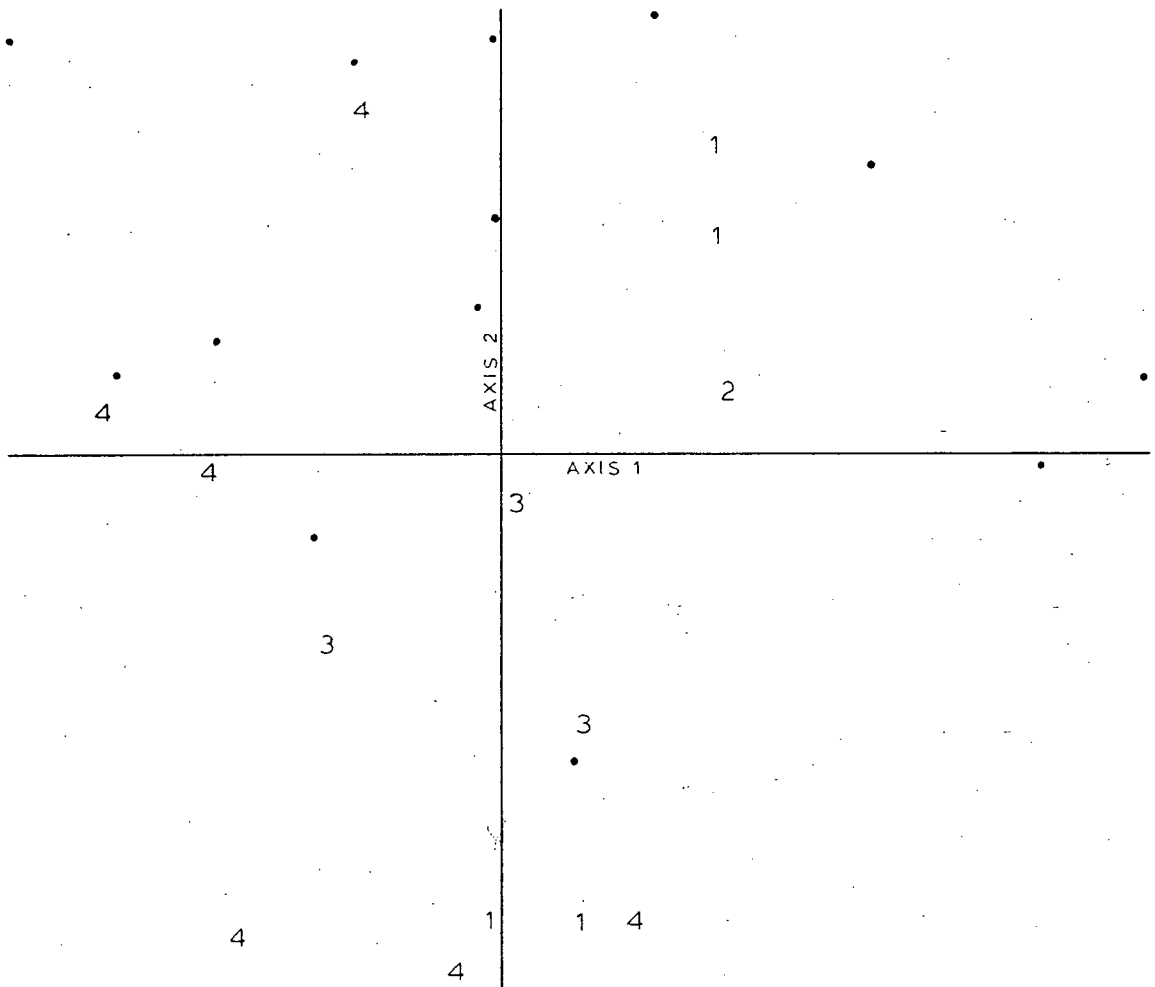


Figure 24 - Plot of cover class codes of *Carex lyngbyei* on the ordination of environmental data from freshwater plots.

1 = <25% cover; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%;

• = absent

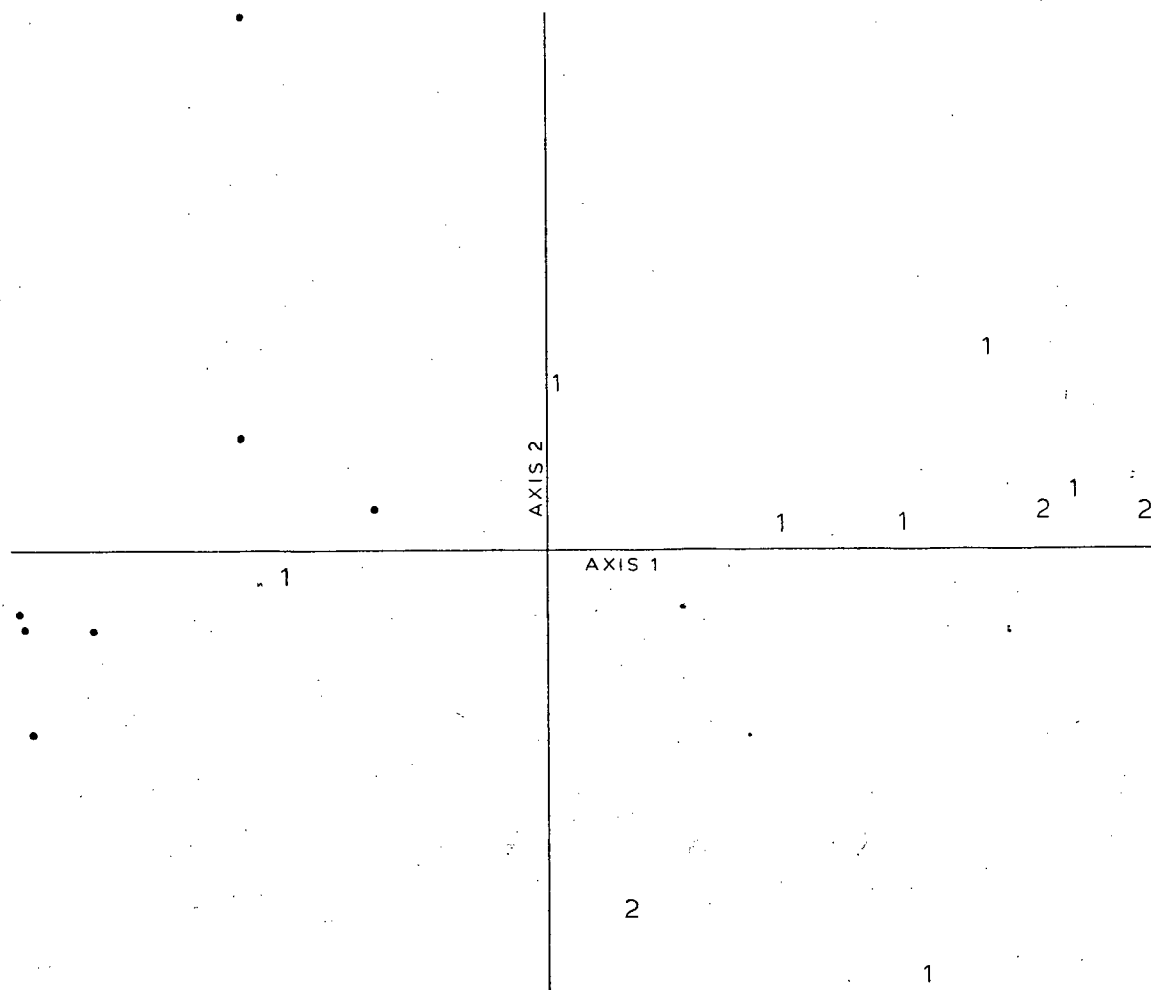


Figure 25 - Plot of cover class codes of Salicornia virginica on the ordination of environmental data from saltwater plots. 1 = <25% cover; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%; • = absent

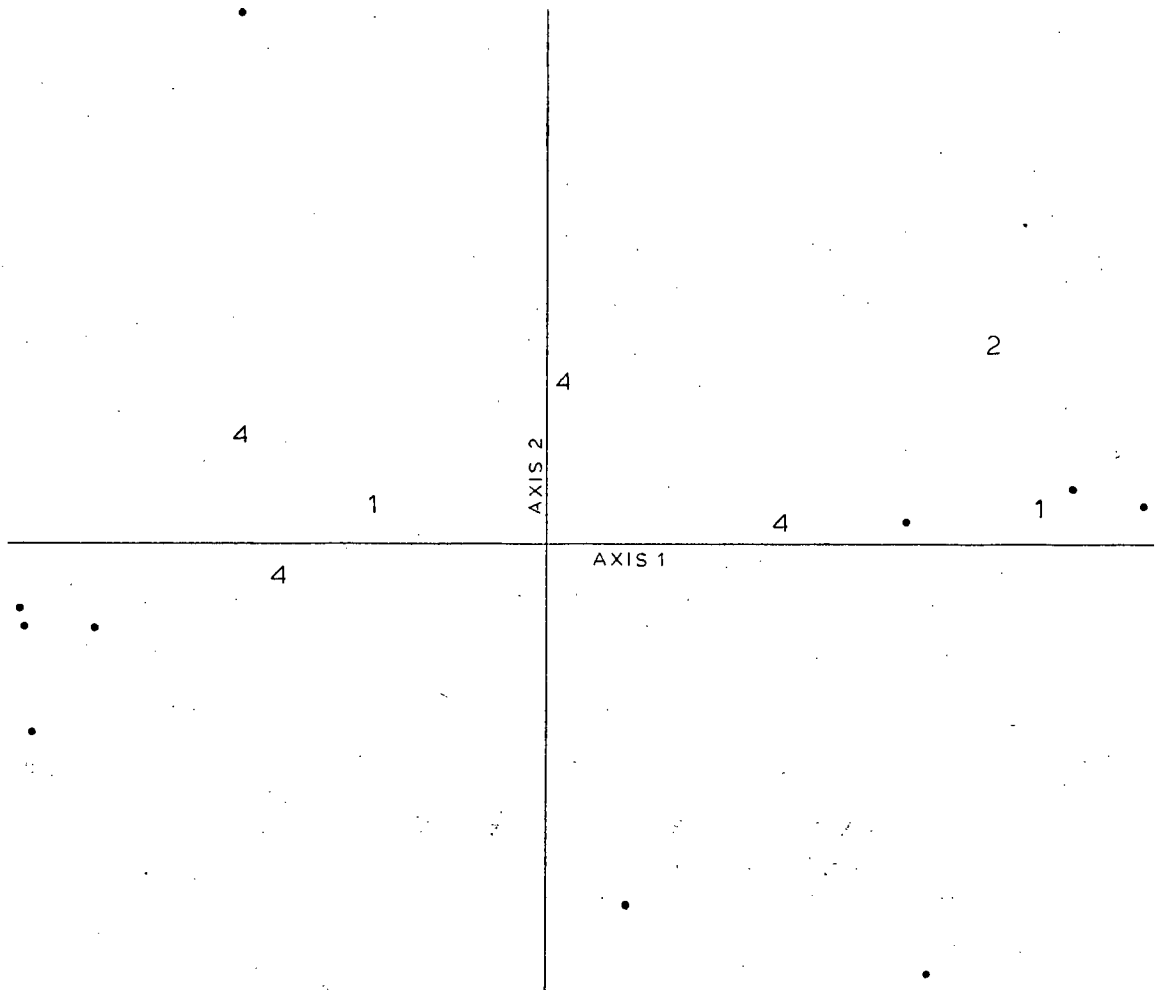
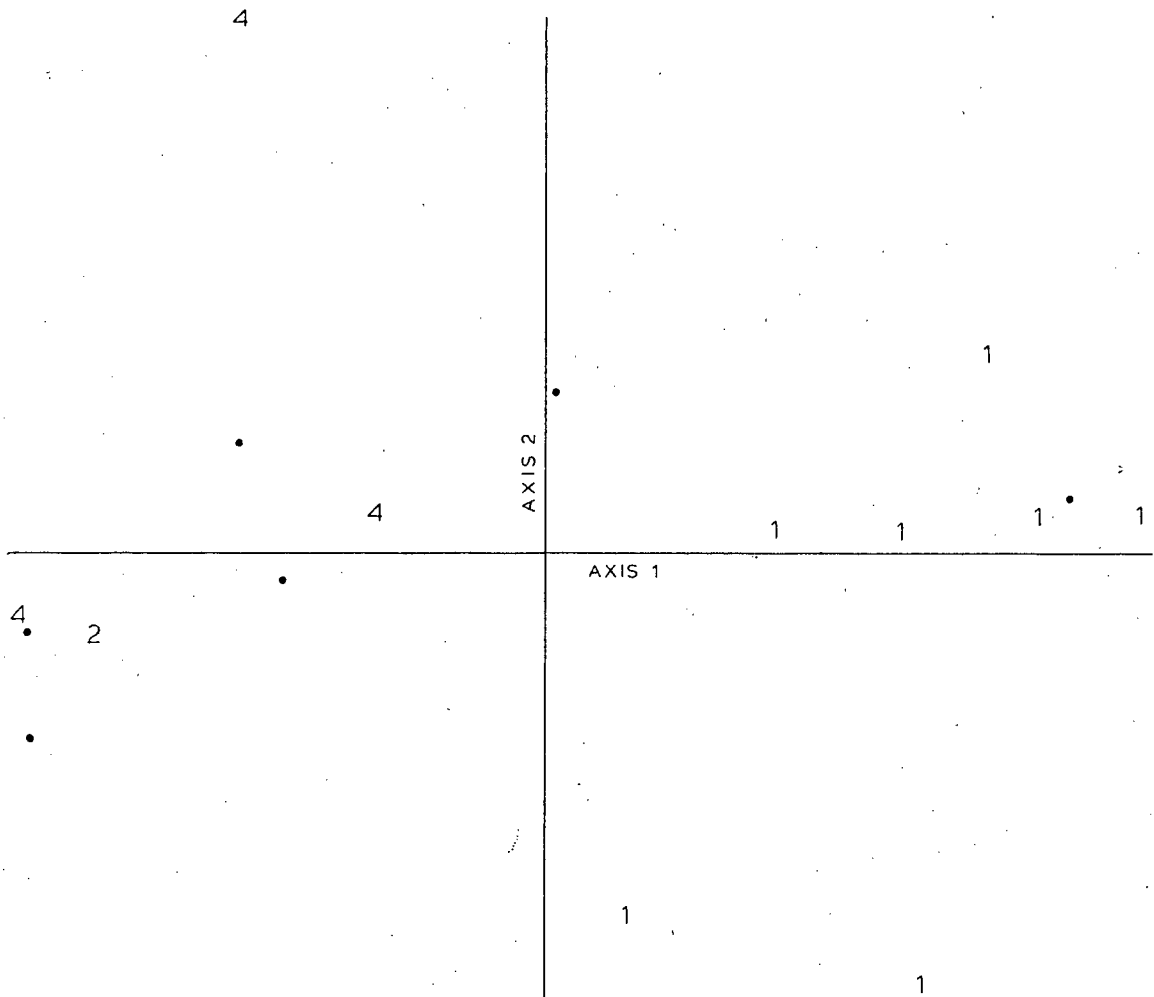


Figure 26 - Plot of cover class codes of Distichlis spicata on the ordination of environmental data from saltwater plots. 1 = <25% cover; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%;
• = absent



8. DISCUSSION

8.1 Data Standardizations

Square root transformation: As may be seen by comparing Fig. 11 with Fig. 13 and Fig. 12 with Fig. 14, the general result of using square root transformed data was that the points on the scatter plots were spread out more evenly. A practical benefit of this was a reduction in the number of plots which were overprinted by the computer. This effect made legible the ordination of the complete cover data set, as shown in Fig. 15. The use of this transformation may thus be helpful for improving the readability of highly congested ordination diagrams.

The square root transformation made previously distinct clumps of plots indistinct, but trends in the data, i.e. the relationships between clumps, became more evident. The overall spatial pattern was preserved with relatively minor distortion, at least on the first and second axes. The percent of total variance accounted for by the principal axes is a little lower with square root transformed data; e.g. 61% for the first three axes (transformed freshwater data) compared with 70% (untransformed).

The variable weightings on the ordination axes corresponded well with those obtained from untransformed data,

at least on the first two axes; on higher axes, the important species were sometimes weighted in quite different proportions. In the untransformed data, there was a tendency for a single species to greatly dominate the weightings, whereas with transformed data the weightings were somewhat more equitable. In the freshwater ordinations, the increased weighting of less important species resulted in easier ecological interpretation of the third axis.

Normalization: By amplifying the effective information content of low-cover quadrats, normalization resulted in the plots being grouped together according to their similarity with respect to the proportionate representation of their dominant species.

As with the square root transformation, the broad patterns of the ordinations were not changed (cf. Figs. 11 and 16, 12 and 17), at least for the first and second axes. The percent variance accounted for on the first three axes was slightly reduced. The species showing strongest correlations with the first and second axes were the same, though differences appeared in the third axis.

In Fig. 16, several distinct groups of quadrats are apparent; these groups constitute floristically distinct entities characterized by their relative abundance of three important species (Agrostis alba, Carex lyngbyei, and Scirpus americanus). A similar pattern of plots is found in the ordination of non-normalized data (Fig. 11), but there the

groups are not distinctly separated. The same principal species govern the axis orientations in either case, but plot position is influenced by relative species abundance in the case of normalized data, and absolute abundance with non-normalized data. For example, Fig. 16 shows a cluster of plots just below the left end of the first axis: these are all proportionately high in Scirpus americanus. In plots A29 and A30, however, the absolute cover of Scirpus americanus is very low; they are located far out on a mudflat where only Scirpus americanus and Ruppia maritima occur, very sparsely. In Fig. 11, however, the two plots appear in a tight cluster, below and to the left of the origin, along with several plots with which they have no species at all in common -- e.g. D3, a dense stand of Typha latifolia, and A0, containing only Eleocharis palustris. Normalization thus emphasized floristic similarity, regardless of species performance. (Refer to Table III for the species composition of the plots.)

The normalization procedure can be criticized on the grounds that it causes important ecological differences between sites to be overlooked -- i.e. site productivity differences, as expressed in overall plant performance. However, the purpose of the ordination may be to assess the relationships among samples on the basis of their resemblance in floristic composition, not on the basis of their resemblance in site productivity. Normalization of data is a procedure that enables the most effective use to be made of floristic information, while sacrificing site productivity

information. An optimal ordination strategy might thus involve the analysis of both normalized and non-normalized data.

Correlation matrix: The correlation matrix is a standardized variance-covariance matrix: each covariance value for a species pair is divided by the standard deviations of the two species. In effect, the variables are standardized to zero mean and unit variance.

The effect of this procedure was that the highest correlation values corresponded to the rarest species, which had many zero values in common. The principal components solution then gave the highest axis weightings to the rarest species, resulting in ordinations in which the great majority of plots were clustered tightly around the origin. When the rarest species (those present in only one or two quadrats) were removed from the data, improved ordinations were obtained, but I found the results difficult to interpret.

Use of the correlation matrix decreased the amount of variance accounted for on the major axes. With the freshwater data, the first three axes accounted for only 34% of total variance.

The correlation matrix does not seem appropriate for use with vegetation data, although satisfactory results might perhaps be obtained with data from very homogeneous stands. Under such favourable conditions, the correlation matrix might

be recommended, if axis generation on the basis of maximum variance did not produce ecologically meaningful results (Austin 1969).

Reciprocal averaging: As noted in Section 7.2, the initial species and quadrat ordinations obtained with RA were disappointing, with one or two quadrats appearing as outliers on the first axis, and all the other quadrats crowded together towards the other end (although with a good spread along the second axis). Examination of the raw data revealed that the anomalous outlying quadrats had very high cover values for uncommon species, which were themselves separated out in the corresponding species ordinations. When outlying plots (and species unique to those plots) were removed from the data, acceptable ordinations were obtained (Fig. 18). This distortion by outliers is a characteristic problem with RA (Gauch, Whittaker & Wentworth 1977), but it is easily dealt with.

Reciprocal averaging has been found superior to PCA by some investigators (Austin 1976; Gauch, Whittaker & Wentworth 1977; Robertson 1978; del Moral 1980) for the ordination of ecological data. RA has been found to produce an efficient ordination in one dimension (del Moral 1980), and Hill (1973) stated that when there is a long floristic gradient, it would always be presented linearly on the first axis. With PCA, by contrast, stands extreme on the first axis are not necessarily extreme on the floristic gradient, and vice versa. Although

RA may yield spurious results on the second axis, with plot position reflecting only the degree of displacement from the first axis (Gauch, Whittaker & Wentworth 1977), this is not always the case, and the second RA axis can sometimes be ecologically meaningful. Del Moral (1980) suggested that this will usually be the case when beta diversity is low. Gauch, Whittaker & Wentworth (1977) found RA much superior to PCA at high beta diversities, and generally preferable at low beta diversities.

8.2 Ecological Interpretation of Ordination Results

8.2.1 Vegetation Data

The PCA ordination of square root transformed cover data from all 103 plots (scatter diagram, Fig. 15; eigenvectors, Table IV) produced a good first-axis separation, accounting for 23% of total variance, of the freshwater plots (Transects A, D, J) on the right, and the saltwater plots (Transects B, C, E, F, G, H) on the left, on the basis of a floristic gradient related to high cover values of community dominants in both plot groups (Carex lyngbyei and Agrostis alba in the freshwater plots; Distichlis spicata, Triglochin maritimum, and Salicornia virginica in the saltwater plots). The second axis, however (14% of total variance), loaded positively with

Carex lyngbyei, Distichlis spicata, and Atriplex patula, and negatively with Scirpus americanus, Scirpus maritimus, and Agrostis alba; does not lend itself to such ready interpretation, and may largely reflect the distortion resulting from high beta diversity.

Table IV - Summary of results of PCA ordination on square roots of species cover data from all plots. Eigenvector elements in the range -0.1500 to +0.1500 not shown

Axis	% variance	Ranked eigenvector elements	Species
1	22.93	0.562	Agrostis alba
		0.513	Carex lyngbyei
		-0.179	Atriplex patula
		-0.249	Triglochin maritimum
		-0.283	Salicornia virginica
		-0.407	Distichlis spicata
2	14.47	0.695	Carex lyngbyei
		0.610	Distichlis spicata
		0.150	Atriplex patula
		-0.116	Agrostis alba
		-0.124	Scirpus maritimus
		-0.238	Scirpus americanus

The PCA ordinations on the freshwater plots (scatter diagrams, Figs. 11, 13; eigenvectors, Table V) separate the plots on the first axis (accounting for 32% of total variance in the ordination of the untransformed data) between those high in Carex lyngbyei on the right and those high in Scirpus americanus on the left. Inspection of the environmental data reveals that this floristic gradient corresponds strongly to

elevation; it is in fact highly conspicuous in the field at Brunswick Point, where a broad belt dominated by Carex lyngbyei in the upper and middle part of the marsh gives way to a wide fringe of Scirpus americanus at the lower levels. On the second axis (28% of total variance), the floristic gradient runs from high cover values of Agrostis alba (top) to high values of Carex lyngbyei (bottom). This does not correspond with any of the environmental gradients sampled, though it may be related to local variations in topography and drainage, with the high-Agrostis group being located in more poorly drained areas where the community is floristically richer, and where Scirpus maritimus tends to replace Carex lyngbyei.

Table V - Summary of results of PCA ordination on species cover data from freshwater plots. Eigenvector elements in the range -0.150 to +0.150 not shown

Axis	% variance	Ranked eigenvector elements	Species
1	31.59	0.912	Carex lyngbyei
		0.232	Agrostis alba
		-0.309	Scirpus americanus
2	27.50	0.893	Agrostis alba
		0.229	Scirpus maritimus
		-0.219	Scirpus americanus
		-0.293	Carex lyngbyei

In the PCA ordination on normalized freshwater data (scatter diagram, Fig. 16; eigenvectors, Table VI), three

floristic nodal groups may be distinguished. At the top of the second axis is a group of plots rich in Agrostis alba and, usually, Scirpus maritimus; at the left end of the first axis is a group of plots rich in Scirpus americanus; and in the lower right corner is a group of plots high in Carex lyngbyei. The other plots either are dominated by some combination of these species, or are not rich in any of them (the group just above and to the left of the origin).

Table VI - Summary of results of PCA ordination on normalized species cover data from freshwater plots. Eigenvector elements in the range -0.150 to +0.150 not shown

Axis	% variance	Ranked eigenvector elements	Species
1	27.89	0.576 0.359 -0.719	Carex lyngbyei Agrostis alba Scirpus americanus
2	22.04	0.688 0.161 -0.184 -0.661	Agrostis alba Scirpus maritimus Scirpus americanus Carex lyngbyei

The PCA ordinations on saltwater data (scatter diagrams, Figs. 12, 14; eigenvectors, Table VII) separated Distichlis spicata-dominated plots (right) from plots dominated by Triglochin maritimum, Salicornia virginica, and Spergularia canadensis (left) on the first axis, and plots dominated by Atriplex patula (top) from those dominated by Salicornia

virginica, Triglochin maritimum, Carex lyngbyei, and/or Distichlis spicata (bottom) on the second axis. The floristic gradient on the first axis does not seem to correspond with a gradient in any of the measured environmental factors, whereas the second axis shows a strong relationship to elevation. The ordination on normalized saltwater data (Fig. 17) added more plots to the Atriplex group at the top and to the Distichlis group in the lower right, while revealing greater detail in the group of plots at left, in particular by isolating a group of five plots which were dissimilar to all other plots (including each other). Taken together, these ordination results suggest four nodal groups of plots: a group dominated by Atriplex patula; a group dominated by Atriplex and Distichlis spicata; a group dominated by Distichlis and other species -- Carex lyngbyei, Triglochin maritimum, Salicornia virginica, and Spergularia canadensis; and a group dominated by Salicornia, Triglochin, and Spergularia.

The RA ordination of freshwater plots (Fig. 18) is similar in part to the PCA ordination, with a strong first-axis separation of the Scirpus americanus-dominated plots at left from the plots dominated by Carex lyngbyei and Agrostis alba at right. The strong separation on both axes of Scirpus validus-dominated plots would not have been predicted from the PCA ordination, in which these plots fall into or near the central swarm. More interesting is the arch-shaped sequence extending from lower left to lower right, which follows a floristic gradient from high-Carex plots at lower right (high-

Table VII - Summary of results of PCA ordination on species cover data from saltwater plots. Eigenvector elements in the range -0.150 to +0.150 not shown

Axis	% variance	Ranked eigenvector elements	Species
1	35.73	0.941	Distichlis spicata
		0.186	Atriplex patula
		-0.168	Salicornia virginica
		-0.176	Triglochin maritimum
2	15.77	0.869	Atriplex patula
		-0.200	Salicornia virginica
		-0.264	Distichlis spicata
		-0.329	Triglochin maritimum

elevation) through a floristically-rich series of plots in which Agrostis is prominent (high to medium elevations) to low-elevation plots dominated by Scirpus americanus. (The dense cluster at right centre is formed by uncommon, low-cover species.) A linear floristic gradient is curved here into the second ordination dimension, but is displayed somewhat more effectively than by PCA.

8.2.2 Environmental Data

The PCA ordination on environmental data from the freshwater and saltwater plots together (scatter diagram, Fig. 19; eigenvectors, Table VIII) clearly separated the freshwater group from the saltwater group on the first (horizontal) axis, accounting for 51% of total variance, with the two groups

appearing on opposite sides of the origin. Silt and clay were weighted negatively on this axis; the other seven variables were weighted positively, especially sodium and potassium. The second (vertical) axis, accounting for 23% of variance, is basically textural and nutritional, with sandy plots toward the bottom, and plots high in cations, silt, and clay toward the top.

Table VIII - Summary of results of PCA ordination on environmental data from freshwater and saltwater plots together

Eigenvector	1	2	3	4	5	6	7	8
Sand	0.3717	-0.3914	-0.1685	-0.1389	-0.0476	0.2370	-0.0058	-0.0114
Silt	-0.3813	0.3462	0.0916	0.1077	0.1934	-0.5785	0.0119	0.0123
Clay	-0.2781	0.4306	0.3282	0.1907	-0.3240	0.6578	-0.0108	0.0073
N	0.3101	0.0361	0.5272	0.1239	0.7287	0.1634	-0.2248	0.0314
K	0.4059	0.1581	-0.0439	0.4342	-0.3708	-0.2311	-0.6181	0.2164
Ca	0.1967	0.5224	-0.2366	-0.5998	0.1060	0.0787	-0.0591	0.5018
Mg	0.3513	0.4409	-0.1332	-0.1276	-0.0109	-0.0332	0.0006	-0.8044
Na	0.4095	-0.2021	-0.0470	0.4424	0.0028	-0.0531	0.7334	0.2299
Elev	0.2203	-0.0839	0.7069	-0.3964	-0.4189	-0.2936	0.1605	0.0140
% variance	50.67	22.87	13.24	5.76	4.40	1.97	0.95	0.13

The ordination of the freshwater plots (scatter diagram, Fig. 20; eigenvectors, Table IX) separated plots along the first axis (39% of total variance) mainly on the basis of texture and cation concentration: high-sand, low-cation plots at right, low-sand, high-cation plots at left. (For the values of the environmental variables at each plot, consult the environmental data table in Appendix B.) Only sand was weighted positively; the strongest negative weighting was for

Table IX - Summary of results of PCA ordination on environmental data from freshwater plots

Eigenvector	1	2	3	4	5	6	7	8
Sand	0.3991	0.3262	0.3623	0.0492	-0.0243	-0.1250	-0.0108	-0.0037
Silt	-0.3430	-0.2394	-0.5115	0.0649	-0.4639	0.2153	-0.0857	0.0032
Clay	-0.3396	-0.3398	-0.0040	-0.2048	0.7581	-0.0579	0.1543	0.0040
N	-0.2509	-0.3406	0.4635	0.4157	-0.2788	-0.1804	0.5621	0.0848
K	-0.4242	0.1729	0.0628	0.4202	0.0740	-0.5161	-0.5461	-0.1989
Ca	-0.3551	0.3753	0.0744	-0.4735	-0.1884	-0.0981	0.3226	-0.5951
Mg	-0.3980	0.3706	0.1222	-0.3039	-0.0996	-0.0719	-0.0166	0.7626
Na	-0.2598	0.3928	0.1392	0.4248	0.2211	0.7216	0.0467	-0.0815
Elev	-0.1139	-0.3775	0.5903	-0.3241	-0.1787	0.3167	-0.4980	-0.1040
% variance	39.34	28.14	13.42	7.18	5.15	4.42	2.22	0.13

potassium. On the second axis (28% of total variance), sodium, calcium, magnesium, and sand contributed strong positive weightings; elevation, nitrogen, and clay were strongly weighted negatively. The result was a separation of generally sandy, cation-rich, low-elevation plots at top from generally high-elevation, fine-textured plots rich in organic matter at bottom. (Ecological interpretation is not facilitated by the loading of sand and cations at opposite ends of the first axis, and at the same end of the second.)

In the ordination of saltwater plots (scatter diagram, Fig. 21; eigenvectors, Table X), the first axis (45% of total variance) was determined by texture and elevation, with sandy, high-elevation plots at right, and lower-elevation plots rich in silt and clay at left. The Boundary Bay plots are thus separated out on the right (Transects G and H) from the Brunswick Point plots on the left (Transects B and C). The second axis (30% of total variance) is largely nutritional, with calcium and magnesium contributing the strongest positive

loadings and sand the only negative loading. The sandy, cation-poor plots H11 and G6 were thus separated out at the bottom, and the silty, cation-rich C8 was isolated at the top. The third ordination axis (11% of total variance; not shown) strongly separated high-nitrogen, high-elevation, low-potassium plots from low-nitrogen, low-elevation, high-potassium plots -- basically an elevation gradient.

Table X - Summary of results of PCA ordination on environmental data from saltwater plots

Eigenvector	1	2	3	4	5	6	7	8
Sand	0.4426	-0.2213	-0.1654	-0.2426	0.1037	0.0290	0.1939	-0.0603
Silt	-0.4370	0.2216	0.1803	0.1911	-0.2035	-0.1178	-0.5296	0.1415
Clay	-0.4275	0.2057	0.1152	0.3611	0.1651	0.2056	0.6990	-0.1561
N	0.2881	0.0081	0.7873	0.0261	-0.1397	-0.4808	0.2117	0.0299
K	0.3022	0.2344	-0.4748	0.5839	-0.1266	-0.4641	0.1061	0.2113
Ca	-0.0113	0.5576	-0.0103	-0.4274	0.3720	-0.0586	0.1133	0.5929
Mg	0.1406	0.5742	-0.0438	-0.1288	0.1920	-0.1616	-0.1712	-0.7346
Na	0.2817	0.4010	0.0498	-0.0550	-0.6965	0.5053	0.1030	0.0569
Elev	0.3960	0.0561	0.2777	0.4800	0.4739	0.4599	-0.2907	0.1093
% variance	45.37	29.79	10.74	6.75	4.19	2.48	0.64	0.03

An examination of the correlation matrices (Table XI) may be helpful. In all the datasets, sand and silt/clay are strongly or very strongly negatively correlated. The nutrient cations are positively correlated, especially calcium with magnesium and potassium with sodium. Elevation and nitrogen do not show such strong correlations as the other variables, but their strongest correlations are with each other (positive), reflecting the greater accumulation of humic matter and peat at high elevations. In the freshwater

dataset, sand is negatively correlated with everything else -- reflecting the difference between the sandy, cation-poor, nitrogen-poor, lower-elevation plots along the Fraser River and the finer-textured plots, richer in cations and organic matter, that occur at higher elevations in northern Brunswick Point and Ladner Marsh and in the more brackish marsh in southern Brunswick Point.

In the saltwater dataset, however, sand is positively correlated with elevation, potassium, sodium, and nitrogen, suggesting a gradient from sandy, cation-rich, nitrogen-rich plots at high elevations to finer-textured, cation-poor, nitrogen-poor plots at lower elevations. This is somewhat misleading, reflecting as it does mainly the geographical variation between the finer-textured, perhaps more brackish, lower-elevation Brunswick Point marshes and the sandier, saltier, higher-elevation marshes at Boundary Bay. In the Brunswick Point marshes, texture does become finer towards the lower elevations; at Boundary Bay, however, the opposite is true. The trends in nitrogen and cations with elevation are not clear, but generally the highest values do occur at higher elevations. Apparently the principal "gradient" exposed by the saltwater PCA ordination was geographical. This implies that beta diversity was too high; the ordination results would probably be improved by ordinating the Brunswick Point and Boundary Bay plots separately.

It is important to realize that the results of an

Table XI - Product-moment correlation coefficients for environmental variables (* = $p < .05$; ** = $p < .01$)

1. Combined freshwater and saltwater plots. Sample size = 44.

Sand	1.000									
Silt	-0.979**	1.000								
Clay	-0.864**	0.744**	1.000							
N	0.374*	-0.410**	-0.216	1.000						
K	0.535**	-0.578**	-0.327*	0.484**	1.000					
Ca	0.004	-0.029	0.057	0.163	0.396**	1.000				
Mg	0.275	-0.315*	-0.121	0.433**	0.772**	0.860**	1.000			
Na	0.506**	-0.542**	-0.322*	0.578**	0.889**	0.457**	0.815**	1.000		
Elev	0.323*	-0.389**	-0.097	0.591**	0.319*	0.008	0.194	0.258	1.000	
	Sand	Silt	Clay	N	K	Ca	Mg	Na	Elev	

2. Freshwater plots. Sample size = 27.

Sand	1.000									
Silt	-0.909**	1.000								
Clay	-0.774**	0.441*	1.000							
N	-0.408*	0.277	0.461*	1.000						
K	-0.389*	0.338	0.326	0.341	1.000					
Ca	-0.167	0.164	0.112	-0.027	0.554**	1.000				
Mg	-0.207	0.185	0.165	0.037	0.697**	0.961**	1.000			
Na	-0.006	0.022	-0.020	0.008	0.542**	0.538**	0.640**	1.000		
Elev	-0.237	0.062	0.416*	0.614**	-0.053	-0.091	-0.043	-0.192	1.000	
	Sand	Silt	Clay	N	K	Ca	Mg	Na	Elev	

3. Saltwater plots. Sample size = 17.

Sand	1.000									
Silt	-0.992**	1.000								
Clay	-0.950**	0.907**	1.000							
N	0.380	-0.352	-0.427	1.000						
K	0.390	-0.396	-0.348	0.066	1.000					
Ca	-0.271	0.269	0.257	-0.027	0.178	1.000				
Mg	-0.055	0.062	0.036	0.147	0.514*	0.912**	1.000			
Na	0.248	-0.224	-0.293	0.360	0.538*	0.496*	0.711**	1.000		
Elev	0.585**	-0.608**	-0.485*	0.608**	0.494*	-0.003	0.284	0.438	1.000	
	Sand	Silt	Clay	N	K	Ca	Mg	Na	Elev	

ordination depend on the choice of variables (Austin 1969). In a vegetation ordination, the variables (species) are pre-selected; in an environmental ordination, however, the investigator makes a subjective decision as to which variables to use. Thus a different choice of variables might have produced very different ordination results.

8.2.3 Species-Environment Diagrams

The projections of cover class codes of important marsh species on the freshwater and saltwater environmental ordinations (Figs. 22-27) reveal clear patterns that can be interpreted ecologically.

Considering first the freshwater series, one sees that Agrostis alba (Fig. 22) performs evenly along the first (textural) axis, but seems to form three performance zones along the second axis (cationic, elevational, textural). The pattern for Scirpus americanus (Fig. 23) is more or less the inverse of the Agrostis pattern. The distribution pattern of Carex lyngbyei (Fig. 24) is similar to that of Agrostis, but its performance pattern is different.

These ordination patterns reflect patterns of species zonation in the marsh itself. Scirpus americanus is found at low elevations (top of diagrams) on both the north and south sides of Brunswick Point, extending lower than Carex or

Agrostis. At middle and upper levels, Carex and Agrostis co-dominate, but Carex outperforms Agrostis at higher elevations (finer-textured, lower in cations, higher in nitrogen; bottom of diagrams).

In the saltwater series, Salicornia virginica (Fig. 25) shows itself to be mostly absent from the Brunswick Point plots at left, but present in all the Boundary Bay plots at right. The first-axis gradient was based on texture and elevation. Examination of the data suggests that texture is probably not the factor controlling Salicornia distribution here; however, the two Brunswick Point plots in which Salicornia does occur are the two highest Brunswick Point plots in the environmental dataset, suggesting a possible role for elevation in restricting the distribution of Salicornia at Brunswick Point.

Distichlis spicata (Fig. 26) seems to show an avoidance of axis extremes, which corresponds to its distribution in the marsh. An important component of the salt marsh flora at middle levels, Distichlis is outcompeted by Atriplex patula at the highest elevations, and does not extend itself to the low levels where colonization of the unvegetated flats is taking place.

Triglochin maritimum (Fig. 27) shows a broad ecological amplitude, apparently tolerant of all major ordination gradient extremes. This corresponds to the distribution observed in the marsh: Triglochin was found on all transects

except Transect J, at Ladner Marsh. However, the figure reveals an interesting pattern: fairly low, uniform cover in the Boundary Bay plots; more variable performance, with some high cover values and some absences, at Brunswick Point. It may be that the Brunswick Point marsh, closer to the influence of the Fraser River, is more susceptible to environmental fluctuations which may not have been detected by my sampling program. This might also be an explanation for the poorer performance of Salicornia at Brunswick Point.

8.3 Plant Communities in the Study Area

In this study, I have emphasized the continuous nature of vegetational variation, rather than attempting to define plant associations, because I feel that the vegetation of the Fraser Delta tidal marshes is best understood by using this approach. A number of other tidal marsh studies have attempted to fit plant associations, rather than individual species, to ecological gradients, with results that tend not to be supported by available data. Some such instances were mentioned in the Literature Review.

A very distinctive zonation pattern, with different species forming successive elevational bands of dominance, is nonetheless a conspicuous and fairly universal feature of tidal marshes, including the Fraser Delta marshes. Moreover, there is a very clear vegetational and environmental

disjunction between the fresh and brackish Fraser Delta marshes on one hand and the salt marshes on the other. Thus it does not seem inappropriate to describe the vegetation in terms of important species-environment nodes that are suggested by ordination results and can be observed in the field. Such a description also facilitates comparisons with tidal marshes elsewhere that have been described in terms of plant associations.

Four of these nodal groups of samples may be informally recognized by analysis of the freshwater data: (1.) a Carex lyngbyei - Agrostis alba group on better-drained sites at high to medium elevations on silty loams, sometimes nitrogen-rich; (2.) an Agrostis alba - Scirpus maritimus group on less well drained sites, tending to be more brackish, at high to medium elevations on silty loams; (3.) a Scirpus americanus group at low elevations in fairly fresh to brackish areas on nitrogen-poor silty clay loams to sandy loams; (4.) a group dominated by Equisetum fluviatile, Scirpus validus, Agrostis alba, and Alisma plantago-aquatica at medium to low elevations on silt loams in the very fresh Ladner Marsh area.

From the saltwater data, four more groups emerge: (1.) an Atriplex patula group at the highest elevations, often with high soil nitrogen and also often with driftwood, on sandy to silty clay loams. In a variant of this group at somewhat lower elevations, Distichlis spicata co-dominates; (2.) a Carex lyngbyei - Distichlis spicata group at higher medium

elevations on loamy sediments with high to medium nitrogen concentrations; (3.) a Salicornia virginica - Triglochin maritimum group at lower medium elevations, displaying two variants: a Salicornia - Triglochin - Distichlis variant at higher elevations, and a Salicornia - Triglochin - Spergularia canadensis variant at lower elevations; (4.) a Spergularia canadensis group at low elevations on sandy loams to loamy sands. Salinity does not seem to play an important role in distinguishing these groups.

To place the Fraser Delta marshes in a regional context, the above species-environment nodal groups were compared with published descriptions of nearby marshlands in the Fraser Delta and neighbouring Washington State.

In the Nisqually salt marsh at the southern end of Puget Sound, Burg, Rosenberg & Tripp (1976) and Burg, Tripp & Rosenberg (1980) described twelve plant associations, the distributions of which they related to topographical and drainage features. Their floristic table and ordination results suggest that these associations are not discrete units, but can be interpreted as species dominance phases along an elevational gradient. Their sequence is similar to that observed in my saltwater plots, with Spergularia marina pioneering at the lowest elevations, zones dominated by Salicornia virginica, Distichlis spicata, Carex lyngbyei, and other species (some not found in the Fraser Delta) at intermediate levels, and a zone dominated by Festuca rubra and

Carex lyngbyei at the highest levels. Atriplex patula, important in the Fraser Delta salt marshes, was not present.

Two important species identified in the Nisqually salt marsh occur in the Fraser Delta only in the freshwater marshes: Juncus balticus and Deschampsia cespitosa. Assuming that their and my species identifications are correct, this illustrates the fact that the ecological roles of species are not necessarily the same at different sites; different community and habitat conditions alter the realized niche.

Farther north, at Bellingham Bay, Disraeli & Fonda (1979) described a brackish marsh similar floristically to the Brunswick Point marsh, with a lower zone dominated by Scirpus americanus and an upper zone dominated by Carex lyngbyei.

On the western side of Lulu Island in the Fraser Delta, Hutchinson (1982) also described a marsh of a similar type to the Brunswick Point marsh. He identified seven plant communities by a hierarchical clustering procedure, relating their distributions to elevation and substrate texture. As at Brunswick Point, the Lulu Island marsh has a lower zone dominated by Scirpus americanus and S. maritimus, and a higher, finer-textured, lower-cation zone dominated by Carex lyngbyei and other species.

Bradfield & Porter (1982) sampled much more extensively at Ladner Marsh than I did in this study, and were able to recognize seven community types (about equal in level of

discrimination to my nodal group variants) from cluster analysis. The distributions of these types were related to physiographic and drainage factors. Only one of these types, the Carex - Agrostis type, would be recognizable in my own data -- a result of the presence of several major species within the area of the Bradfield & Porter study that were not found in my own study area. This illustrates that the freshwater marshes of the lower Fraser River are quite different in character from the marshes at the delta front. I have not found descriptions in the literature of similar marshes outside of the lower Fraser River.

9. CONCLUSIONS

(1.) Transforming species cover data values to their square roots prior to ordination can lead to more readable ordination diagrams by spreading out the points. Reduction of the bias from overemphasis of high-cover species may expose data trends not otherwise evident, without causing major change in plot scores on the first two PCA axes, though higher axes may be considerably changed.

(2.) Normalization of species cover value data prior to ordination exposes sample relationships based on relative rather than absolute species abundances. Effective use is thus made of floristic information, while site productivity information is sacrificed. As an optimal ordination strategy for vegetation data, the analysis of both normalized and non-normalized data is recommended.

(3.) Use of the correlation matrix for ordination of vegetation data is not recommended for general purposes.

(4.) Reciprocal averaging is highly sensitive to anomalous samples, but may produce good vegetation ordinations, at least along the first axis, when such samples are removed from the data. RA and PCA produced vegetation ordinations of equivalent quality, but the RA ordinations of environmental data were inferior.

(6.) Ordination of environmental data exposes environmental gradients directly; the results can be a worthwhile aid to the interpretation of vegetation ordinations. The projection of species data on an environmental ordination can suggest relationships between species performance and environmental factors.

(7.) The performance and distribution of dominant plant species in the Fraser Delta tidal marshes were shown to be related to substrate texture, substrate nitrogen and cation levels, and site elevation.

(8.) On the basis of floristic and environmental factors, the sample plots were separated into two main groups: one representing the brackish marshes of northern and western Brunswick Point and the freshwater marshes of Ladner Marsh; the other representing the salt marshes of southeastern Brunswick Point and Boundary Bay. Each group may be subdivided by floristic and environmental differences: the Ladner Marsh plots from the north and west Brunswick Point plots, and the southeast Brunswick Point plots from the Boundary Bay plots.

(9.) Based on floristic and environmental distinctions, eight field-recognizable species-environment sample groups, with variants, are informally recognized. These are dominated respectively by: (i) Carex lyngbyei and Agrostis alba; (ii) Agrostis alba and Scirpus maritimus; (iii) Scirpus americanus; (iv) Equisetum fluviatile, Scirpus validus, Agrostis alba, and

Alisma plantago-aquatica; (v) Atriplex patula (variant: Atriplex patula - Distichlis spicata); (vi) Carex lyngbyei and Distichlis spicata; (vii) Salicornia virginica and Triglochin maritimum (variants: Salicornia virginica - Triglochin maritimum - Distichlis spicata, and Salicornia virginica - Triglochin maritimum - Spergularia canadensis); (viii) Spergularia canadensis.

(10.) The marshes of the study area are similar to other brackish and salt marshes that have been described in the Fraser Delta and in Washington, but are mostly dissimilar to the fresh Fraser River marshes.

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APPENDIX A. NAMES OF SPECIES SAMPLED, WITH AUTHORITIES

Achillea millefolium L.
Agropyron repens (L.) Beauv.
Agrostis alba L. var. alba
Agrostis alba L. var. palustris (Huds.) Pers.
Alisma plantago-aquatica L.
Aster eatonii (Gray) Howell
Atriplex patula L. var. hastata (L.) Gray
Atriplex patula L. var. patula
Atriplex patula L. var. zosteraefolia (Hook.) C. L. Hitchc.
Bidens cernua L.
Callitriche L. sp.
Caltha asarifolia DC.
Carex lyngbyei Hornem.
Chara braunii Gm.
Cotula coronopifolia L.
Cuscuta salina Engelm.
Deschampsia cespitosa (L.) Beauv.
Distichlis spicata (L.) Greene
Eleocharis palustris (L.) R. & S.
Elymus glaucus Buckl. var. breviaristatus Davy
Elymus mollis Trin. in Spreng.
Equisetum fluviatile L.
Festuca arundinacea Schreb.
Glaux maritima L.
Grindelia integrifolia DC. var. macrophylla (Greene) Cronq.
Hordeum brachyantherum Nevski
Hygrohypnum luridum (Hedw.) Jenn.
Juncus articulatus L.
Juncus balticus Willd.
Juncus bufonius L.
Juncus gerardii Loisel.
Lathyrus L. sp.
Leptodictyum riparium (Hedw.) Warnst.
Lilaea scilloides (Poir.) Hauman
Lilaeopsis occidentalis Coult. & Rose
Limosella aquatica L.
Lythrum salicaria L.
Mentha arvensis L.
Mimulus guttatus DC. var. guttatus
Myosotis laxa Lehm.
Oenanthe sarmentosa Presl
Plantago maritima L.
Polygonum aviculare L.
Potentilla pacifica Howell
Puccinellia nutkaensis (Presl) Fern.
Puccinellia nuttalliana (Schult.) A. S. Hitchc.
Ruppia maritima L.
Sagittaria latifolia Willd.

Salicornia virginica L.
Scirpus americanus Pers.
Scirpus maritimus L.
Scirpus validus Vahl
Sium suave Walt.
Sonchus arvensis L.
Spergularia canadensis (Pers.) G. Don
Spergularia marina (L.) Griseb.
Trifolium oliganthum Steud.
Triglochin maritimum L.
Typha latifolia L.
Zostera americana den Hartog

Nomenclature is according to Hitchcock et al. 1969, except: Chara braunii Gm. (a green alga), Hygrohypnum luridum (Hedw.) Jenn. and Leptodictyum riparium (Hedw.) Warnst. (mosses), and Zostera americana den Hartog (which keys to Z. nana Roth in Hitchcock et al.).

APPENDIX B. ENVIRONMENTAL DATA

Explanation of abbreviations: SAMPL = sample plot (initial letter designates transect); SAND = percent by weight of sand in soil sample; SILT = percent by weight of silt in soil sample; CLAY = percent by weight of clay in soil sample; TXTCLASS = textural classification of soil sample (L = loam, LS = loamy sand, S = sand, SCL = sandy clay loam, SiCL = silty clay loam, SiL = silt loam, SL = sandy loam); COND = electrical conductivity of soil sample in mS cm^{-1} ; N = percent by weight of nitrogen (total) in soil sample; K = parts per million of potassium in soil sample; CA = parts per million of calcium in soil sample; MG = parts per million of magnesium in soil sample; NA = parts per million of sodium in soil sample; PH = pH of soil sample; ELEV = elevation of sample plot above local chart datum; %ELEV = standardized sample plot elevation as described in section 7.3.

SAMPL	SAND	SILT	CLAY	TXTCLASS	COND	N	K	CA	MG	NA	PH	ELEV	%ELEV
A 0	27.5	60.	12.5	SiL	5.4	.04	31.6	105.	110	290	1.82	44.9	
A 1	25.	60.	15.	SiL	10.4	.05	30.	155.	280	700	2.22	54.7	
A 2	27.5	57.5	15.	SiL	8.4	.06	45.	137.5	245	550	2.53	62.6	
A 3	27.5	57.5	15.	SiL	5.0	.10	50.	82.5	160	365	2.71	67.0	
A 4											2.73	67.5	
A 5	25.	60.	15.	SiL	9.4	.06	67.5	280.	580	625	2.59	63.9	
A 6	15.	52.5	32.5	SiCL	4.5	.11	37.5	40.	120	425	2.92	72.1	
A 7											2.80	69.1	
A 8	7.5	60.	32.5	SiCL	5.6	.14	72.5	140.	275	560	2.88	67.9	
A 9											2.84	70.1	
A10	5.	65.	30.	SiCL	8.8	.14	77.5	272.5	710	855	2.88	71.1	
A11	7.5	65.	27.5	SiL-SiCL	7.8	.12	45.	285.	525	325	2.92	72.0	
A12											3.00	74.2	
A13											3.00	74.2	
A14	12.5	62.5	25.	SiL	9.1	.13	57.5	372.5	735	625	3.11	76.7	
A15											3.10	76.6	
A16											3.20	79.0	
A17	7.5	67.5	25.	SiL	8.1	.14	57.5	460.	825	415	3.15	77.9	
A18					11.4	.14	39.9	209.	371	703	3.20	79.1	
A19	30.	47.5	22.5	L	12.	.12	39.	335.	608	608	3.09	76.4	
A20					11.	.12	91.7	231.6	405	714	3.08	76.0	
A21	22.5	57.5	20.	SiL	10.	.17	35.9	135.2	311	877	3.10	76.4	
A22					14.2	.13	51.3	295.1	599	1001	3.03	74.9	
A23	25.	55.	20.	SiL	12.	.12	67.5	237.5	540	1380	5.1	2.99	73.9
A24	20.	57.5	22.5	SiL	21.	.08	61.3	254.	578	1356	4.4	2.68	66.2
A25	7.5	70.	22.5	SiL	18.	.11	82.5	415.	915	1335	4.7	2.81	69.4
A26	22.5	55.	22.5	SiL	14.	.12	40.	240.	464	864	2.91	71.9	
A27					15.4	.11	50.2	301.3	591	837	2.08	51.3	
A28	32.5	50.	17.5	SiL-L	16.	.06	42.6	246.8	485	706	5.3	2.37	58.4
A29	57.5	32.5	10.	SL	23.	.02	57.5	72.5	165	1130	6.6		
A30	62.5	27.5	10.	SL	25.	.02	70.	162.5	125	510	6.0		
B 1	27.5	52.5	20.	SiL	46.	.24	250.	315.	1115	8400	3.75	80.4	
B 2	15.	65.	20.	SiL	39.	.24	180.6	249.2	867	5272	3.50	75.1	
B 3					39.	.19	217.5	225.	840	7100	3.39	72.8	
B 4	20.	55.	25.	SiL	42.	.21	405.5	224.5	905	6372	3.24	69.5	
B 5					40.	.13	148.	416.	896	3240	3.29	70.6	
B 6	7.5	65.	27.5	SiL-SiCL	35.	.14	250.	187.5	670	5450	3.19	68.4	

SAMPL	SAND	SILT	CLAY	TXTCCLASS	COND	N	K	CA	MG	NA	PH	ELEV	%ELEV
B 7												3.20	68.7
B 8	0.	70.	30.	SiCL	33.	.15	265.	190.	690	5250		3.11	66.8
B 9												3.18	68.2
B10	17.5	57.5	25.	SiL	32.5	.08	185.	272.5	775	4650		2.59	55.6
B11												2.59	55.6
B12	27.5	50.	22.5	L	30.	.05	157.5	227.5	660	4250		2.59	55.5
C 1	12.5	70.	17.5	SiL								3.92	84.1
C 2	27.5	52.5	20.	SiL	26.		152.5	212.5	700	2080		3.64	78.0
C 3	17.5	62.5	20.	SiL	30.	.13						3.66	78.6
C 4					41.	.28	221.4	278.8	951	6421		3.61	77.4
C 5	12.5	57.5	30.	SiCL	36.	.19	255.	322.5	965	6000	6.3	3.54	75.9
C 6					38.	.21	166.2	253.3	823	5082		3.53	75.6
C 7					46.	.18	210.8	450.4	1236	6143		3.37	72.3
C 8	5.	65.	30.	SiCL	40.	.14	285.	577.5	1625	7500	5.6	3.27	70.2
D 1	17.5	65.	17.5	SiL	3.5	.24	31.	25.	58	400		3.40	83.9
D 2	2.5	72.5	25.	SiL	2.3	.10	38.7	54.1	129	156		3.33	82.1
D 3												3.24	80.1
D 4	5.	67.5	27.5	SiL-SiCL	3.1	.14	36.9	62.7	140	280		3.48	85.9
D 5					3.3	.26	600.	56.3	113	390		3.19	78.8
D 6	5.	65.	30.	SiCL	3.8	.26	76.6	119.5	196	319	5.2	3.07	75.9
D 7					4.7	.23	83.3	154.2	258	408		3.06	75.5
D 8	10.	65.	25.	SiL	5.	.14	92.5	235.	640	300	4.2	2.95	72.8
E 1					35.	.20	152.3	132.9	486	3403			
E 2	50.	37.5	12.5	L	31.	.16	77.5	102.5	395	3150	4.2		
E 3					28.	.13	101.3	138.8	593	3900			
E 4	30.	50.	20.	SiL-L	28.	.21	252.5	167.5	645	4900			
E 5					48.	.32	625.	320.	1285	9950			
E 6	42.5	42.5	15.	L	52.	.35	370.	145.	575	4350	5.5		
E 7					46.	.30	390.4	233.	974	8413			
E 8	75.	15.	10.	SL	33.	.07	220.	205.	830	3890	3.9		
E 9	60.	27.5	12.5	SL	47.	.19	252.5	220.	395	2600			
F 1	57.5	30.	15.	SL	29.	.17	142.5	132.5	495	3950	5.0		
F 2					28.5	.07	98.4	84.8	299	2314			
F 3	75.	20.	5.	LS	32.	.11	143.3	100.	367	2620			
F 4					41.	.20	218.7	109.3	820	4961			
F 5	80.	17.5	2.5	LS	28.	.09	84.8	45.1	414	2705			
G 1	57.5	32.5	10.	SL	38.	.28	590.	507.5	825	5500	3.9	3.53	80.0
G 2	60.	30.	10.	SL	46.	.23	315.	315.	1030	7500	4.2	3.22	72.9
G 3	55.	35.	10.	SL	58.	.38	440.	332.5	1250	9650	4.7	3.26	73.6
G 4					48.	.26	412.5	375.	1523	10800		3.13	70.9
G 5	72.5	20.	7.5	SL	58.	.14	415.	290.	1035	8500	4.5	3.20	72.5
G 6	72.5	17.5	10.	SL	56.	.23	177.5	175.	585	3550	4.4	3.13	70.8
G 7	60.	25.	15.	SL	49.		600.	350.	1350	10800	4.1	2.87	64.9
G 8	85.	10.	5.	LS	40.		382.5	192.5	735	6995	5.6	3.05	69.1
G 9					38.	.11	142.5	150.	600	4200		3.54	80.1
G10					25.	.09	86.3	127.5	405	2610		3.50	79.2
H 1	62.5	22.5	15.	SL	39.	.43	282.5	292.5	1060	8500	5.7	4.24	95.9
H 2	55.	22.5	22.5	SCL							6.0	4.26	96.4
H 3	67.5	10.	22.5	SCL							5.6	4.28	96.8
H 4						.72						4.22	95.5
H 5	70.	15.	15.	SL							5.3	4.14	93.7
H 6					83.	.84	865.	598.	2697	29906		4.15	93.9
H 7	60.	22.5	17.5	SL		.61					5.3	4.10	92.7
H 8	70.	17.5	12.5	SL	62.	.18	622.5	267.5	1140	5450	5.8	4.07	92.2
H 9					57.	.26	799.	364.	1193	10425		4.01	90.7
H10	82.5	7.5	10.	LS	58.	.13	490.	250.	1040	9550		3.93	88.9
H11	87.5	5.	7.5	S	52.	.31	182.5	125.	515	4600	5.0	3.76	84.8
J 1	50.	35.	15.	L	1.3	.06	6.	60.	60	17		3.45	77.2
J 2	45.	40.	15.	L	1.9	.10	8.5	70.	70	65	5.5	3.50	78.3
J 3					2.2	.01	6.2	71.3	86	20.		3.43	76.6
J 4	5.	67.5	27.5	SiL-SiCL	2.2	.08	6.6	60.	45	110	5.4	3.42	76.6
J 5					1.8	.13	8.1	72.	72	54		3.04	68.0
J 6	2.5	72.5	25.	SiL	3.2	.08	10.	142.5	130	110	6.3	2.91	65.1
J 7					2.4	.06	8.7	191.3	131	41		2.39	53.5
J 8	10.	72.5	17.5	SiL	2.8	.03	14.1	192.5	65	55	6.8		
J 9					1.	.05	5.1	75.	51	38		2.48	55.5