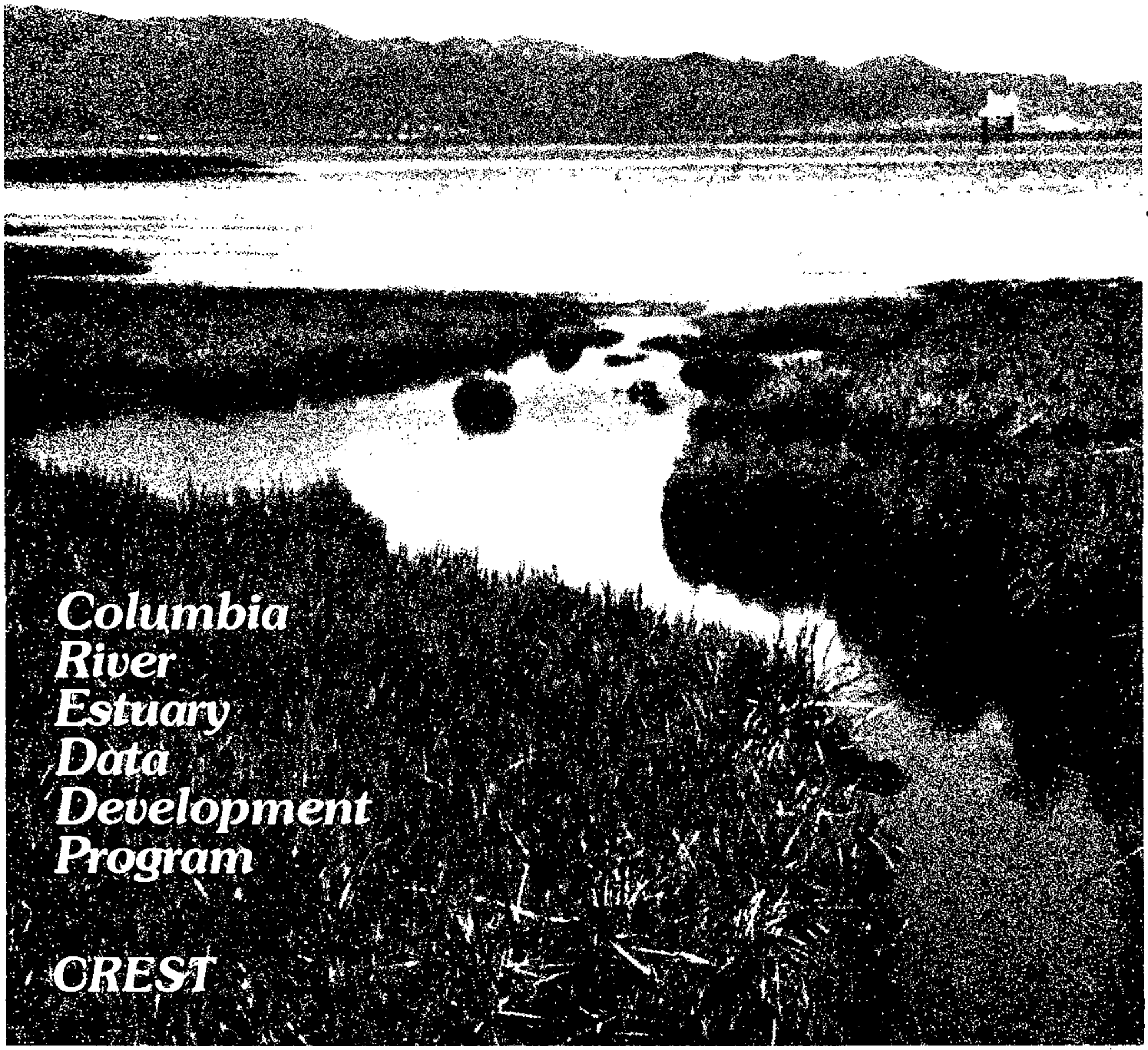
TIDAL MARSH PLANT PRODUCTION IN THE COLUMBIA RIVER ESTUARY



Final Report on the Emergent Plant Primary Production Work Unit of the Columbia River Estuary Data Development Program

TIDAL MARSH PLANT PRODUCTION IN THE COLUMBIA RIVER ESTUARY

Contractor:

Woodward-Clyde Consultants
3467 Kurtz Street
San Diego, California 92110

Principal Investigator:

Keith B. Macdonald
P.O. Box 60310
San Diego, California 92106

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This Report Was Prepared By

Keith B. Macdonald, Principal Investigator

With Assistance From

Ted P. Winfield, Project Manager

PREFACE

The Columbia River Estuary Data Development Program

This document is one of a set of publications and other materials produced by the Columbia River Estuary Data Development Program (CREDDP). CREDDP has two purposes: to increase understanding of the ecology of the Columbia River Estuary and to provide information useful in making land and water use decisions. The program was initiated by local governments and citizens who saw a need for a better information base for use in managing natural resources and in planning for development. In response to these concerns, the Governors of the states of Oregon and Washington requested in 1974 that the Pacific Northwest River Basins Commission (PNRBC) undertake an interdisciplinary ecological study of the estuary. At approximately the same time, local governments and port districts formed the Columbia River Estuary Study Taskforce (CREST) to develop a regional management plan for the estuary.

PNRBC produced a Plan of Study for a six year, $6.2 million program which was authorized by the U.S. Congress in October 1978. For the next three years PNRBC administered CREDDP and $3.3 million was appropriated for the program. However, PNRBC was abolished as of October 1981, leaving CREDDP in abeyance. At that point, much of the field work had been carried out, but most of the data were not yet analyzed and few of the planned publications had been completed. To avoid wasting the effort that had already been expended, in December 1981 Congress included $1.5 million in the U.S. Water Resources Council (WRC) budget for the orderly completion of CREDDP. The WRC contracted with CREST to evaluate the status of the program and prepare a revised Plan of Study, which was submitted to the WRC in July 1982. In September, after a haitus of almost one year, CREDDP work was resumed when a cooperative agreement was signed by CREST and the WRC to administer the restructured program and oversee its completion by June 1984. With the dissolution of the WRC in October 1982, the National Oceanic and Atmospheric Administration (NOAA) assumed the role of the WRC as the federal representative in this cooperative agreement.

CREDDP was designed to meet the needs of those groups who were expected to be the principal users of the information being developed. One such group consists of local government officials, planning commissions, CREST, state and federal agencies, permit applicants, and others involved in planning and permitting activities. The other major anticipated user group includes research scientists and educational institutions. For planning purposes, an understanding of the ecology of the estuary is particularly important, and CREDDP has been designed with this in mind. Ecological research focuses on the linkages among different elements in the food web and the influence on the food web of such physical processes as currents, sediment transport and salinity intrusion. Such an ecosystem view of the estuary is necessary to predict the effect of estuarine alterations on natural resources.

Research was divided into thirteen projects, called work units. Three work units, Emergent Plant Primary Production, Benthic Primary Production, and Water Column Primary Production, dealt with the plant life which, through photosynthesis and uptake of chemical nutrients, forms the base of the estuarine food web. The goals of these work units were to describe and map the productivity and biomass patterns of the estuary's primary producers and to describe the relationship of physical factors to primary producers and their productivity levels.

The higher trophic levels in the estuarine food web were the focus of seven CREDDP work units; Zooplankton and Larval Fish, Benthic Infauna, Epibenthic Organisms, Fish, Avifauna, Wildlife, and Marine Mammals. The goals of these work units were to describe and map the abundance patterns of the invertebrate and vertebrate species and to describe those species' relationships to relevant physical factors.

The other three work units, Sedimentation and Shoaling, Currents, and Simulation, dealt with physical processes. The work unit goals were to characterize and map bottom sediment distribution, to characterize sediment transport, to determine the causes of bathymetric change, and to determine and model circulation patterns, vertical mixing and salinity patterns.

Final reports on all of these thirteen work units have been published. In addition, these results are integrated in a comprehensive synthesis entitled The Dynamics of the Columbia River Estuarine Ecosystem, the purpose of which is to develop a description of the estuary at the ecosystem level of organization. In this document, the physical setting and processes of the estuary are described first. Next, a conceptual model of biological processes is presented, with particular attention to the connections among the components represented by the work unit categories. This model provides the basis for a discussion of relationships between physical and biological processes and among the functional groups of organisms in the estuary. Finally, the estuary is divided into regions according to physical criteria, and selected biological and physical characteristics of the habitat types within each region are described. Historical changes in physical processes are also discussed, as are the ecological consequences of such changes.

Much of the raw data developed by the work unit researchers is collected in a magnetic tape archive established by CREDDP at the U.S. Army Corps of Engineers North Pacific Division Data Processing Center in Portland, Oregon. These data files, which are structured for convenient user access, are described in an Index to CREDDP Data. The index also describes and locates several data sets which were not adaptable to computer storage.

The work unit reports, the synthesis, and the data archive are intended primarily for scientists and for resource managers with a scientific background. However, to fulfill its purposes, CREDDP had developed a set of related materials designed to be useful to a wide range of people.

Guide to the Use of CREDDP Information highlights the principal findings of the program and demonstrates how this information can be used to assess the consequences of alterations in the estuary. It is intended for citizens, local government officials, and those planners and other professionals whose training is in fields other than the estuary-related sciences. Its purpose is to help nonspecialists use CREDDP information in the planning and permitting processes.

A detailed portrait of the estuary, but one still oriented toward a general readership, is presented in The Columbia River Estuary: Atlas of Physical and Biological Characteristics, about half of which consists of text and illustrations. The other half contains color maps of the estuary interpreting the results of the work units and the ecological synthesis. A separate Bathymetric Atlas of the Columbia River Estuary contains color bathymetric contour maps of three surveys dating from 1935 to 1982 and includes differencing maps illustrating the changes between surveys. CREDDP has also produced unbound maps of the estuary designed to be useful to resource managers, planners and citizens. These black-and-white maps illustrate the most recent (1982) bathymetric data as contours and show intertidal vegetation types as well as important cultural features. They are available in two segments at a scale of 1:50,000 and in nine segments at 1:12,000.

Two historical analyses have been produced. Changes in Columbia River Estuary Habitat Types over the Past Century compares information on the extent and distribution of swamps, marshes, flats, and various water depth regimes a hundred years ago with corresponding recent information and discusses the causes and significance of the changes measured. Columbia's Gateway is a two-volume set of which the first volume is a cultural history of the estuary to 1920 in narrative form with accompanying photographs. The second volume is an unbound, boxed set of maps including 39 reproductions of maps originally published between 1792 and 1915 and six original maps illustrating aspects of the estuary's cultural history.

A two-volume Literature Survey of the Columbia River Estuary (1980) is also available. Organized according to the same categories as the work units, Volume I provides a summary overview of the literature available before CREDDP while Volume II is a complete annotated bibliography.

All of these materials are described more completely in Abstracts of Major CREDDP Publications. This document serves as a quick reference for determining whether and where any particular kind of information can be located among the program's publications and archives. In addition to the abstracts, it includes an annotated bibliography of all annual and interim CREDDP reports, certain CREST documents and maps, and other related materials.

To order any of the above documents or to obtain further information about CREDDP, its publications or its archives, write to CREST, P.O. Box 175, Astoria, Oregon 97103, or call (503) 325-0435.

FOREWORD

This contract was initiated under the Pacific Northwest River Basins Commission (PNRBC) as a cooperative venture between Science Applications Inc. (SAI), Boulder, Colorado and Woodward-Clyde Consultants (WCC), San Diego, California. Contract Manager Edward A. Wolf (SAI) provided field assistants and laboratory facilities in Astoria, Oregon. Principal Investigator Keith B. Macdonald and Project Manager Ted P. Winfield (both WCC) provided technical leadership for the program, overseeing field research and performing the data analysis and interpretation. Woodward-Clyde assumed management of the contract when it was resumed under the Columbia River Estuary Study Taskforce (CREST).

Numerous individuals contributed to the successful completion of this project. We thank them all, and are especially grateful for the following contributions:

David P. Anderson, initially hired by SAI and subsequently as an independent consultant, deserves special credit as the critical link in our Astoria research team. He hired and supervised an excellent group of clip-quadrat field assistants from Clatsop Community College, performed the laboratory analyses, collected the August 1981 species cover data, and acted as boat handler and field surveyor.

Early discussions with Harold V. Kibby (U.S. Environmental Protection Agency, Corvallis Environmental Research Laboratory) and John L. Gallagher (University of Delaware, Lewes) contributed to our initial field program sampling design and procedures. James Von Loh (WCC) and Duncan W. Thomas (Missouri Botanical Garden, St. Louis) confirmed our tentative marsh plant taxonomic identifications. Donald M. LaVigne (consultant, San Diego) and David Guggenhiem (EcoAnalysis, Ojai, CA) assisted in the design and execution of our data analysis program. David McIntire (Oregon State University, Corvallis) generously performed divisive clustering and canonical discriminant analysis on our species distribution data, and together with Larry Small (Oregon State University) provided the conceptualization of estuary-wide primary production processes.

U.S. Army Corps of Engineers Astoria staff worked with David Anderson and Duncan Thomas to measure our marsh sample location elevations relative to local tide levels.

Jack Damron, David Fox, David McIntire, Duncan Thomas, Joy Zedler (San Diego State University), and one anonymous reviewer, each contributed to discussions of our results and provided very helpful comments on preliminary drafts of this Final Report.

Margaret Cavallin and Cynthia Heyman (both WCC) drafted the text figures and Robert Collins (Tonga WordPro, San Diego) prepared the draft and final manuscripts.

Completion of both the computer data analysis and this Final Report, were made possible through additional funding provided by Woodward-Clyde Consultants, Environmental Systems Division and Keith B. Macdonald & Associates, Inc., San Diego.

In conclusion, we particularly appreciate the patience and persistence of Program Manager Jack Damron and Technical Representative David S. Fox whose steady leadership contributed very significantly to the successful completion of this Work Unit and Final Report. Thank You!

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EXECUTIVE SUMMARY

The Emergent Plant Primary Production Work Unit of the Columbia River Estuary Data Development Program (CREDDP) describes the species composition, standing crop, and primary production dynamics of the tidal marsh vegetation found within the estuary.

An estuary-wide field reconnaissance conducted in October 1979 confirmed the floristic diversity of Columbia River Estuary tidal marshes and suggested that their species composition reflected: salinity changes from the marine estuary mouth to freshwater conditions upstream, and low marsh to high marsh elevation changes. Twenty-two broadly representative tidal marsh study sites located to examine these two environmental gradients were subsequently selected for intensive study.

Percent species cover and aboveground biomass data sets, collected from the 22 tidal marsh study sites in both July 1980 and August 1981, yielded 67 different plant species. An additional 15 species were collected nearby but did not occur within the sample quadrats. Despite this diversity, the great majority of plant cover and biomass within the marshes was accounted for by only 20 of the total 82 species recorded. Lyngby's sedge (Carex lyngbyei) was by far the most abundant and widespread species throughout the marshes.

The species percent cover data were examined using both divisive clustering combined with cannonical discriminant analysis, and agglomerative cluster analysis. Both procedures yielded results in good agreement with the subjective four-fold subdivision of estuary marsh types developed from our field reconnaissance. The four major tidal marsh types are each characterized by distinctive groups of species and relative abundance patterns, as described in Section 3.1.2 of the Final Report.

Brackish low marshes (567 hectares/1,400 acres) fringe much of the shoreline of Baker, Trestle and Young's Bay. Brackish high marsh (316 hectares/780 acres) is also best developed in Trestle and Young's Bays. Freshwater tidal marshes extend upriver from Tongue Point (RM-18). Low marsh habitats (2,268 hectares/5,600 acres) are widespread throughout the islands of Cathlamet Bay, fringe much of Gray's Bay, and occur on the downstream portions of Tronson, Quinns, Grassy, and Fitzpatrick Islands, near Aldrich Point (RM-30). Freshwater high marshes (576 hectares/1,400 acres) are present along the eastern shores of Gray's Bay and are more broadly developed across portions of Marsh, Horseshoe and Welsh Islands. (Additional wetland habitats within the estuary include brackish shrub swamp (53 hectares) and freshwater shrub/ forested swamp (2,357 hectares) that were excluded from this study.)

Seasonal patterns of net aboveground marsh plant standing crop were established from replicate clip-quadrats harvested at each study site during April, May, June, July and October 1980, and August 1981. Biomass data for live shoots, attached standing dead material, and unattached plant litter, were treated separately. Mean net aboveground total (live plus standing dead) standing crop values, measured near the peak of the 1980 growing season, indicated no statistically significant ($p>0.05$) differences among the four tidal marsh categories. The overall mean value (± standard error) for all marsh sites was 864 ± 41 g dry wt/m^2. Comparable data collected near the 1981 growth season peak indicated that standing crop values from the freshwater low marshes were significantly ($p<0.01$) lower than those from the other three marsh groups; the overall mean was 892 ± 43 g dry wt/m^2.

An estuary-wide overview of seasonal biomass changes was obtained by averaging all tidal marsh standing crop samples on a month-to-month basis. Mean net aboveground live standing crop (± standard error) was at its lowest in April (112 ± 22 g dry wt/m^2), climbed rapidly through the end of June (735 ± 95 g dry wt/m^2), and held steady through August. By mid-October however, estuary-wide marsh biomass had declined substantially again (257 ± 34 g dry wt/m^2). Attached standing dead plant material was virtually absent in April (12 ± 5 g dry wt/m^2) but showed a steady increase through mid-October (205 ± 32 g dr wt/m^2). Detached plant litter showed little variation from month-to-month. The highest mean value was recorded in April 1980 (223 ± 69 g dry wt/m^2). Except for the April 1980 sampling period when marsh plant growth was just getting underway, these litter values represented only a small portion of the aboveground total (live and attached dead) marsh plant biomass.

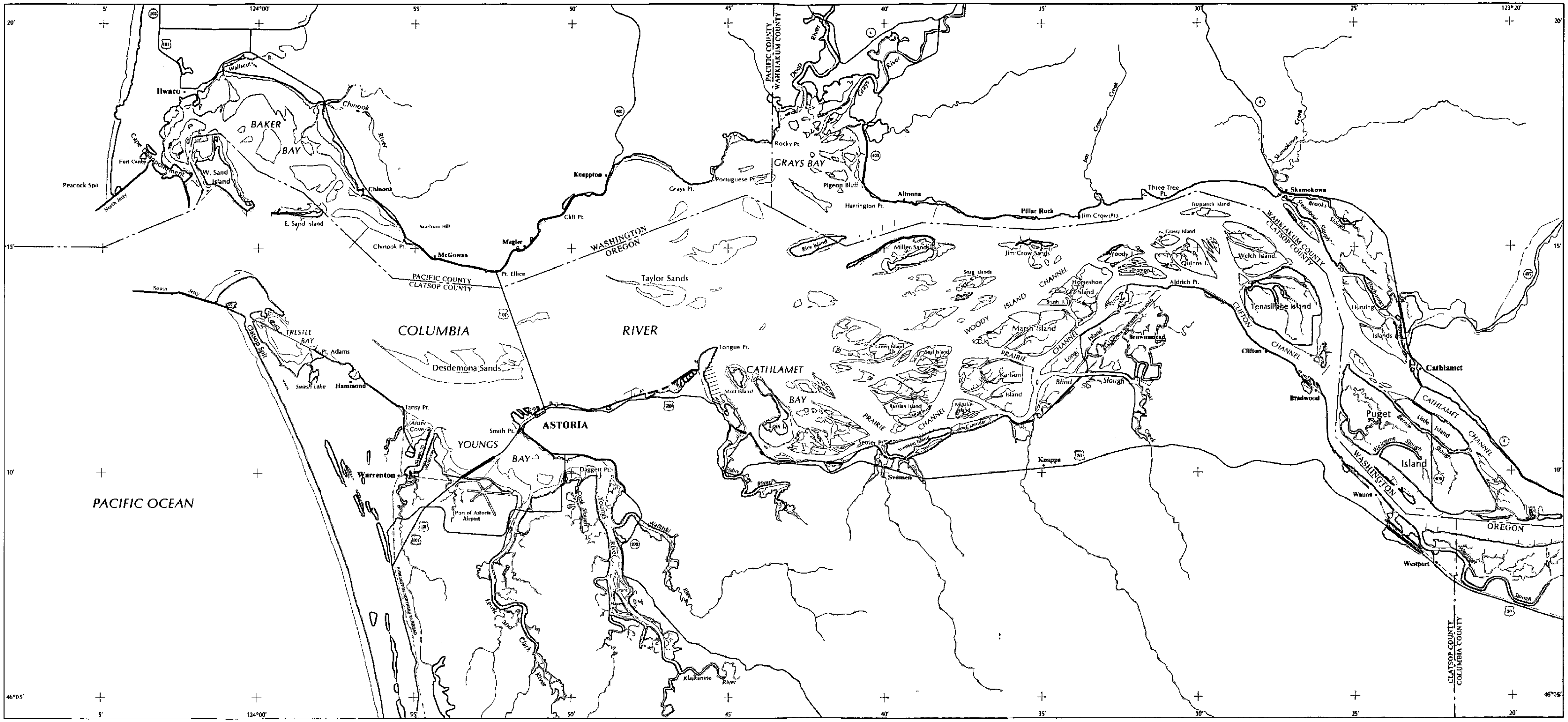
Net belowground live root biomass data were collected from replicate soil cores taken at each study site in April, June, July and October 1980. Live root biomass was always substantially higher than the aboveground live biomass, and seasonal patterns of root biomass abundance were the opposite of aboveground biomass trends. Root biomass was highest in April (20 times greater than aboveground biomass), lowest at the end of June (less than double aboveground biomass values), and was on an uptrend again in July and October. The reciprocal relationship in above and belowground biomass supports the concept that late in the growing season some perennial species (Carex lyngbyei, for example) translocate biomass and nutrients from aerial shoots to overwintering root systems. Subsequently this stored material supports and accelerates the spring burst of growth typical of many marsh plants in cooler latitudes.

Net annual aboveground primary production estimates for each marsh site were calculated from the 1980 sequential standing crop harvests using the Smalley Method. Values ranged from a low of 364 g dry wt/m^2/year at Lois Island freshwater low marsh, to a high of 1,730 g dry wt/m^2/yr for brackish low marsh Carex stands at East Trestle Bay. When production estimates were sorted among the four major tidal marsh types and pooled, no statistically significant ($p>0.05$) differences were found. This suggests that all marsh types are equally productive, with an overall mean estimated net annual aboveground production value (± standard error) of 964 ± 100 g dry wt/m^2/yr.

The general absence of statistically significant differences among biomass measurements and primary production estimates from the four marsh types may be real. It could also reflect sampling problems associated with high within- and between-marsh variability. Among five indirect environmental variables tested, surface salinity regimes yielded the most significant regressions against estimated net annual aboveground primary production values from the different tidal marshes; site elevation was also important. While the relationships are clearly not simple ones, tidal marsh net aboveground primary production does exhibit significant trends -- increasing both upriver from the estuary mouth and at higher intertidal elevations.

Decomposition and loss rates of plant material from the marsh surface were measured during three litter bag experiments (initiated in May, July, and October 1980, respectively) designed to measure loss rates for different plant types, marsh elevations, and estuary locations. The overall results of the experiments suggest marsh elevation has no significant effect ($p>0.05$) upon decomposition rates. Some significant differences ($p<0.05$) were noted among decomposition rates for different plant types, more succulent species decomposing faster than more fiberous species at the same location. The most striking difference however, was that marsh plants at upriver freshwater sites decomposed substantially faster and more completely, than the same species at brackish water sites nearer the estuary mouth.

Net tidal marsh production represents a dynamic balance among several ongoing processes that account for the difference between true total, or "gross" production and the residual "net" production estimated here (964 g dry wt/m^2/year, aboveground). Some of these processes have been tentatively quantified as follows: leaching of dissolved organic matter from live plants, 200 g dry wt/m^2/yr; utilization by herbivores (nutria, muskrat, and beaver), 145 g dry wt/m^2/yr; translocation to plant roots in the fall 370 g dry wt/m^2/yr; and minimum detrital export, 460 g dry wt/m^2/yr.



Columbia River Estuary

Scale 1:160,000

0 1 2 3 4 5 6 7 8 9 10 Kilometers

0 1 2 3 4 5 6 Miles

Map produced in 1983 by Northwest Cartography, Inc.
for the Columbia River Estuary Data Development Program

- Shoreline (limit of non-aquatic vegetation)
- Intertidal vegetation
- Shoals and flats
- Lakes, rivers, other non-tidal water features
- Major highways
- Cities, towns
- Railroads
- Other cultural features

The Columbia River Estuary

1. INTRODUCTION

This report summarizes the final results of the Emergent Plant Primary Production Work Unit of the Columbia River Estuary Data Development Program (CREDDP). Research was initiated in September 1979. When the Pacific Northwest River Basins Commission (PNRBC) was abolished by the federal government in September 1981, a literature review had been completed (CREDDP 1980), field and laboratory procedures had been established, and marsh vegetation samples from 1980 and 1981 growth seasons had been collected and quick-frozen. Laboratory analysis was about half completed by September 1981; and some preliminary results had been presented earlier in the year (SAI/WCC 1981). When research resumed under the Columbia River Estuary Study Taskforce (CREST) in November 1982, laboratory work was completed and data analysis and report preparation begun.

The report describes the species composition, standing crop, and production dynamics of the extensive areas of tidal marsh vegetation that fringe the shores of the Columbia River Estuary and form many of its islands. The role of marsh production is discussed within a conceptual framework of the entire estuarine ecosystem. For additional information concerning these broader relationships, the reader may refer to the CREDDP integration report entitled The Dynamics of the Columbia River Estuarine Ecosystem (Simenstad et al., 1984).

1.1 PREVIOUS STUDIES

The Columbia River Estuary is one of only four major estuaries along the entire Pacific Coast of North America receiving sufficient freshwater outflow to maintain extensive areas of both brackish (marine-estuarine) and freshwater tidal marshes. San Francisco Bay-San Joaquin Delta (Atwater et al. 1979) on the central California Coast to the south, Fraser River Delta at the Canadian Border (Forbes 1972, Kistritz et al. 1983), and Cook Inlet, Alaska (Macdonald et al. 1979), are the other three examples. Prior to initiation of the research reported here, and concurrent CREST studies by Dr. Duncan W. Thomas (Thomas 1980a, 1980b, 1983, In Press), Columbia River Estuary tidal marshes were the least known of these four examples.

The earliest accurate information on Columbia River Estuary tidal marshes comes from U.S. Coast Survey Charts of the estuary made between 1870 and 1878 (Thomas 1983). It was a century later however, before Franklin and Dyrness (1973) provided the first brief floristic descriptions of the Columbia's marshes and swamps. Jefferson (1974) was perhaps the first to realize the impact of the immense freshwater flows on the marshes (Thomas, In Press). She described *Carex lyngbyei* - *Scirpus validus* and *Scirpus validus* assemblages from the estuary, and noted the absence of salt marsh species common in other Oregon coastal marshes, even at the mouth of the river.

James Tabor (Oregon Cooperative Wildlife Research Unit 1976) provided a much more complete description of the tidal marshes, including a species list (recently modified by Thomas 1980a, 1980b) and quantitative vegetation transect studies for six sites within the estuary. James W. Good summarized and integrated Tabor's work with other available marsh data in the Columbia River Estuary Inventory (CREST 1977).

The only additional tidal marsh studies conducted within the estuary prior to September 1979 all related to the U.S. Army Corps of Engineers, Dredge Material Research Program, marsh reestablishment project at Miller Sands (WCC 1976, Clairain et al. 1978, Heilman et al. 1978, Greer and Heilman 1978, McVay et al. 1978). Different aspects of natural and propagated marsh vegetation are discussed, including, aboveground peak biomass, (recent spoil areas, 54 grams dry weight/m^2; longer established natural marsh, 674 g dry wt/m^2), primary production, and fertilizer treatment experiments.

1.2 PROJECT OBJECTIVES

Tidal marshes -- characterized by high levels of primary plant production and providing essential breeding, rearing and feeding grounds for many species of fish and wildlife -- are already widely recognized as critical national resource areas. Seasonal changes in the tidal marshes of the Columbia River Estuary are particularly striking and emphasize their potential contribution to overall estuary ecosystem function.

In the late summer, at the height of the growing season, the tidal marsh fringes and islands of the estuary provide a vista of thousands of hectares of dense herbaceous vegetation often a meter or more tall. By year-end or early winter however, almost bare flats replace these marsh vistas and only a stubble of dead plant stems hints at earlier production. A major portion of the season's growth of marsh sedges, grasses and herbs is thus contributed to the estuary. Whether this material is utilized within the estuarine aquatic system, or perhaps is flushed out to the marine continental shelf beyond, remains unknown.

With this potential contribution to the estuary in mind, the TIDAL MARSH PLANT PRODUCTION Work Unit was designed to:

1. Determine the species composition and aerial extent of emergent tidal marshes in the Columbia River Estuary;

2. Determine seasonal changes in the abundance and distribution of tidal marsh plant biomass (grams dry weight/m^2) throughout the estuary and from these data estimate and map net annual plant production rates (g dry wt/m^2/year);

3. Determine marsh plant decomposition rates (percent dry weight plant material lost/time) and thus indirectly estimate the potential carbon contribution from the marshes to the estuary ecosystem.

While specific program objectives emphasized descriptive data, the broader CREDDP goal of developing an integrated, conceptual ecosystem process model was addressed by testing biological distributions (e.g. primary production, plant decomposition rates) against documented environmental gradients (e.g. tidal range, salinity). More specific pathways for carbon transfer between the tidal marshes and the estuary (e.g. wetland herbivory, dissolved organic matter) were also identified.

1.3 CONCEPTUAL FRAMEWORK OF RESEARCH

A large ecosystem study program such as CREDDP requires some integrating structure to assure that the various component projects remain adequately focused on total project goals. The general ecosystem modeling paradigm used in the CREDDP integration report is therefore briefly quoted here (taken from McIntire and Amspoker 1984), to provide a conceptual framework for the Tidal Marsh Primary Production Work Unit.

"A hierarchial model of an estuarine ecosystem from a biological perspective is illustrated in Figure 1. Estuarine Biological Processes can be investigated as a system with two coupled subsystems: Primary Food Processes and Consumption. The Primary Food Processes subsystem represents the dynamics of variables associated with the accumulation and degradation of plant biomass and detritus, while the consumption subsystem is concerned with the dynamics of macrofauna as they function as consumers of living plant biomass and detritus. The subsystems within Primary Food Processes are Primary Production, which represents the production dynamics of autotrophic organisms, and Detrital Decomposition, a process that is concerned with the breakdown of dead organic material. The process of Consumption is partitioned mechanistically into four coupled subsystems: Deposit Feeding, Suspension Feeding, Wetland Herbivory, and Predation. Structural details of these subsystems are described in The Dynamics of the Columbia River Estuarine Ecosystem (Simenstad et al., 1984)."

"The target subsystem for the research presented in this report was Primary Production (Figure 2). The process of primary production generates inputs of light energy and nutrients and outputs of dissolved organic matter and respiratory products, variables represented by arrows to or from the perimeter of the circle. In addition, the process is also influenced by physical variables and processes (e.g., sediment properties, temperature and hydrologic factors) which are indicated collectively by the dotted ellipse. The Primary Production subsystem has three state variables, the biomasses of benthic algae, phytoplankton, and vascular plants. Inputs and outputs acting directly on the state variables include consumption by macroconsumers, transfer to a detrital state variable after natural mortality, and imports and exports into and out of the spatial area under consideration (McIntire and Amspoker 1984)."

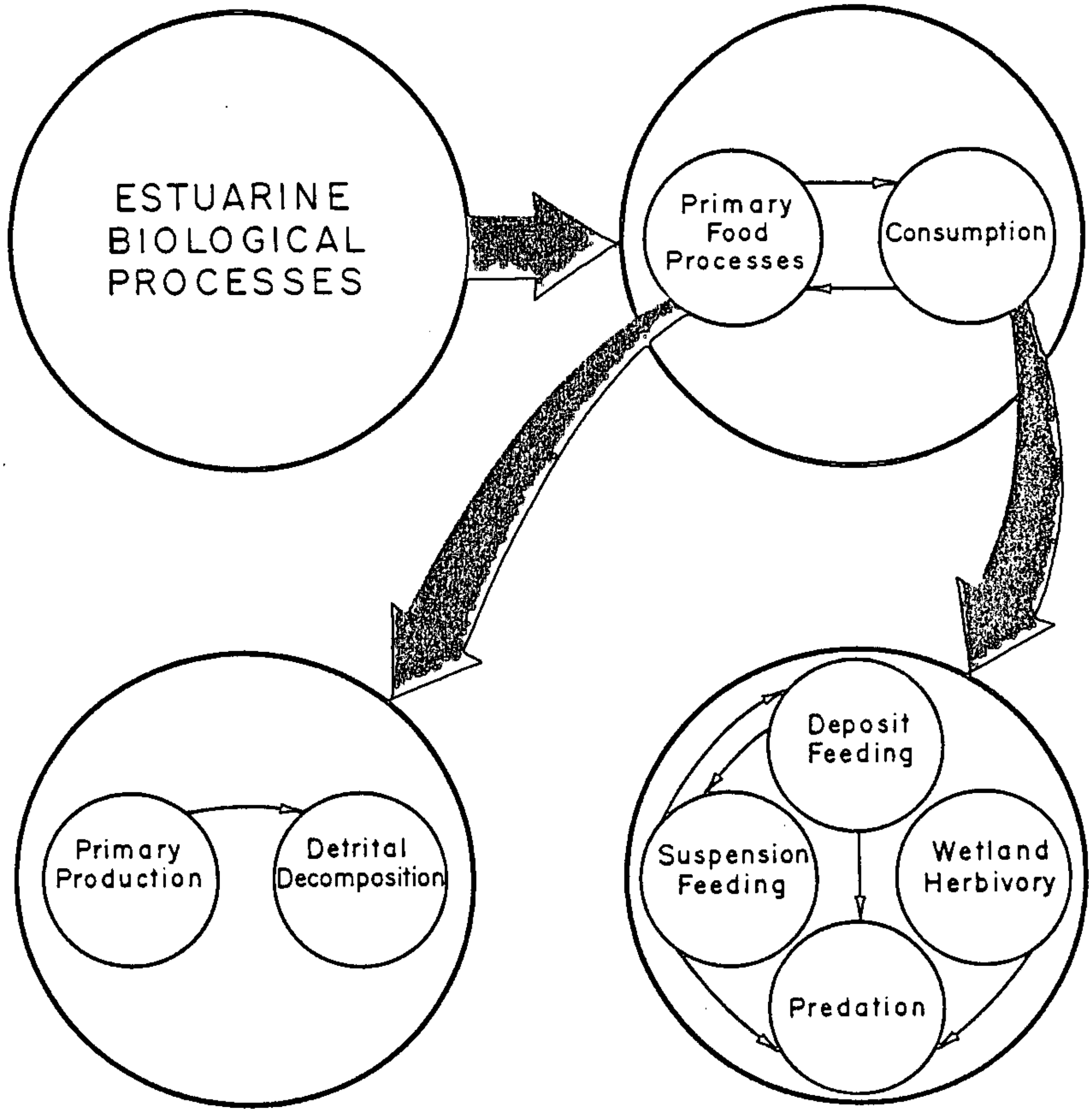


Figure 1. Systems Diagram of Estuarine Biological Processes and Associated Subsystem (McIntire and Amspoker 1984).

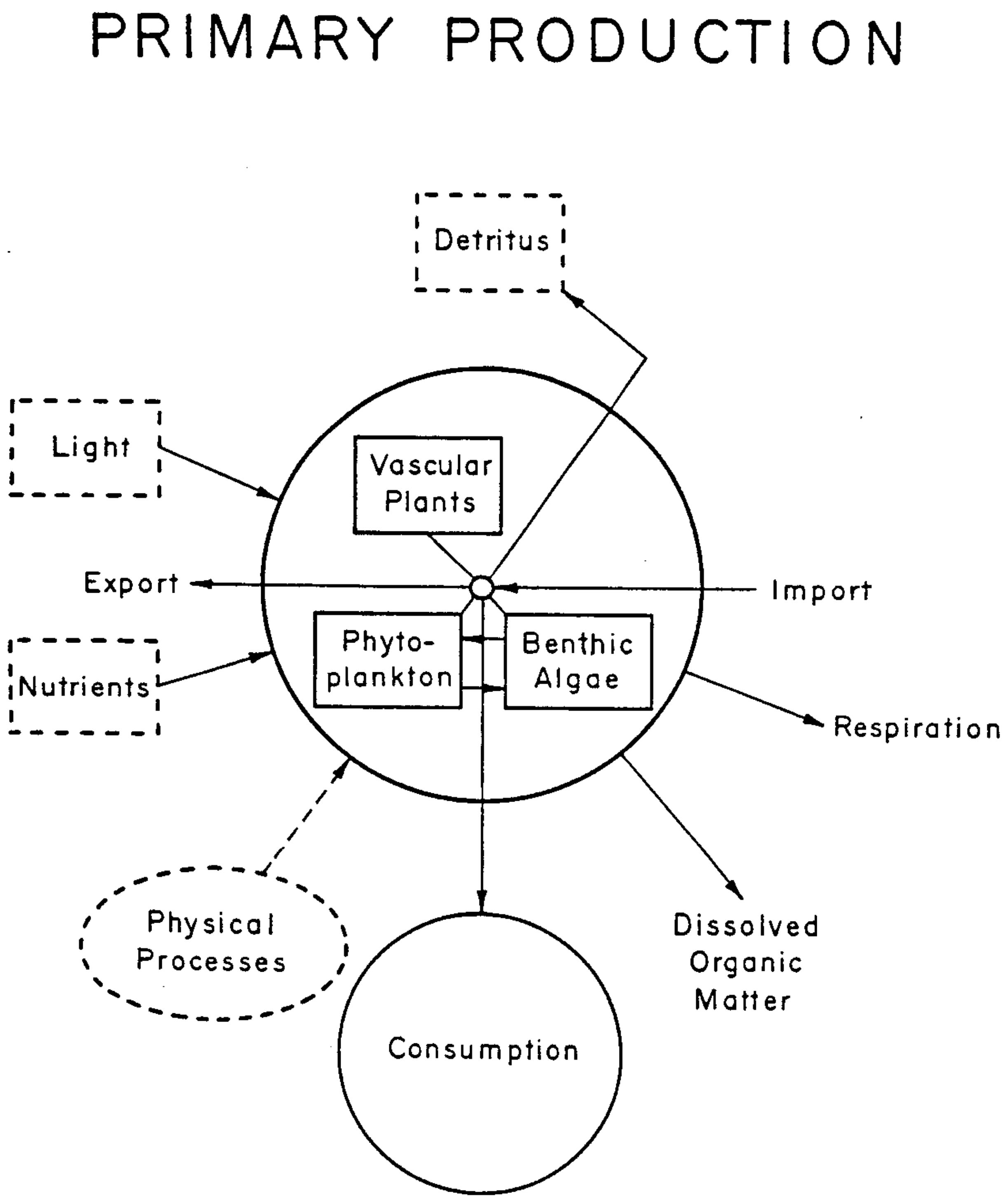


Figure 2. Systems Diagram Illustrating the Primary Production Subsystem and Associated State Variables with Relevant Inputs and Outputs (McIntire and Amspoker 1984).

Emergent vascular hydrophytes are the dominant functional group of autotrophs in the tidal marshes of the Columbia River Estuary. Submergent vascular hydrophytes (aquatic plants) and benthic macroalgae were only occasionally present.

This report deals almost exclusively with the dynamics of emergent vascular hydrophytes -- the tidal marsh plants. Research concerning phytoplankton, and benthic algae and submergent vascular hydrophytes is described in the Water Column Primary Production (Frey et al. 1984) and Benthic Primary Production (McIntire and Amspoker, 1984) Work Units, respectively.

2. METHODS AND MATERIALS

All field sampling, experimental and laboratory techniques used throughout the program, as well as all statistical methods and multivariate analyses used during data interpretation, are widely used, well documented, standard procedures. The methodological descriptions that follow have therefore been kept to a minimum.

2.1 SAMPLING STRATEGY

The CREDDP study area extends from the mouth of the Columbia River Estuary, 49 river miles upstream to the eastern end of Puget Island (RM 49). This region encompasses approximately 150 square miles (almost 389km^2). Photo interpretation and mapping studies, completed since the initiation of the Tidal Marsh Plant Production Work Unit in September 1979 (Thomas 1980a, Northwest Cartography, Inc. 1983), indicate that tidal marsh and swamp habitats occupy almost 22.8 square miles (59km^2), more than 15 percent of the CREDDP study area.

Review of previously published studies (see Section 1.1) and an estuary-wide field reconnaissance conducted in October 1979, provided the basis for development of a tidal marsh sampling strategy. The distribution of broadly representative marsh vegetation types appeared to reflect two principal physical gradients: (1) a change in salinity from more marine or brackish conditions near the estuary mouth to clearly freshwater conditions further upstream, and (2) changes that accompanied increasing intertidal elevation as one moved from low marsh to high marsh habitats at any specific location. The field reconnaissance also confirmed the tremendous floristic diversity of Columbia River Estuary marshes. Not only were species assemblages much richer than those of the more typical 'coastal salt marshes' described from other Oregon and Washington estuaries (Jefferson 1974), they also varied significantly among the individual bay systems (e.g. Baker Bay, Gray's Bay, etc.) tributary to the main estuary.

Based on the above considerations, 15 localities dispersed around the estuary were selected as representative of the more common tidal marsh vegetation types present. Numbers of high and low marsh sites were chosen in approximate proportion to the estimated relative areas of these habitats within upstream and downstream portions of the estuary. Since no elevation data were available at the start of the program, individual sites were subjectively judged to be high or low marsh on the basis of previous general descriptions of species assemblages (CREST 1977).

Subdivision of marsh vegetation types at some localities resulted in a total of 22 study sites being selected for intensive investigation. Subsequent CREDDP research has confirmed that the study sites chosen are broadly representative of tidal marsh types developed under the different physical environmental regimes represented within the estuary.

Once selected, each of the 22 intensive study sites was permanently staked for identification. With the exception of the Puget Island site which was sampled only once in July 1980, all study sites were subsequently quantitatively sampled during April through October 1980, and again in August 1981. Quantitative sampling included investigation of species composition of the marsh vegetation and aboveground-belowground net standing crop measurements. Three litterbag experiments were used to determine marsh plant decomposition rates at selected localities.

In the final year of the program, published environmental data that might indirectly reflect physical variables controlling species composition and primary production of the marshes were reviewed and tabulated. A joint U.S. Army Corps of Engineers-CREDDP team also conducted an elevation survey, measuring the height of each sample site marker stake relative to mean lower low water (MLLW) tidal datum, or its equivalent.

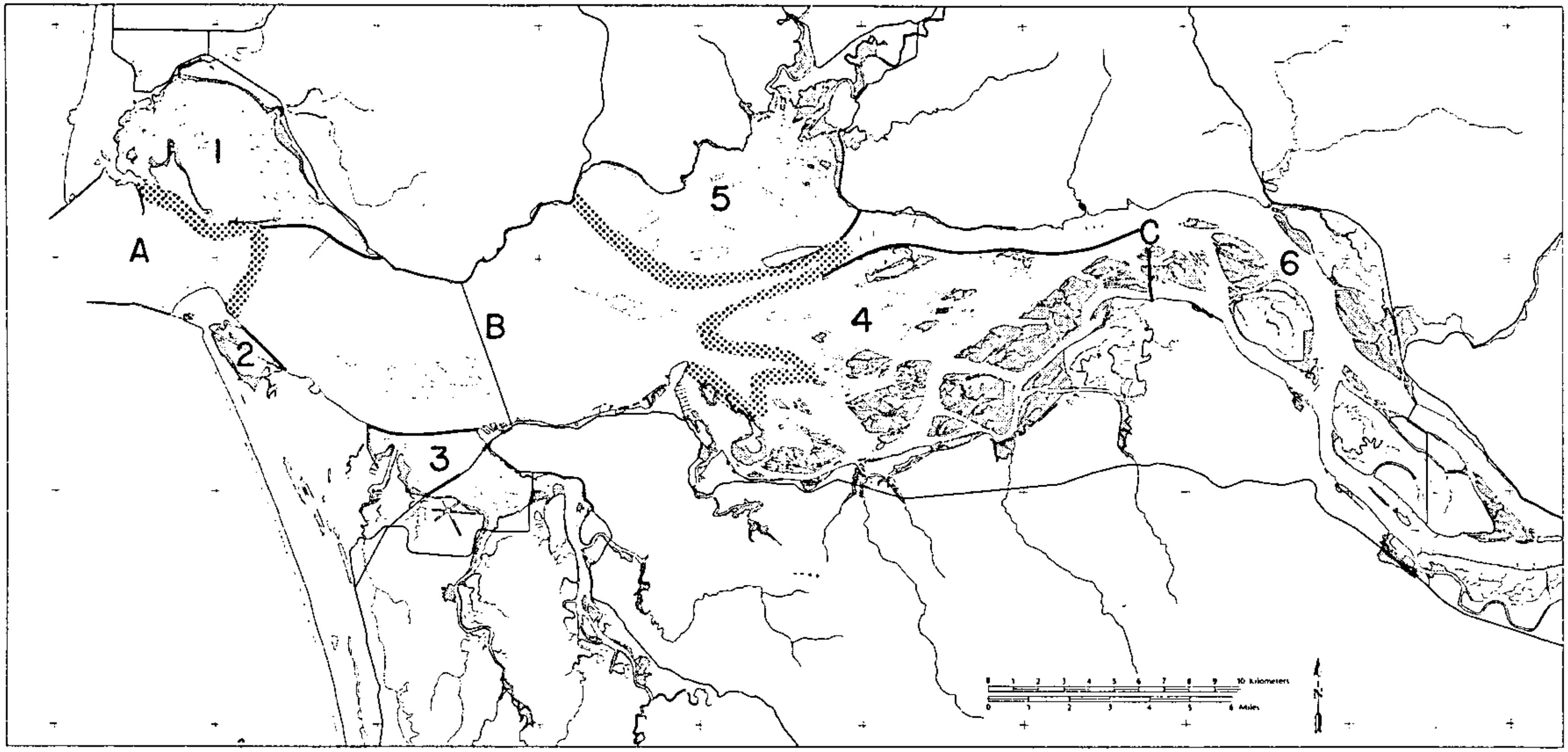
Columbia River Estuary salinity zone boundaries defined by CREDDP research are shown in Figure 3, along with the estuary marsh regions chosen for study. The quantitative distribution of tidal marsh and swamp habitat types (based on Thomas' [1980a] aerial-photo mapping, redrawn and planimetered by Northwest Cartography, Inc.) among the estuary marsh regions is summarized in Table 1. The 15 low and high elevation (as originally subjectively defined) tidal marsh localities chosen for intensive study are shown in Figure 4, and CREDDP coordinates for every study site are listed in Table 2.

2.2. PLANT COVER AND SPECIES COMPOSITION

Quantitative species composition data were collected from each study site at the approximate peak of two successive growing seasons, in late July 1980 and again in early August 1981. Twenty-one sites were sampled both times; the *Typha* high marsh at the eastern tip of Puget Island was sampled only once in July 1980.

2.2.1 Randomization Procedure

Replicate quadrat samples for species percent cover data and biomass data were always located using the following randomization procedure: At each tidal marsh study site the permanent marker stake was set within a broad, prescribed area of visually uniform marsh vegetation. Temporary, flagged stakes were used to mark north-south and east-west axes centered on the permanent marker stake. Random number tables were then used to select both the compass quadrant to be sampled, and paced coordinates within the quadrant for specific sample quadrat locations. The same prescribed area of vegetation was sampled during each successive sampling period, however previously sampled quadrats were never reoccupied. As a result of the randomization procedure, the data collected can be considered statistically, "as representative" of actual species distributions or biomass values, as any other set of samples that might have been collected within the same prescribed area of marsh vegetation.



Salinity Zone Boundaries:

A. Ocean Zone

B. Estuarine Mixing Zone
(Brackish Water)

C. Tidal Fluvial Zone
(Freshwater)

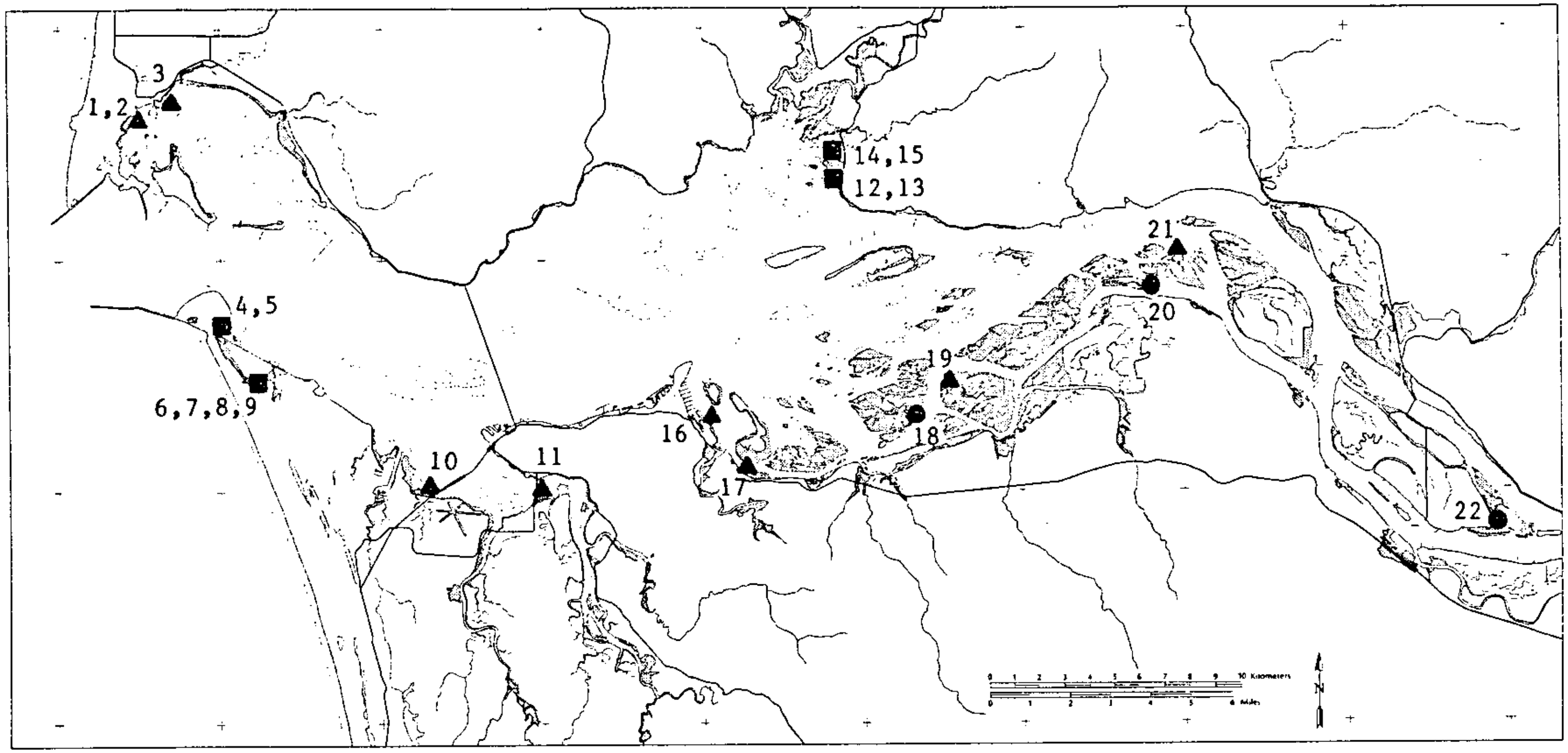
Estuary Marsh Study Regions:

1. Baker Bay
2. Trestle Bay
3. Young's Bay
4. Cathlamet Bay
5. Gray's Bay
6. Fluvial Zone

Figure 3. Columbia River Estuary: Salinity Zone Boundaries and Estuary Marsh Study Regions. (Tidal marsh and swamp habitats shaded.)

Table 1. Quantitative Distribution of Columbia River Estuary Tidal Wetland Types: Areas in Hectares (Acres). (See Figure 3 for study region locations.)

Salinity Regime	Tidal Wetland Type		
Study Region	Low Marsh	High Marsh	Swamp
Brackish Water Habitats			
Baker Bay	219 (541)	21 (51)	19 (47)
Trestle Bay	66 (164)	58 (144)	2 (4.5)
Youngs Bay	285 (704)	135 (333)	50 (124)
Other	<3 (4)	>1 (3)	<1 (1)
Freshwater Habitats			
Cathlamet Bay	1,832 (4,525)	279 (689)	1,762 (4,352)
Grays Bay	276 (682)	31 (76)	268 (663)
Fluvial Zone	174 (431)	115 (285)	334 (825)
Estuary-wide Totals	2,855 (7,051)	640 (1,582)	2,436 (6,017)



▲ Tidal Low Marsh Study Site ● Tidal High Marsh Study Site ■ Low & High Marsh Study Sites

Figure 4. Sampling Sites for the Investigation of Tidal Marsh Plant Production in the Columbia River Estuary.

Table 2. CREDDP Coordinates for each Study Site in the Columbia River Estuary Marsh Plant Production Work Unit.

Study Site	CREDDP Coordinates
Baker Bay:	
1. Baker Bay-China Cove, *Carex* Low Marsh	4-2.7 - 18.1
2. Baker Bay-China Cove, *Scirpus* Low Marsh	4-2.6 - 18.1
3. Baker Bay-Ilwaco, Low Marsh	4-1.8 - 18.2
Trestle Bay:	
4. West Trestle Bay, Low Marsh	3-59.5 - 13.4
5. West Trestle Bay, High Marsh	3-59.8 - 13.4
6. East Trestle Bay, *Carex* Low Marsh	3-59.1 - 12.6
7. East Trestle Bay, Low Marsh	3-59.1 - 12.6
8. East Trestle Bay, Middle Marsh	3-59.1 - 12.5
9. East Trestle Bay, High Marsh	3-59.1 - 12.5
Young's Bay:	
10. Young's Bay-Outer, Low Marsh	3-53.1 - 10.1
11. Young's Bay-Inner, Low Marsh	3-50.1 - 9.9
Gray's Bay:	
12. Gray's Bay-Outer, Low Marsh	3-41.0 - 16.7
13. Gray's Bay-Outer, High Marsh	3-40.8 - 16.7
14. Gray's Bay-Inner, Low Marsh	3-40.9 - 17.2
15. Gray's Bay-Inner, High Marsh	3-40.8 - 17.2
Cathlamet Bay:	
16. Army Corps Dock, Low Marsh	3-44.7 - 11.3
17. Lois Island, Low Marsh	3-42.1 - 10.5
18. Russian Island, High Marsh	3-38.3 - 11.8
19. Karlson Island, Low Marsh	3-37.4 - 12.5
20. Tronson Island, High Marsh	3-31.6 - 14.4
Fluvial Zone:	
21. Quinns Island, Low Marsh	3-30.2 - 15.1
22. Puget Island, *Typha* High Marsh	3-20.4 - 9.5

2.2.2 Percent Cover Data

Plant cover data were recorded and averaged from five replicate $0.5m^2$ quadrats randomly placed at each intensive study site. The abundance of each species, as a percentage of total quadrat area, was recorded within ten-percent cover classes (i.e. Class 1 - one to ten percent, Class 2 - from 11 to 20 percent, etc.). Since the marsh vegetation was often multilayered, with a shorter groundcover growing beneath a taller marsh plant canopy, total cover recorded as described frequently exceeded 100 percent (range: 46 to 144 percent of quadrat area). The mid-value of each ten percent cover increment (i.e. interval 1 to 10% used 5 as a value, interval 11 to 20% used 15 as a value, etc.), averaged over all five quadrats examined at each site, was subsequently used to estimate the mean cover by each species at each study site. For inter-site comparisons, total cover data (i.e. absolute cover) were converted to relative abundance values by normalizing each study site plant cover total to 100 percent (i.e. percent cover data).

2.2.3 Percent Live Biomass

The species composition of the marsh vegetation was also quantified by weighing (as dry weights) individual species contributions to the total net aboveground live standing crop. At each study site, nine randomly placed replicate $0.1m^2$ clip-quadrats were harvested to ground level; the live material was sorted by species and oven dried at approximately 93°C to a constant weight. The resulting dry weights, averaged over the nine replicates, were used to derive percent live biomass species composition data.

2.2.4 Plant Taxonomy

Preliminary species identifications were made in the field and voucher specimens returned to the laboratory for confirmation. Plant taxonomist James Von Loh, of Woodward-Clyde Consultants, San Diego, California, confirmed much of the initial material. In the summer of 1980, Dr. Duncan W. Thomas established an herbarium of Columbia River Estuary wetland plants at the CREST office in Astoria, Oregon. All of our material was subsequently checked against the herbarium specimens with the assistance of both Thomas and David Anderson.

The plant names used in this report follow Hitchcock and Cronquist (1973) as far as possible, as does Thomas' herbarium material (Thomas 1980a, 1980b, In Press). Some common names were taken from Peck (1961).

2.3 STANDING CROP MEASUREMENTS

2.3.1 Net Aboveground Standing Crop

Net aboveground standing crop data for emergent tidal marsh vegetation were collected April 14-18, May 28-31, June 29-July 1, July 29-31, and October 9-13, 1980, and again in early August 1981. Nine randomly placed 0.1m² clip-quadrats were harvested at each study site during each sampling period. The same quadrat location randomization procedure was used as described above in 2.2.1. All live vegetation and attached standing dead material (attached to a living shoot and of the same years growth) within each quadrat, was clipped at ground level and bagged. Loose dead plant material (litter) from each quadrat was collected and bagged separately. All material was quick-frozen and stored until processed.

In the laboratory, the frozen live and attached dead plant samples were thawed, gently washed to remove sediment, including volcanic ash, and sorted into live and dead material by species. The sorted sub-samples were each placed in weighed, predried and labelled paperbags and oven dried at approximately 93°C to a constant weight. This was checked by repeatedly redrying for two hour intervals. When additional redrying failed to change the weight by one-percent or more, a constant weight had been achieved. The oven dried material was always allowed to cool to room temperature in a desiccator before weighing.

Litter samples were thawed, washed and dried to a constant weight in a similar manner, but the were not sorted by species.

All data were converted to a square-meter basis (i.e. grams dry weight/m^2). Means and standard deviations for each nine-replicate sample set were than calculated separately for live, attached dead, and litter components.

The possibility of systematic differences in species dry weights obtained from quick-frozen stored samples, rather than freshly harvested material, was tested using five fresh and five frozen, identical samples of *Carex lyngbyei* and *Potentilla pacifica*. In both cases t-tests confirmed there was no statistically significant ($p > 0.10$) difference between treatments.

2.3.2 Net Belowground Standing Crop

Net belowground standing crop data for live root material were obtained from two sediment cores (8 cm inside diameter, 20 cm long) collected within two of the randomly located clip-quadrats at each study site. Quick-frozen until processed, the root material was rinsed free of sediment over a series of fine mesh screens. Live root material, readily identified on the basis of firmness and color, was hand-picked and oven dried at 93°C to constant weight. Means and standard deviations were calculated for each root material sample-pair, and their means extrapolated to estimate live root material biomass on a per square-meter basis (i.e. grams dry weight live roots/m^2).

2.3.3 Wet Weight-Dry Weight-Ash Free Dry Weight Relationships

Marsh plant dry weights as a percentage of freshly harvested wet weights, were determined for a number of key species collected between May and October 1980, from five different estuary localities. Dry weight: wet weight ratios were also determined for mixed-species live root samples collected at 18 study sites throughout the estuary, in May 1980.

Ash-free dry weight (AFDW) determinations, as a percentage of dry weights, were made to investigate the relative abundance of organic matter among different biomass components (e.g. live aerial shoots, attached standing dead, litter, live roots) of several key species, at various location around the estuary and at different times of year.

The AFDW determinations typically utilized at least three replicate subsamples (range: n=2 to 10) of thoroughly mixed and finely ground marsh plant material from the dry weight measurements. The subsamples were again oven-dried for at least 2 hours at 93°C, cooled, and weighed. They were then ashed in a muffle-furnace at 500 to 550°C for at least an hour or until a constant weight was achieved. The remaining ash material was kept in a dessicator until cool and then weighed. The AFDW (i.e. organic matter content) was obtained by subtracting the final ash weight from the initial dry weight. Results are expressed as percentages of the dry weight. Laboratory tests indicated that experimental errors accounted for approximately ± one percent of the AFDW determinations, considerably less than the random variation of many samples.

2.4 PRIMARY PRODUCTION ESTIMATES

While several approaches are available to estimate tidal marsh net annual aboveground plant production, all of the methods used in this program rely on aboveground standing crop data-sets as input. Aboveground production is emphasized since this is the most likely source of marsh detritus and organic matter contributed to the broader estuary ecosystem.

2.4.1 Simple Harvest Methods

The simplest procedure for estimating net annual aboveground plant production is to harvest the end of growing season peak live standing crop. Among our data sets, values from June or July 1980 and August 1981 would represent such peak measurements. These net production estimates are usually increased somewhat when peak <u>total</u> standing crop measurements, including both live shoots and attached standing dead material of the same season's growth, are used.

While the majority of marsh vegetation disappears each winter, some species, most notably *Carex lyngbyei*, produce short "overwintering" shoots in the late summer or fall that remain dormant over the winter and then grow very rapidly as conditions improve again the following spring. Allowance for such plant biomass carried over from the previous year is made by the "maximum minus minimum" standing crop estimate of net annual production. For this project, net aboveground standing crop totals measured at each study site in April 1980 were used as an estimate of overwintering plant biomass, and subtracted from the comparable peak total values recorded the following June and July.

All three approaches described above usually underestimate true net production however, for they do not adequately allow for the mortality and disappearance of leaves and other plant parts during the growing season.

2.4.2 Smalley Method

The most widely used procedure to overcome the mortality and loss problem noted above is provided by the Smalley Method of net production estimation (Smalley 1958, Turner 1976, Reimold and Linthurst 1977) which takes into account incremental changes in both living and dead aboveground standing crop over successive sampling periods throughout the growing season. Production is computed as follows:

1. If there is an increase in standing crop of both live and attached dead material (between successive sampling periods), the net production is the sum of the increases.

2. If both live and attached dead standing crops decrease, then production is zero.

3. If live standing crop increases but attached dead standing crop declines, net production is equal to the increase in live material.

4. If the attached standing dead biomass increases but live biomass declines, they are added algebraically; if the result is negative, production is zero; if the result is positive, then the resulting value represents net production.

The sum of the resultant values obtained by applying the above assessment to successive sampling periods throughout the year provides the estimated net annual aboveground production (grams dry weight/m^2/-year).

2.4.3 Smalley Species Peak Method

The Smalley method described above is usually applied to sample site total biomass values irrespective of their species composition. Marsh plant growth is not synchronous however; some species achieve their peak abundances early in the growing season (Lysichitum americanum, for example) while others produce their greatest biomass as late as August (Aster subspicatus, for example). Carex lyngbyei, the most widespread species of the estuary tidal marshes, peaks in June.

As usually applied, the Smalley method averages out these seasonal growth differences among species. A higher estimate of net aboveground primary production is usually obtained when the Smalley calculation is performed separately on each species and the resulting net production values are summed. We have called this approach the "Smalley Species Peak" method.

2.5 LITTERBAG EXPERIMENTS

Standard litterbag techniques (Cruz 1973) were used to measure decomposition and loss rates of plant material from the marsh surface. Three successive litterbag experiments were initiated in May 1980, July 1980, and October 1980; each lasted for 33, 28, and 38 weeks, respectively. Each experiment was designed to measure loss rates for different plant types (grasses, herbs and reed-like species) at high and low tidal marsh elevations, in downriver brackish water and upriver freshwater estuary locations.

Known wet weights of freshly harvested plant material were sewn into ~$1mm^2$-mesh nylon litterbags and staked out on selected tidal marshes. Dry weight equivalents for the bagged material were estimated from wet weight: dry weight ratios determined on separate replicate samples of the same plants. At four- to 11-week intervals over the course of each experiment, three bags of each species were returned from each location to the laboratory. After each bag was gently rinsed to remove accumulated sediment, the plant material was taken out and oven dried at 80°C to a constant weight.

The resulting dry weights were averaged, for each species at each location, and plotted as percentages of the initial estimated dry weight of plant material still remaining after given numbers of weeks of the experiment. At the termination of each experiment, the total percentage dry weight loss was noted.

The results obtained during each separate experiment were tested for statistical significance (α=0.05) using analysis of covariance which tests for differences between slopes (i.e. plant material lost/time). Experiment dry weight values were transformed prior to testing, using a log transform [log (x+1)] to correct for non-linearity. Student-Newman-Kuels tests were subsequently used to identify which species-location pairs in each experiment exhibited significantly different (α=0.05) decomposition rate slopes.

2.6 ENVIRONMENTAL VARIABLES

Other than study site elevations, direct measurements of environmental variables were beyond the scope of the work unit. Instead published environmental data that might indirectly reflect important physical variables were examined and tabulated.

U.S. Army Corp of Engineers and CREDDP staff, using local benchmarks, water level elevations, and level-line surveys, measured the elevation (feet) of each tidal marsh sample site above mean lower low water, or its local equivalent (MLLW, or upstream of Altoona, Ordinary Low Water Columbia River Data, OLWCRD).

The shortest distance (km) between each study site and the midpoint of a line joining the rivermouth jetties, (measured at waterlevel and passing around headlands and islands) was used as a measure of "ocean influence". Such a measure might indirectly reflect upriver changes in tidal patterns, salinity regimes, freshwater influx, dissolved nutrient availability, etc.

The estimated mean diurnal tidal range (feet) at each study site, and mean surface water salinity values (ppt) -- under conditions of high river flow and low river flow -- at points projected from each study site onto the centerline of the estuary navigation channel, were all provided from the Columbia River Estuary Circulatory Processes Work Unit by Dr. David Jay (see also Jay 1984).

2.7 DATA ANALYSIS

2.7.1 Data Processing

Field and laboratory data sheets were carefully checked for completeness and correctness, and submitted for keypunching and verification. Punchcard records were transferred to tape, entered onto a DEC PDP-11/23 minicomputer, and checked through a series of inhouse quality control programs. Once clean, all data were transferred to an IBM 3081 mainframe computer for database management (using RAMIS II) and analysis. All multivariate statistical applications were performed using EAP (Ecological Analysis Package, Smith 1981) and SAS (Statistical Analysis System, SAS 1981) program packages. Additional analyses were also performed by Dr. C. David McIntire using programs established on a CYBER 170/720 computer at the Oregon State University Computer Center, Corvallis, Oregon.

Data obtained by the Marsh Plant Primary Production Work Unit were organized into four data files. Documentation for these files is presented in Appendix D; each file is accessible through the U.S. Army Corps of Engineers, North Pacific Division Computer Services facility in Portland, Oregon.

2.7.2 Tidal Marsh Vegetation Types

Data describing species distributions and relative abundance within marsh vegetation sampled at the various study sites were available as both mean percent cover and mean percent biomass records (n=5 per study site, in both cases). Percent cover data were the more complete, with all species identified separately. Information was somewhat reduced among percent biomass data sets for some species remained lumped together for dry weight determinations. Because of this difference, multivariate analyses of study site species assemblages were performed on the percent cover data only.

Inspection of our study site species percent cover data and review of Duncan Thomas' (1980a) more broadly based marsh vegetation descriptions, provided two subjective interpretations of the species assemblages that characterize Columbia River Estuary tidal marshes.

Objective separation of these subjectively defined tidal marsh vegetation types was examined using two cluster analysis procedures and canonical discriminant analysis. Cluster analysis (Sneath and Sokal 1973) procedures classify objects into groups based on their overall similarity. The method can be applied in two modes: Q-Mode, or station by station comparisons, in which the similarity between samples is measured on the basis of their overall species composition; and R-Mode, or species-by-species comparisons, in which the distribution patterns of different species are compared on the basis of their occurrence among various sampling stations. The analytical procedures used are outline below.

Data Preparation

Plant species with mean percent cover values lower than 0.1 percent were adjusted to 0.1 as a minimum to prevent premature exclusion. Taxa having a frequency of occurrence in the entire database of one or two were then eliminated if their percentage value(s) did not exceed one percent. This removed a total of 16 taxa from consideration. Percent cover data for the remaining species were normalized using log transforms; data for July 1980 (22 study sites) and August 1981 (21 study sites) were combined for the analysis. The final data matrix consisted of 43 study sites and 49 species.

Divisive Cluster Analysis

Polythetic divisive hierarchial clustering progressively splits an entire data set into smaller and smaller groups, with divisions being based on resemblance over all attributes -- rather than the presence or absence of single species (Boesch 1977, Gauch 1982). The specific procedure used by McIntire was the same as for the Columbia River Estuary benthic diatom floras and is more fully described in the CREDDP integration report (Simenstad et al., 1984).

Canonical Discriminant Analysis

McIntire subsequently used canonical discriminant analysis to display the divisive clustering structure in a simple two-dimensional graph. This procedure involves establishment of two discriminant axes, each representing different components of total species composition, which maximize between-site variation. When individual study site percent cover values are projected onto the discriminant axes site locations are maximally separated.

If the marsh vegetation types yield substantially different species cover data, then study sites sharing similar vegetation will appear as discrete clusters, separated from other locality groupings representing different marsh types. Conversely, if all marsh vegetation types are similar, no meaningful separation will be seen.

Agglomerative Cluster Analysis

The same raw data matrix used for divisive clustering was also used for agglomerative cluster analysis. Here however, the species cover data were normalized using a square root transformation.

Polythetic agglomerative hierarchical clustering (performed here by Donald M. LaVigne, San Diego, California) also uses information on all of the species. Initially each sample is assigned to a single member cluster. These are subsequently agglomerated into a hierarchy of larger and larger clusters until finally a single cluster contains all the samples. This is by far the most widely used approach in ecological studies (Sneath and Sokal 1973, Boesch 1977, Gauch 1982).

The procedure begins by generating a matrix of similarity coefficients among the various entities being clustered -- species abundances at each study site, for example. Coefficient values can be regarded as measurements of the relative "ecological distance" between closely spaced similar samples or less similar, more distant samples.

The newly developed ZAD index (Zero Adjusted Distance; Smith and Bernstein, In Preparation) was used to measure Q-mode inter site-distances (i.e. overall similarity of species abundance data collected at different study sites). Most similarity or distance measures approach maximum values and then level off, losing their sensitivity to larger magnitudes of actual biological change. The ZAD index is designed to overcome this problem and continues to increase steadily with biological change.

R-mode inter-species distances (i.e. degree of distributional overlap of various species among all 22 study sites) were calculated in two steps. The widely used Bray-Curtis distance index (see Boesch 1977) was used to measure distributional overlap among species. Two-step and step-across procedures (see Smith 1981) then converted the Bray-Curtis overlap distances to distances which measure the relative habitat preference of the species. The final distance values are thus proportional to the dissimilarity of the habitats (our 22 study sites) in which the species being compared are found.

The results of both Q-mode (study sites) and R-mode (species) hierarchical clustering, accomplished using a flexible sorting strategy $\beta=0.25$), are displayed as dendrograms (tree diagrams). In addition, two-way coincidence tables display standardized raw data in symbol form, as a matrix of species verses study sites, sorted by their order of appearance in the dendrograms.

2.7.3 Standing Crop and Primary Production

Means, standard deviations, standard errors (of mean values) and ranges, were calculated wherever appropriate replicate field observations or laboratory measurements were available. Standard statistical procedures (t-tests, for example) were used to test differences between means, with $p<0.05$ being the level chosen for significance.

Analysis of variance F-value procedures (Scheffer 1969) were used to test for significant differences among mean net annual aboveground production estimates from the four tidal marsh types, as well as their mean net aboveground total standing crop values for July 1980 and August 1981.

Analysis of covariance, combined with Student-Newman-Kuels tests, was used to identify significantly different decomposition rates among plant material set out at different elevations and locations around the estuary.

Interrelationships among the physical variables selected to describe tidal marsh habitats throughout the estuary were examined using a matrix of correlation coefficients and Principal Components Analysis (Gauch 1982).

Finally, multiple regression procedures (R-square procedure, multiple regression analysis, and stepwise regression) were used to examine possible relationships between Smalley net annual aboveground primary production estimates for tidal marsh study sites around the estuary and physical environmental measurements selected as characteristic of these same locations.

3. RESULTS AND INTERPRETATION

The different data sets collected during the Columbia River Estuary Tidal Marsh Plant Production research program are presented in the following sections. Results obtained using the analytical procedures described in the preceding methods section are also outlined below.

3.1 MARSH VEGETATION TYPES

Prior to the initiation of this study very little information had been published describing the tidal marsh vegetation of the Columbia River Estuary. Among our initial goals therefore were the following:

1. Description of the distribution and general vegetative characteristics of Columbia River Estuary tidal marshes.

2. Collection of quantitative species cover data to characterize the more widespread and distinctive tidal marsh plant assemblages.

3. Multivariate analysis of marsh plant cover data to provide objective testing of any preliminary estuary-wide tidal marsh classification.

3.1.1 Species Richness

Taken together, the quantitative cover and biomass quadrats yielded 67 different plant species. An additional 15 species were collected nearby but did not occur within the sample quadrats. This total of 82 species is almost exactly half the estuary-wide floral list of 165 species assembled by Duncan Thomas (Thomas 1980a). This apparent discrepancy in part reflects Thomas' collections from tidal swamps (scrub-shrub and forested wetlands) and nontidal wetlands, excluded from the tidal marsh production work unit. His goal was also to document all species occurrences, including those of occasional and rare plants.

Presence-absence data for all taxa collected during this study at each tidal marsh study site are presented in Table 3. Numbered study site locations at the top of the table are listed in order of increasing distance from the estuary mouth. Their order corresponds with the listing of CREDDP coordinates presented in Table 2.

Four separate data sets were collected that describe species relative abundances among the various study sites sampled, in quantitative terms. These are the percent cover data and percent aboveground biomass data, each collected in both July 1980 and August 1981. All four data sets are presented in Appendix A. For ease of comparison the four data sets from each study site are shown together (Tables A-1 through A-22).

Table 3. Species Presence-Absence Data for Columbia River Estuary Sample Sites, All Data Sets Combined. Species Ordered to Emphasize Upriver Compositional Changes.

SPECIES	SAMPLE SITES (ESTUARY MOUTH → UPRIVER) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Fucus distichus edentatus	*																					
Orthocarpus castillejoides	+																					
Cotula coronopifolia			+																			
Carex obnupta					*																	
Vicia gigantea					*																	
Hordeum brachyantherum							+															
cf. _Vallisneria americana_							+															
Achillea millefolium								+														
Elymus glaucus								+														
Scirpus sp.	*	+				+				*												
Triglochin maritimum	*	*	*	*			*				*											
Scirpus americanus	*	*	*									*	*									
Agrostis alba	*			*	*	+	*	*	*		*		+		*	*	*	*		*		
Lilaeopsis occidentalis	*			*						+	*	*				*	*	*	*	*	*	
Scirpus validus	*									*	*	*	+	*					*		*	+
Carex lyngbyei	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Zannichellia palustris			*				+															
Festuca arundinacea			+		*				*				*		*							
Lotus corniculatus			+										*		*	+						
Aster subspicatus			+		*				*			*	*	*		*					*	
Potentilla pacifica				*	*		*	*	*	+	*				*	*				*		
Lathyrus palustris					*			*	*													
Juncus balticus					*		*		*			*			*							
Oenanthe sarmentosa					*			+		*	*		*		*			*				
Rumex crispus					*						*		*		*			*				
Deschampsia caespitosa						+	*					*	*	*	*			*	*	*	*	

* Present in Sample quadrats. + Present nearby but absent from sample quadrats.

Table 3. (Continued).

SPECIES	SAMPLE SITES (ESTUARY MOUTH → UPRIVER) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Trifolium wormskjoldii							+				+				*					*		
Typha angustifolia										*						*						*
Scirpus microcarpus											*				*							
Equisetum sp.											+					*						
Rumex conglomeratus											*					*						
Eleocharis palustris											*	*	*	*		*	*		*	*	*	
Typha latifolia											+		*									*
Alisma plantago-aquatica											*	*	*	*		*	*	*	*	*	*	+
Elodea canadensis												*	*	*			*					
Polygonum hydropiperoides												*		*		*	*	*	*		*	
Sium suave												*	*	*		*	+	*	*	*	*	
Juncus oxymeris												*	*	*		*	*	*	*	*	*	+
Mimulus guttatus												*	*	*	*	*	*	*		*	*	+
Sagittaria latifolia												+		*		*	*	*	*	*	*	*
Equisetum fluviatile													*		*							
Caltha asarifolia													*		*			*		*		
Habenaria dilatata													+		*			*		+		
Ranunculus sp.														*		*			*		*	
Littorella sp.														*		*	*					
Isoetes echinospora														*		*		*				
Galium cymosum															*							
Hypericum formosum															+							
Heracleum lanatum															+							
Iris sp.															+							
Juncus nevadensis															*							
Mentha sp.															*							
Typha sp.															*							
Mentha piperita															*					*		
Myosotis laxa															*	*	+			*		

* Present in Sample quadrats. + Present nearby but absent from sample quadrats.

Table 3. (Continued).

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
	SAMPLE SITES (ESTUARY MOUTH → UPRIVER)																					
Lysichitum _americanum_															+			*		*		+
Aster sp.															*				*	*		*
Helenium sp.																*						
Fontinalis sp.																*		*				
Callitriche sp.																*	*	*	*			
Epilobium _watsonii_																*		*		*		
Bidens _cernua_																*	*			*		
Phalaris _arundinacea_																*	*		*	*		*
Ceratophyllum sp.																	*					
Gratiola _neglecta_																	*					
Limosella _aquatica_																	*					
Tillaea _aquatica_																	*					
Najas sp.																	*					
Boltonia _asteroides_																	*		*			
Helenium _autumuale_																		+				
Aster _modesta_																		*	+			
Mentha _arvensis_																		*		*		
Senecio _triangularis_																		+		*		
Galium sp.																				*		
Helenium _grandiflorum_																				*		
Lupinus sp.																				+		
Prunella _vulgaris_																				+		
Veratrum _californicum_																				+		
Beckmannia _syzigachne_																						+
Iris _pseudacorus_																						*
Juncus _effusus_																						+
Plantago _lanceolata_																						*

* Present in Sample quadrats. + Present nearby but absent from sample quadrats.

Despite variations among the four sets of relative abundance values recorded from each study site, data inspection confirms that only a small subset of the total 82 species recorded is usually responsible for the majority of plant cover and biomass within the tidal marshes. These species, each accounting for at least five-percent of the total plant cover at one or more of the 22 quantitative sample sites in July 1980, are listed in Table 4. Note that *Carex lyngbyei* occurred at every site and was the most abundant species (in terms of percent cover, net aboveground live biomass, or both) at 12 to 15 of the 22 study sites depending upon the data set used.

3.1.2 Marsh Vegetation Types

The initial description of Columbia River Estuary tidal marsh and swamp vegetation prepared by Dr. Duncan W. Thomas (Thomas 1980a) included generalized species lists and distributional data for 19 different marsh vegetation types. In his more recent floristic summary (Thomas In Press) he reduced this number to seven: four different tidal marsh types, and three distinctive swamp assemblages.

Our own field observations (October 1979 through August 1981) confirm that the species composition of the tidal marsh vegetation varies considerably both within and between individual marsh localities, as well as to a lesser extent from year to year. The most striking differences however, are clearly those between marshes developed under freshwater verses brackish water conditions, and higher verses lower intertidal elevations. This four-fold subdivision of tidal marsh types throughout the estuary was subsequently confirmed by the more objective multivariate analyses described in later sections.

Brief descriptions of the four principal tidal marsh floral assemblages represented in the Columbia River Estuary follow below. These descriptions are based on our own and Thomas' field observations as well as subjective inspection of species abundance data, such as presented in Table 4 and Appendix A.

Brackish Low Marshes

These marshes are characterized by simple plant assemblages in which only one or two species account for the majority of cover and biomass (Table 4: sites 1 to 4, 6, 7, 10 and 11). *Scirpus americanus* (Three-square bulrush), *Carex lyngbyei* (Lyngby's sedge) and *Agrostis alba* (Creeping bentgrass) are generally the common dominants, each reaching prominence at successively higher elevations across the low marshes. *Triglochin maritimum* (Seaside arrow-grass), a common saltmarsh species, is another characteristic plant although never found in great abundance.

Carex stands at Baker Bay were unusual in that clumps of the marine brown alga *Fucus distichus edentatus* commonly occurred, attached to the substrate among the *Carex* plants. Another locally distinctive feature among the brackish low marshes was the occurrence of dense stands of *Typha angustifolia* (Lesser cattail) at Outer Youngs Bay.

Table 4. Relative Abundance, as Mean Percent Cover, of Different Species Among Columbia River Estuary Tidal Marsh Sample Sites, July 1980. Species Ordered to Emphasize Upriver Compositional Changes. (Only species >5.0 percent cover at one or more sites are listed.)

	Brackishwater Low Marsh								Brackishwater High Marsh			Freshwater Low Marsh						Freshwater High Marsh				
SPECIES/SITES:	1	2	3	4	6	7	10	11	5	8	9	12	14	16	17	19	21	13	15	18	20	22
Fucus distichus (rockweed)	18																					
Scirpus americanus (bulrush)	*	77	33									*						*				
Agrostis alba (creeping bentgrass)	+			6	+	80		4	38	39	27								3	*		
Scirpus validus (bulrush)	5						1	1					19			19		+				+
Carex lyngbyei (lyngby's sedge)	77	23	63	91	100	16	82	87	14	51	2	21	35	74	12	67	85	58	30	82	43	+
Aster sp.			+						5		7	9		+		*	3	7	3	*		33
Potentilla pacifica (Pacific silverweed))				+		2	+		33	2	41			+					6		5	
Lilaeopsis occidentalis				2	+		+	*				4		7	1		1			*	2	
Lathyrus palustris (marsh pea)									6	9	15											
Juncus balticus (Baltic rush)						1			5	+	8	32						+				
Deschampsia caespitosa (tufted hairgrass)					+	1						11	13			4	3	7	6	2	8	
Oenanthe sarmentosa (water parsley)								6		+								+	3	2		
Typha angustifolia (cattail)							17							1								11
Eleocharis palustris (creeping spikerush)								+				4	+	12	52	8	1	+	+		2	
Elodea canadensis (waterweed)												13	8		9			20				
Sium suave (water parsnip)												4		*	+	+	3	9		5	*	
Juncus oxymeris (rush)												2	8	3	16	2	5	*		1	5	+
Lotus corniculatus (birdsfoot trefoil)														+				+	6			
Caltha asarifolia (yellow marsh marigold)																		*	8		2	
Sagittaria latifolia (wappato)													17		4	*				2		*
Mentha sp. (mint)																			25			
Lysichitum americanum (skunk cabbage)																			+		27	+
Typha latifolia (Narrow-leaved cattail)																						52

*Present in sample quadrats but mean cover <0.5 percent. +Present nearby but absent from sample quadrats.

A variety of additional species were recorded as occasionals within various low marsh sample quadrats: Deschampsia caespitosa (Tufted hairgrass), Lilaeopsis occidentalis (Western lilaeopsis), Potentilla pacifica (Pacific silverweed), Scirpus validus (Softstem bulrush), and Zannichellia palustris (Horned pondweed).

The Inner Youngs Bay site yielded the richest low marsh flora (15 species) and included a number of species more commonly associated with the freshwater marshes further upriver. These included: Alisma plantago-aquatica (Water plantain), Eleocharis palustris (Creeping spike rush), Equisetum sp. (Horsetail), Oenanthe sarmentosa (Pacific water-parsley), Scirpus microcarpus (Small-fruited bulrush), and Typha latifolia (Common cattail).

Brackish High Marshes

Three of these marshes were sampled, all in Trestle Bay (Table 4: sites 5, 8, and 9). Their vegetation was more complex than that of the brackish low marshes, with increasing numbers of species appearing at higher elevations. Carex lyngbyei and Agrostis alba remained important but several additional species, scarce or absent from the low marshes, also contributed significantly to both cover and biomass. These included Potentilla pacifica, Lathyrus palustris (Marsh pea), Juncus balticus (Baltic rush), and Aster sp. (probably A. subspicatus, Douglas' aster). Other occasional species included Carex obnupta (Slough sedge), Festuca arundinacea (Reed Fescue), Oenanthe sarmentosa, Rumex crispus, (Curlyleaved dock) and Vicia gigantea (Giant vetch).

Freshwater Low Marshes

East of Tongue Point (RM-18) freshwater tidal marshes replace the brackish marshes of the lower estuary. The freshwater marsh vegetation is more variable both within and between sites than the brackish marsh; it also yields greater numbers of species. Freshwater low marshes (Table 4: sites 12, 14, 16, 17, 19, and 21), for example, yielded 13 to 26 species per site, compared with only 4 to 15 species per site from brackish low marshes.

Overall species composition between brackish and freshwater marshes also differs considerably. Of the 82 plant species recorded during this study, 13 were collected from brackish sites only; 21 from both brackish and freshwater sites; and the remaining 48 species were found only in freshwater marshes. Partly because of this species richness and variability, distinctions between low and high freshwater marsh types are less obvious than those noted between low and high brackish marshes.

Tidal freshwater habitats yielded a group of widely distributed marsh plants that were commonly recorded from both low and high marsh study sites. Carex lyngbyei, already noted as a brackish marsh dominant, remained the most widespread and abundant of all species encountered at freshwater sites. Aster spp., Deschampsia caespitosa, and Alisma plantago-aquatica, all recorded from lower estuary brackish marshes, increased substantially in abundance within the freshwater marshes.

Four additional species, not represented in the lower estuary, also commonly occurred at both low and high freshwater marsh study sites: Elodea canadensis (Rocky mountain waterweed), Mimulus guttatus (Common monkey-flower), Sagittaria latifolia (Broad-leaved arrowhead), and Sium suave (Hemlock water parsnip). Less common but widely dispersed "occasionals" among both low and high freshwater marsh sites included: Callitriche sp. (Water starwort), Isoetes echinospora (Quillwort), Myosotis laxa (Smaller forget-me-not), and Phalaris arundinacea (Reed canary-grass).

In addition to the ubiquitous species noted above, a second major species group contained plants sometimes found at high marsh study sites, but more commonly present or abundant in freshwater low marshes. This group included several species also recorded from brackish marshes: Lilaeopsis occidentalis, Scirpus validus, and Juncus balticus -- as well as new species not found in the lower estuary: Eleocharis palustris (Creeping spike-rush), Juncus oxymeris (pointed rush), and Polygonum hydropiperoides (Mild water pepper). Two additional common species, Littorella sp. (Plantain) and Ranunculus sp. (Buttercup), were apparently restricted to freshwater low marsh sites.

Freshwater High Marshes

The freshwater high marshes sampled (Table 4: sites 13, 15, 18, 20, and 22) were also more variable and yielded greater numbers of species (14 to 28 species per site, compared with only 5 to 10 species at brackish sites) than their brackish lower estuary counterparts.

In addition to the broadly distributed group of freshwater marsh plants already noted above, Agrostis alba, Lotus corniculatus, and Potentilla pacifica -- while sometimes found at low marsh sites -- were more characteristic and abundant at freshwater high marsh localities. Both Agrostis and Potentilla were less abundant in the upper estuary however, than among lower estuary brackish marshes.

Several species present in the upper estuary were only noted at high marsh study sites. For example, Caltha asarifolia (Western marsh marigold), Equisetum fluviatile (Swamp horsetail), Festuca arundinacea, Habenaria dilatata (Boreal bog orchid), Rumex crispus, and Oenanthe sarmentosa -- although each rarely contributed more than a few percent to the total cover. Other species, while less frequently encountered, contributed more significantly to high marsh plant cover when they did occur: Mentha sp.(mint) 25 percent cover at Inner Grays Bay, Lysichitum americanum (Yellow skunk cabbage) 17 percent cover at Tronson Island, and Typha latifolia 52 percent cover at Puget Island, for example.

Compositional Variability

Information on the variability of species assemblages among the different marsh types can be gained by comparing the study site data sets presented in Appendix A. Changes in species composition and relative abundance within a single study site might reflect natural sampling variability, or real year-to-year compositional changes.

Comparisons among low and high marsh study sites, as at East Trestle Bay (Table 5) for example, also provide quantitative data on changes in species composition that accompany increasing intertidal elevations. East Trestle Bay is characteristic in that several species occupy broad elevational ranges, but exhibit significant changes in relative abundance across the elevational gradient. Note also that marsh vegetation at this brackish water site is relatively simple when compared with the diverse freshwater assemblages recorded further up the estuary (See Appendix A, Table A-17 Lois Island, and Table A-20 Tronson Island, for example).

Additional Wetland Habitats

In addition to the tidal marshes described above, swamps, wetlands with shrub or tree-dominated vegetation, account for some 2,410 hectares (5,950 acres) of intertidal habitats within the estuary. This Work Unit did not include studies of the swamp vegetation, however, Thomas' (1980a and In press) estuary-wide wetlands reconnaissance provides the following description of these habitats.

Brackish Scrub-Shrub Wetlands

Now limited to Youngs Bay, these assemblages occur as a mosaic, mixed with brackish high marsh. The dominant woody shrub species include Salix hookeriana (Coast willow), Lonicera involucrata (Black twin-berry), Rubus spectabilis (Salmon berry), Picea sitchensis (Sitka spruce), and occasionally Alnus rubra (Red alder). The understory vegetation includes most of the same species previously noted from the brackish high marshes.

Freshwater Scrub-Shrub Wetlands

This extensive wetland type is dominated by Salix sitchensis (Sitka willow). Salix lasiandra (Red willow), Cornus stolonifera (Red osier dogwood) and Spiraea douglasii (Western spiraea) are also important woody shrub species. The understory vegetation is commonly dominated by Lysichitum americanum.

Freshwater Forested Wetlands

This now scarce and unusual habitat co-occurs as a mosaic with the freshwater scrub-shrub wetlands described above. While the same shrub species remain important, tall trees of Picea sitchensis are the striking dominant. Thomas (1980a) notes that well developed areas have a hummock-hollow topography, with many upland forest species occurring on the hummocks and wetland species in the hollows.

3.1.3 Estuary-Wide Distribution Patterns

Based upon Duncan Thomas' (1980a) photo-mapping studies, the approximate estuary-wide areal extent of the various wetland habitats described above is as follows:

Table 5. East Trestle Bay Marsh: Changes in Species Relative Abundance (as Percent Aboveground Live Biomass) With Increasing Elevation, July 1980.

Species	Elevation (Feet Above MLLW)			
	7.17	7.85	8.43	8.83
Carex lyngbyei	99.0	32.4	39.7	3.0
Agrostis alba	0.5	61.3	37.0	16.0
Juncus balticus	-	3.5	1.5	11.6
Potentilla pacifica	-	1.0	12.5	40.8
Festuca arundinacea	-	-	7.6	-
Lathyrus palustris	-	-	~1.7	-
Lathyrus sp./Aster sp.	-	-	-	~19.4
Other	0.5	1.8	-	9.2

	Hectares	(Acres)
Brackish Low Marsh	567	(1,400)
Brackish High Marsh	316	(780)
Freshwater Low Marsh	2268	(5,600)
Freshwater High Marsh	567	(1,400)
Brackish Shrub Swamp	53	(130)
Freshwater Shrub/Forested Swamp	2357	(5,820)
Total	6128	(15,130)

Table 1 includes a more detailed distributional breakdown of marsh and swamp vegetation types within the estuary; the marsh maps included in the CREDDP Atlas (Fox et al., 1984) illustrate their specific locations. Brackish low marsh habitats fringe much of the shoreline of Baker, Trestle and Youngs Bays. Brackish high marsh is also best developed in Trestle and Young's Bays, brackish shrub swamp in Youngs Bay. Freshwater tidal marshes extend upriver from Tongue Point (RM-18). Low marsh habitats are widespread throughout the islands of Cathlamet Bay (Lois, Russian, Seal, Green, Minaker, and the western portion of Karlson Island), fringe much of Grays Bay, and occur on the downstream portions of Tronson, Quinns, Grassy, and Fitzpatrick Islands, near Aldrich Point (RM-30). Freshwater high marshes are present along the eastern shores of Grays Bay and are more broadly developed across portions of Marsh, Horseshoe and Welsh Islands.

Shrub and tree-dominated freshwater swamp habitats are best developed in the Prairie Channel-Blind Slough area of Cathlamet Bay (Karlson, Marsh and Long Islands) and further upriver at Welsh (RM-34) and Hunting (RM-37) Islands.

3.2 CLUSTER ANALYSIS

Separation of the marsh vegetation types described above by more objective criteria was examined using both divisive cluster analysis combined with cannonical discriminant analysis, and agglomerative cluster analysis.

3.2.1 Divisive Cluster Analysis

McIntire found a six-cluster structure generated by the divisive clustering algorithm to be the most interpretable pattern in the marsh plant species cover matrix (Table 6). His own description of the clustering results is as follows.

"Cluster 1 consists primarily of low marsh sites in brackish water. However, the dominance of Carex lyngbyei, a euryhaline species, at four sites in the middle estuary groups these samples with the brackish water sites. Other taxa predominant in some of the samples of

Table 6. Six-Cluster Structure of Plant Species Percent Cover Data (1980/1981 Combined) Produced by Divisive Q-Mode Cluster Analysis.

Cluster	Location	Year	Description
1	Baker Bay - China Cove	1980	_Carex_ Low Marsh
	Baker Bay - China Cove	1981	_Carex_ Low Marsh
	Baker Bay - China Cove	1980	_Scripus_ Low Marsh
	Baker Bay - China Cove	1981	_Scirpus_ Low Marsh
	Baker Bay - Ilwaco Harbor	1980	Low Marsh
	Baker Bay - Ilwaco Harbor	1981	Low Marsh
	Trestle Bay - West	1980	Low Marsh
	Trestle Bay - West	1981	Low Marsh
	Trestle Bay - East	1980	_Carex_ Low Marsh
	Trestle Bay - East	1981	_Carex_ Low Marsh
	Youngs Bay - Outer	1980	Low Marsh
	Youngs Bay - Outer	1981	Low Marsh
	Youngs Bay - Inner	1980	Low Marsh
	Youngs Bay - Inner	1981	Low Marsh
	Army Corps Pier	1980	Low Marsh
	Grays Bay - Outer	1980	Low Marsh
	Grays Bay - Outer	1980	High Marsh
	Karlson Island	1980	Low Marsh
	Quinns Island	1980	Low Marsh
	Quinns Island	1981	Low Marsh
2	Grays Bay - Inner	1980	High Marsh
	Grays Bay - Inner	1981	High Marsh
	Grays Bay - Outer	1981	High Marsh
	Russian Island	1980	High Marsh
	Russian Island	1981	High Marsh
	Tronson Island	1980	High Marsh
	Tronson Island	1981	High Marsh
3	Lois Island	1980	Low Marsh
	Lois Island	1981	Low Marsh
	Grays Bay - Inner	1980	Low Marsh
	Grays Bay - Inner	1981	Low Marsh
	Grays Bay - Outer	1981	Low Marsh
	Karlson Island	1981	Low Marsh
4	Puget Island	1981	_Typha_ High Marsh
5	Army Corps Pier	1981	Low Marsh
6	Trestle Bay - West	1980	High Marsh
	Trestle Bay - West	1981	High Marsh
	Trestle Bay - East	1980	Low Marsh
	Trestle Bay - East	1981	Low Marsh
	Trestle Bay - East	1980	Mid Marsh
	Trestle Bay - East	1981	Mid Marsh
	Trestle Bay - East	1980	High Marsh
	Trestle Bay - East	1981	High Marsh

Cluster 1 included Triglochin maritimum, Scirpus americanus, and Eleocharis palustris. Cluster 2 includes 7 samples from high marsh sites in the middle estuary. Some of the dominant taxa in these samples were Oenanthe sarmentosa, Lotus corniculatus, Mimulus guttatus, Carex lyngbyei, and Deschampsia caespitosa. Samples from low marsh sites in the middle estuary were in the six components of Cluster 3. Again, Carex lyngbyei was abundant in all of these samples. Other dominant taxa associated with Cluster 3 included Alisma plantago-aquatica, Sagittaria latifolia, Eleocharis palustris, and Juncus oxymeris. Clusters 4 and 5 are one-sample clusters which were separated from the other groups on the basis of several dominant taxa. Cluster 4 represents a marsh on Puget Island dominated by Typha latifolia, whereas Cluster 5 is a sample from a low marsh near Tongue Point where Myosotis laxa and Equisetum sp. were abundant. The latter taxon was also abundant in one sample from Young's Bay and two samples from Gray's Bay. Cluster 6 is composed of eight samples from Trestle Bay, only two of which were from the low marsh. The abundant species in these samples were Lathyrus palustris, Potentilla pacifica, Carex lyngbyei, Juncus balticus, and Agrostis alba."

Canonical Discriminant Analysis

Following the divisive cluster analysis, McIntire used canonical discriminant analysis to display the clustering structure of Table 6 in a simple two-dimensional graph (Figure 5). The two axes used to create Figure 5 retained 88.2 percent of the among-group variation and successfully separated the clusters of similar marsh types. Again in McIntire's own words,

"....the brackish water groups (Clusters 1 and 6) are relatively close, while the discrete and unique nature of the high marsh samples from the middle estuary is apparent. The low marsh samples from the middle estuary and the sample from the Typha marsh on Puget Island (Clusters 3 and 4) have a greater affinity for the brackish water clusters than for Cluster 2, the high marsh samples from the middle estuary. These relationships are indicative of the presence of a few euryhaline species that were abundant at both brackish water and freshwater locations. Cluster 5, dominated by Myostis laxa, Carex lyngbyei, Eleocharis palustris, Juncus oxymeris, Equisetum sp., and Isoetes echinospora, is well separated from all the other clusters. Of these taxa, Myostis laxa and Isoetes echinospora were primarily responsible for this separation."

Overall, the results obtained from divisive clustering and canonical discriminant analysis are in good agreement with the subjectively separated marsh vegetation types described above (Section 3.1.2). In particular, Clusters 1, 2, 3, and 6 are approximately equivalent of brackish water low marsh, freshwater high marsh, freshwater low marsh, and brackish water high marsh, respectively. The fact that in all but four cases (Army Corps Pier, Outer Gray's Bay, and Karlson Island) the same study sites clustered together for both July 1980 and August 1981 percent cover data, also suggests a robust and meaningful classification.

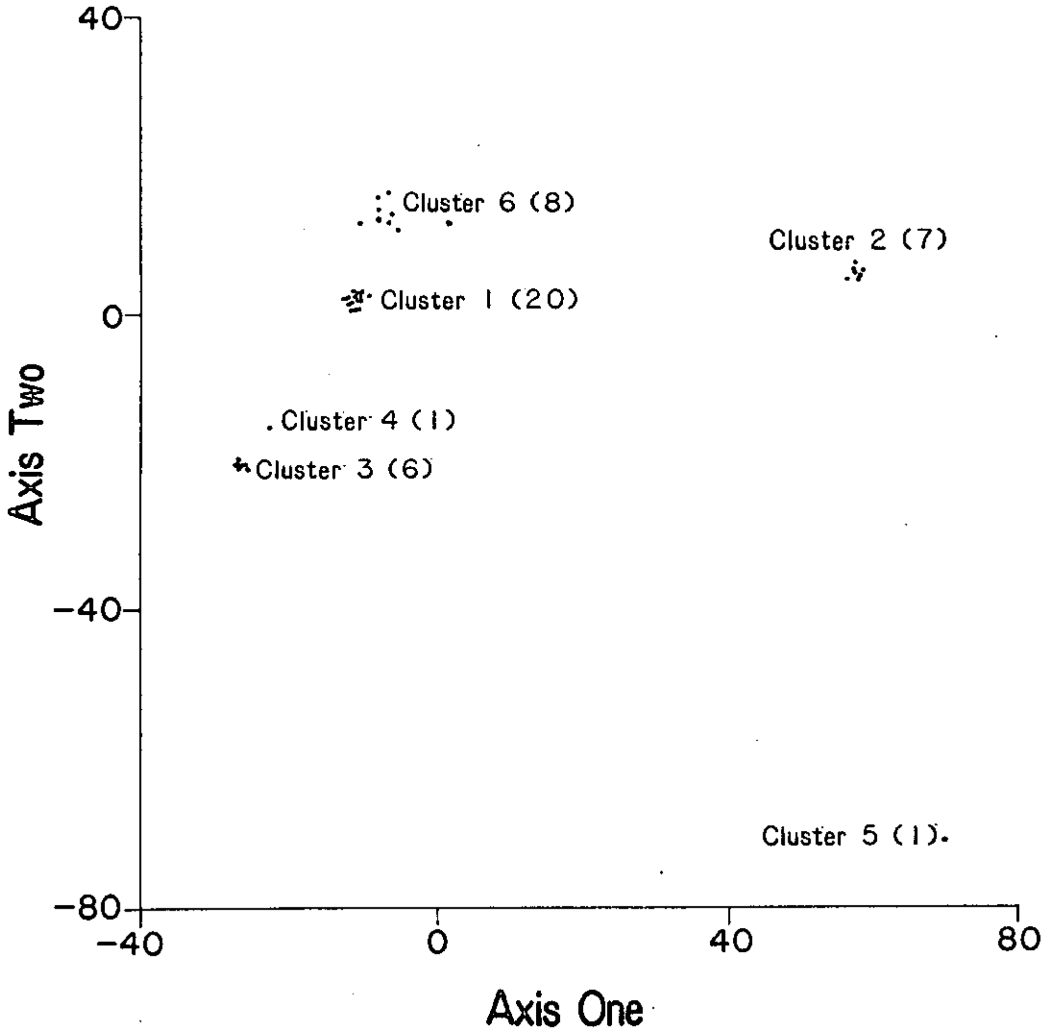


Figure 5. Two Dimensional Ordination of the Six-Cluster Structure from Table 6 Produced by Canonical Discriminant Analysis.

The more obvious differences between the subjectively separated marsh vegetation types and clustering results are the inclusion of five freshwater sites among the brackish water low marshes of Cluster 1, and the isolation of the August 1981 Army Corps Pier low marsh site as Cluster 5. As noted by McIntire, the Cluster 1 freshwater sites shared relatively high percentages of Carex cover (20 to 85%), a feature also typical of the brackish water low marshes of Cluster 1.

Significant differences in species relative abundances were noted at the Army Corps Pier site between July 1980 and August 1981 (Appendix A, Table A-16). In July 1980, Carex lyngbyei (73.5%) and Eleocharis palustris (11.8%) together accounted for 85.3 percent of the total plant cover. In August 1981 however, the same two species accounted for only 49.6 percent of the cover. Equisetum sp. (16.5%), Isoetes echinospora (11.4%), and Myosotis laxa (9.5%), virtually absent before, now accounted for 37.4 percent of the plant cover. The scarcity of other sites sharing a similar species composition explains the isolation of the August 1981 sample.

3.2.2 Agglomerative Cluster Analysis

Q-mode (study site) and R-mode (species) agglomerative clustering techniques were applied separately to the July 1980, August 1981, and combined 1980-1981, species percent cover data sets.

July 1980 Percent Cover Clusters

Overall similarities among marsh vegetation sampled at each study site in July 1980 are illustrated in the Q-mode dendrogram presented in Figure 6. (Sites that cluster at lower distance coefficients share more similar vegetation than sites joined together at higher distance coefficients.) Four well separated clusters are apparent (numbered on the righthand side of the figure). The Typha spp. high marsh at the eastern tip of Puget Island is identified as a single-site cluster. The brackish water marsh sites are divided among two clusters: Cluster 2, principally high marsh sites and Cluster 4, entirely low marsh sites. Except for Puget Island all of the freshwater marsh sites are grouped together in Cluster 3. There is no clear separation of freshwater high and low marsh sites, however.

The R-mode dendrogram developed from the July 1980 cover data is presented in Figure 7. Species sharing the greatest similarity in distribution among study sites, cluster at the lowest distance coefficient values. Four major species clusters (Clusters A through D) are identified. Species marked with asterisks were absent from the July 1980 data set; note that they are still clustered, but at higher distance coefficients than the meaningful species clusters.

The two-way table developed from the July 1980 clustering data (Figure 8) indicates which clusters of species are responsible for separation of the study site groups. The species in Cluster A are clearly responsible for separating the brackish water marshes (Clusters 2 and 4) from the freshwater marshes (Cluster 3) which are character-

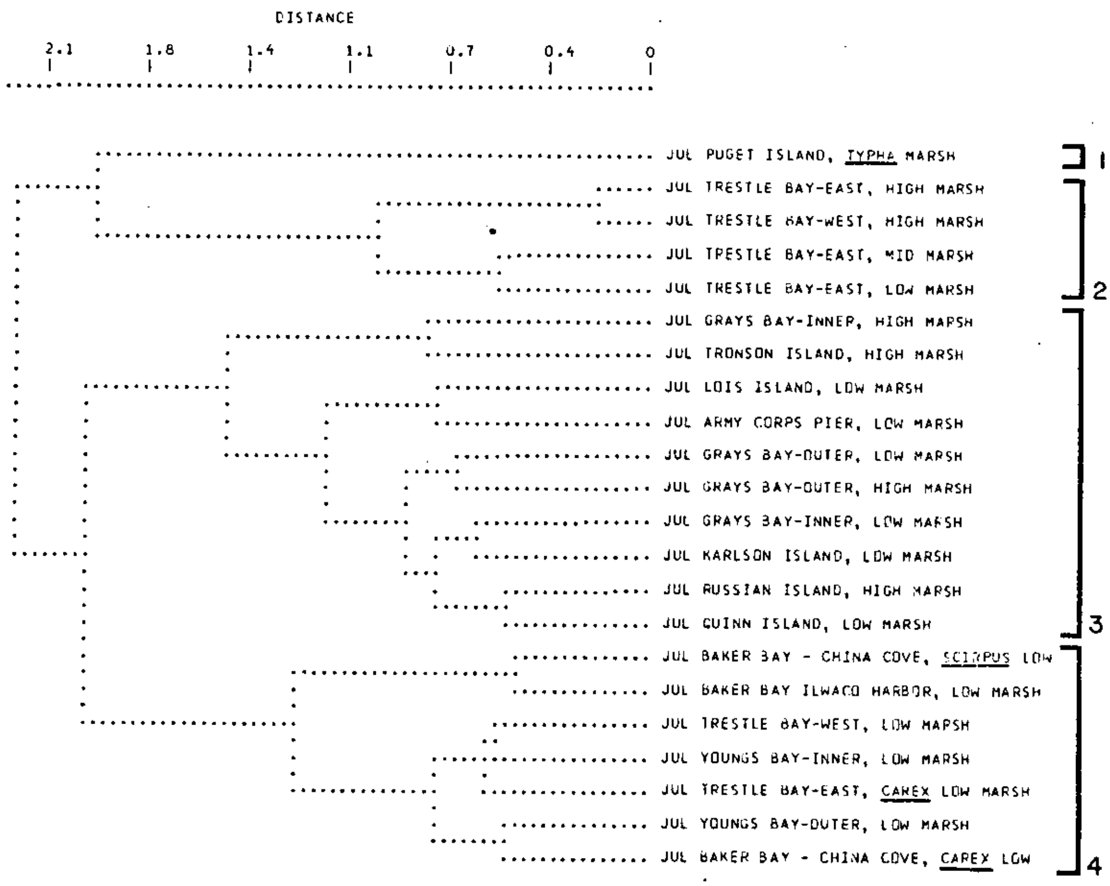


Figure 6. Q-Mode (Study Site) Dendrogram Based on ZAD Indices Calculated from Species Percent Cover Data, July 1980. (Numbered brackets identify study site clusters.)

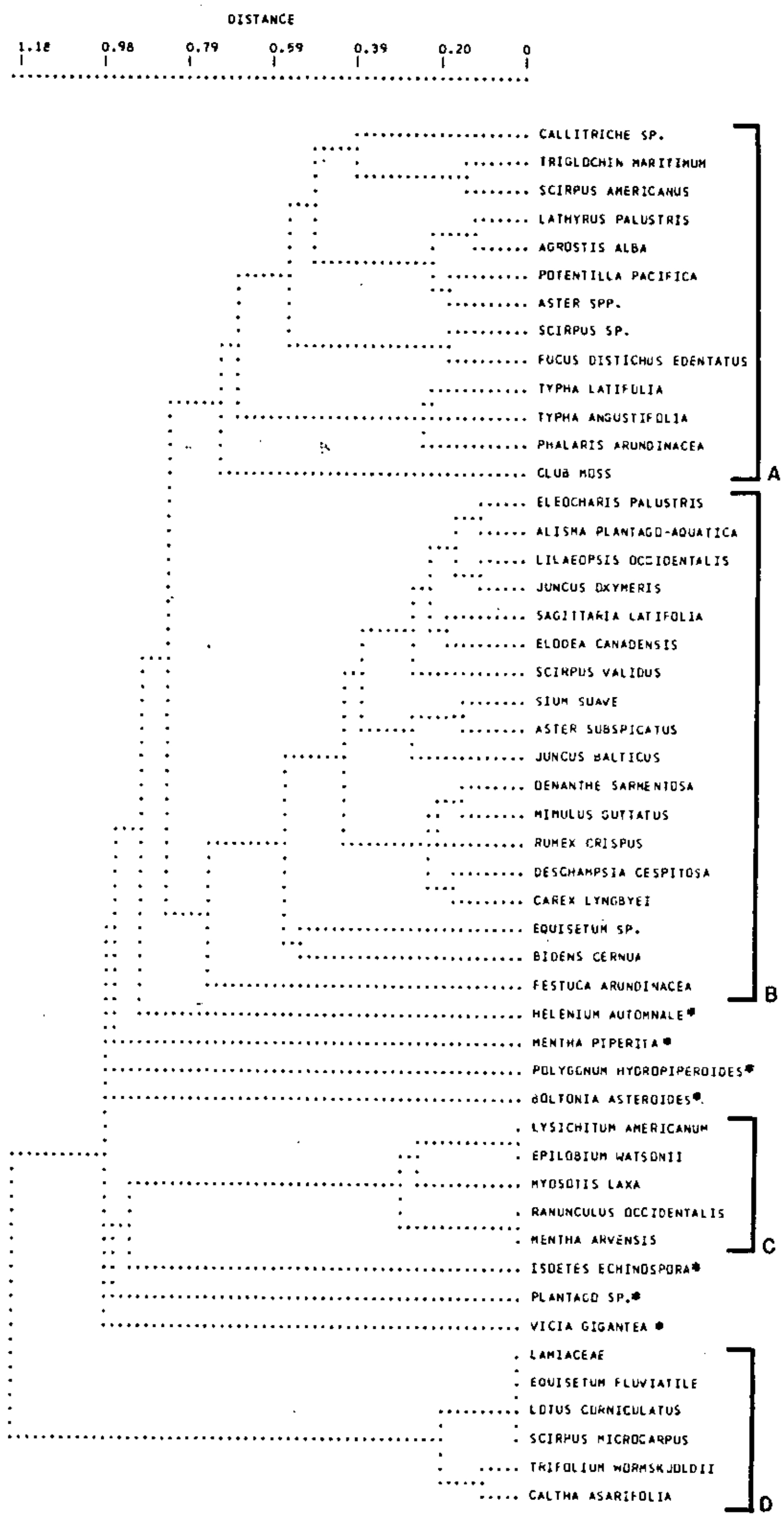


Figure 7. R-Mode (Species) Dendrogram Based on Bray-Curtis Indices Calculated from Species Percent Cover Data, July 1980. (Lettered brackets identify species clusters; Lamiaceae = Mentha sp.; *taxon absent.)

SPECIES\STUDY SITES	1	2				3										4							
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	
CALLITRICHE SP.																							
TRIGLOCHIN MARITIMUM																.	*	+				.	
SCIRPUS AMERICANUS										.	.					*	+					.	
LATHYRUS PALUSTRIS		+	-	-																			
AGROSTIS ALBA		+	+	+	*	.								.				-	-				
POTENTILLA PACIFICA		*	+	.	.	-	-																
ASTER SPP.	*	+	-			-					.		.										
SCIRPUS SP.																			-		-	+	
FUCUS DISTICHUS EDENTATUS																						-	
TYPHA LATIFOLIA	-																						
TYPHA ANGUSTIFOLIA	+								.												+		
PHALARIS ARUNDINACEA	+							-															
CLUB MOSS																							A
ELEOCHARIS PALUSTRIS							.	*	+	-			-		.								
ALISMA PLANTAGO-AQUATICA								+	+				.	.					.				
LILAEOPSIS OCCIDENTALIS							+	-	*	+				.	-			+	.				
JUNCUS OXYMERIS							+	*	-	-	.	+	-	-	+								
SAGITTARIA LATIFOLIA	.							+				*	.	-									
ELODEA CANADENSIS								-		+	+	-											
SCIRPUS VALIDUS												+	+						.				
SIUM SUAVE							.		.	+	+			+	+								
ASTER SUBSPICATUS										+	+				-								
JUNCUS BALTICUS		-	-		.					*													
OENANTHE SARMENTOSA						-								-					+				
MIMULUS GUTTATUS						+	*	.		.	.	.		*	.								
RUMEX CRISPUS						.								+									
DESCHAMPSIA CESPITOSA					.	+	+			+	+	+	-	-	-								
CAREX LYNGBYEI		.	-	+	-	-	-	-	+	-	+	-	+	+	+	-	+	+	+	+	+	+	
EQUISETUM SP.									-														
BIDENS CERNUA								-															
FESTUCA ARUNDINACEA																							B
HELENIUM AUTOMNALE																							
MENTHA PIPERITA																							
POLYGONUM HYDROPIPEROIDES	Absent																						
BOLTONIA ASTEROIDES																							
LYSICHITUM AMERICANUM							-																
EPILOBIUM WATSONII							-																
MYOSOTIS LAXA						.	+																
RANUNCULUS OCCIDENTALIS							+							-									
MENTHA ARVENSIS							+							-									C
ISOETES ECHINOSPORA																							
PLANTAGO SP.	Absent																						
VICIA GIGANTEA																							
LAMIACEAE						-																	
EQUISETUM FLUVIATILE						-																	
LOTUS CORNICULATUS						-																	
SCIRPUS MICROCARPUS						-																	
TRIFOLIUM WORMSKJOLDII						+	.																
CALTHA ASARIFOLIA						+	-				.												D
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	

Figure 8. Two Way Table: Distribution and Relative Abundance of Species Occurrences Among Study Sites, July 1980. [Relative abundances standardized by species means (x) as follows: (.) <0.5x; (-) 0.5 to 1.0x; (+) = 1.0 to 2.0x; (*) >2.0x; blanks indicate absence.] Lamiaceae = Mentha sp.

ized by the species in Cluster B. R-mode Clusters C and D consist mostly of species restricted to single study sites (Tronson Island, high marsh and Inner Gray's Bay, high marsh, respectively).

August 1981 Percent Cover Clusters

The Q-mode dendrogram developed from the August 1981 species percent cover data (Figure 9) is very similar to that for July 1980. (Study site clusters have been numbered to correspond with those identified in Figure 6) Since the Puget Island *Typha* marsh was not resampled in August 1981, it does not appear. The only other change from Figure 5, is that Inner Young's Bay low marsh, probably the brackish marsh site experiencing the greatest freshwater influence, is now grouped with the major freshwater marsh site cluster (Cluster 3).

The species distribution patterns appearing in the R-mode dendrogram for August 1981 (Figure 9) are more complex than in Figure 7, with six rather than four species clusters being identified (Clusters A through F). The two-way table (Figure 11) indicates that species Clusters A and D (each smaller subsets of Clusters A and B in Figure 8), are again mainly responsible for separating the brackish water (Figure 9, Clusters 2 and 4) and freshwater marsh sites (Figure 9, Cluster 3). Cluster E contains species that share rather broad ranges throughout the estuary, including *Carex lyngbyei*. Clusters B, C, and F are each restricted to a different pair of freshwater sites, including one low marsh (Army Corps Pier) and four high marshes (Inner and Outer Gray's Bay, Russian Island, and Tronson Island).

1980-1981 Combined Data Clusters

The Q-mode dendrogram for the combined data sets (Figure 12) yielded a straightforward clustering structure that again separated the brackish marshes (Clusters 2 and 4) from the freshwater sites (Clusters 3A and 3B). Now, more clearly than before, marsh elevation appears to play a role in the clustering. Six of the eight records grouped into Cluster 2 are brackish high marshes, and all 13 of the records in Cluster 4 are brackish low marshes. Similarly, nine of the 11 records in Cluster 3A (fully expanded, as indicated with the dotted line) are freshwater high marshes, and ten of the 11 records in Cluster 3B are freshwater low marshes. The remaining station in Cluster 3B is again Inner Young's Bay low marsh, already noted as a brackish site, but with strong freshwater affinities.

The R-mode dendrogram for the combined data sets (Figure 13) may now be broken down into eight separate clusters (species Clusters A through H) which join together at higher distance coefficients into three large groups (Clusters A, B and C; D, E and F; G and H, respectively).

Inspection of the two-way table (Figure 14) indicates that smaller, more specific groups of species are now more readily identified as being responsible for separating specific clusters of study sites. Species Cluster A, for example, dominated by *Agrostis alba* and *Potentilla pacifica*, and with lesser amounts of *Lathyrus*

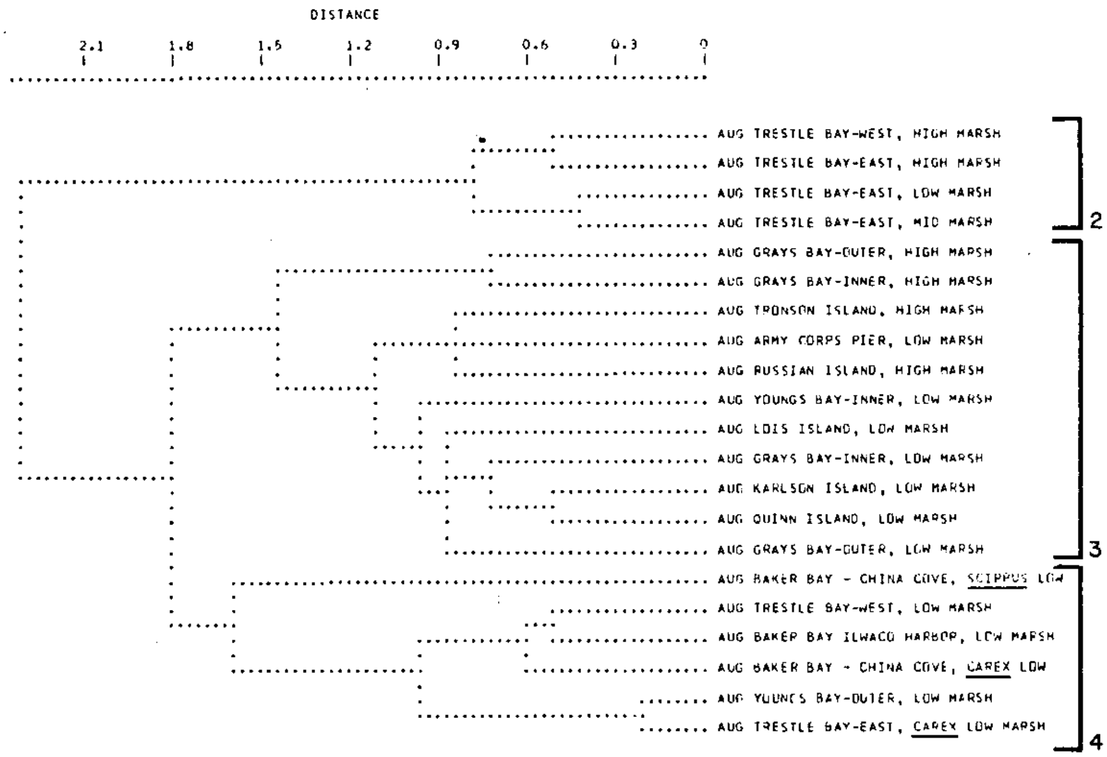


Figure 9. Q-Mode (Study Site) Dendrogram Based on ZAD Indices Calculated from Species Percent Cover Data, August 1981. (Numbered brackets identify study site clusters.)

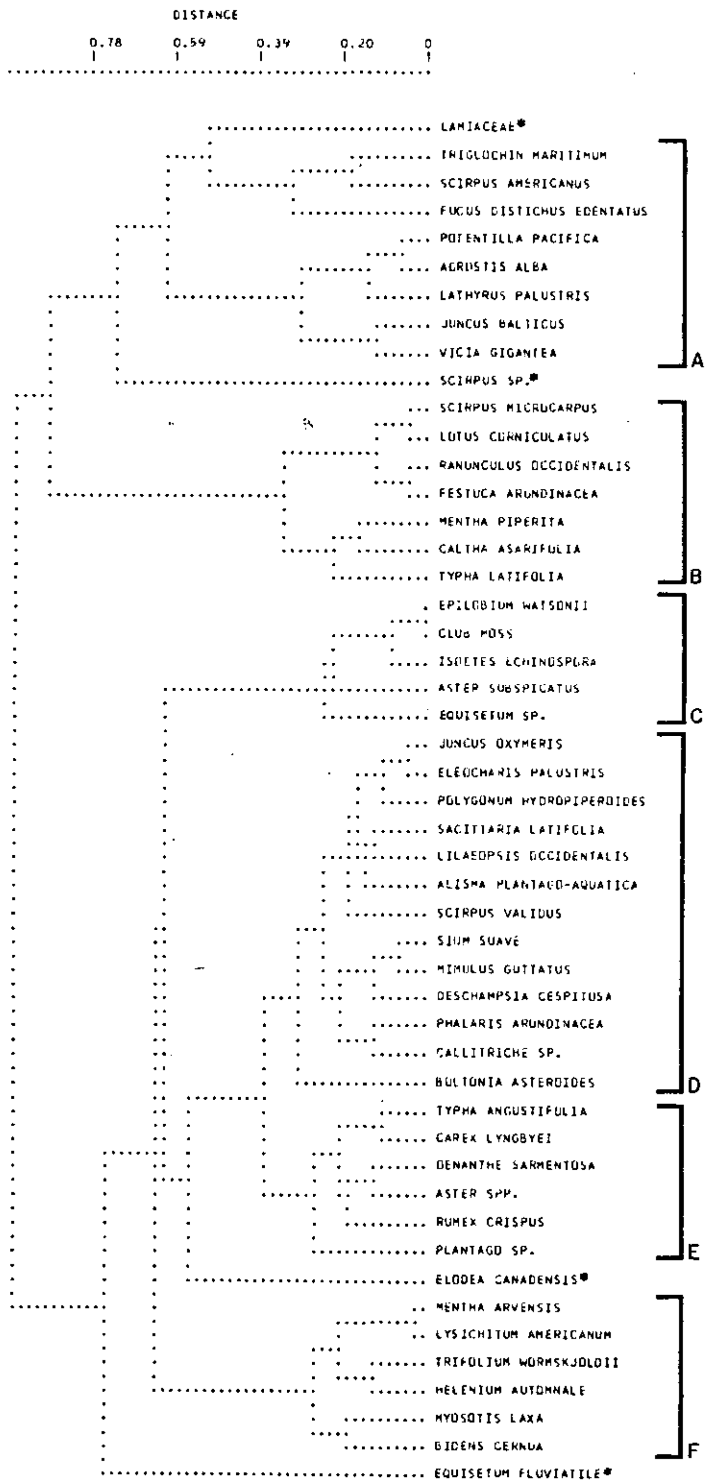


Figure 10. R-Mode (Species) Dendrogram Based on Bray-Curtis Indices Calculated from Species Percent Cover Data, August 1981. (Lettered brackets identify species clusters; Lamiaceae = Mentha sp.; * taxon absent.)

SPECIES\STUDY SITES	2				3											4						
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	
LAMIACEAE																						
TRIGLOCHIN MARITIMUM			.							.						+	+	+				
SCIRPUS AMERICANUS					-										.	*		+	.			
FUCUS DISTICHUS EDENTATUS																			-			
POTENTILLA PACIFICA	*	*	-	+		.	-	.									.					
AGROSTIS ALBA	+	+	*	*			-	.			.						-		.			
LATHYRUS PALUSTRIS		+		-																		
JUNCUS BALTICUS	*	+	-			.																
VICIA GIGANTEA	-																					A
SCIRPUS SP.																						
SCIRPUS MICROCARPUS					+	-				.												
LOTUS CORNICULATUS					+	-																
RANUNCULUS OCCIDENTALIS					+	-																
FESTUCA ARUNDINACEA	.	.			+	+																
MENTHA PIPERITA						+	.															
CALTHA ASARIFOLIA						+	+		.													
TYPHA LATIFOLIA						-																B
EPILOBIUM WATSONII								+	-													
CLUB MOSS								+	-													
ISOETES ECHINOSPORA								+	-			.										
ASTER SUBSPICATUS								-														
EQUISETUM SP.					-	-		+														C
JUNCUS OXYMERIS					.		-	-	.		*	+	+	+	-							
ELEOCHARIS PALUSTRIS					.		-	-		+	+	+	-	-	+							
POLYGONUM HYDROPIPEROIDES								-	-		+	+	+	.	+							
SAGITTARIA LATIFOLIA							-	.	.		+	*	-	+								
LILAEOPSIS OCCIDENTALIS							+		.	.	+		.	.	*		+		+			
ALISMA PLANTAGO-AQUATICA					+		.	.		+	+	+	.	.								
SCIRPUS VALIDUS										-		+	*	-	-				-	-		
SIUM SUAVE					.		-	.	*			+	+	-								
MIMULUS GUTTATUS							-	.	+		-	+										
DESCHAMPSIA CESPITOSA					-		+		-			+	+		-							
PHALARIS ARUNDINACEA							-	-					+									
CALLITRICHE SP.								-	-		-		*									
BOLTONIA ASTEROIDES											.		+									D
TYPHA ANGUSTIFOLIA					.			.												*		
CAREX LYNGBYEI	.	.	-	-	-	+	-	+	+	+	.	.	-	+	+		+	+	+	+	+	
OENANTHE SARMENTOSA	.				-	-			-	*										.		
ASTER SPP.		+			+	-	-		+			+			+							
RUMEX CRISPUS	-				-				*	-												
PLANTAGO SP.									-						+							E
ELODEA CANADENSIS											-											
MENTHA ARVENSIS							+		-													
LYSICHITUM AMERICANUM							+		-													
TRIFOLIUM WORMSKJOLDII							-															
HELENIUM AUTOMNALE							+	.														
MYOSOTIS LAXA						.	+	+														
BIDENS CERNUA							+	.			+											F
EQUISETUM FLUVIATILE																						
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	

Figure 11. Two Way Table: Distribution and Relative Abundance of Species Occurrences Among Study Sites, August 1981. [Relative abundances standardized by species means (x) as follows: (.) <0.5x; (-) 0.5 to 1.0x; (+) = 1.0 to 2.0x; (*) >2.0x; blanks indicate absence.] Lamiaceae = Mentha sp.

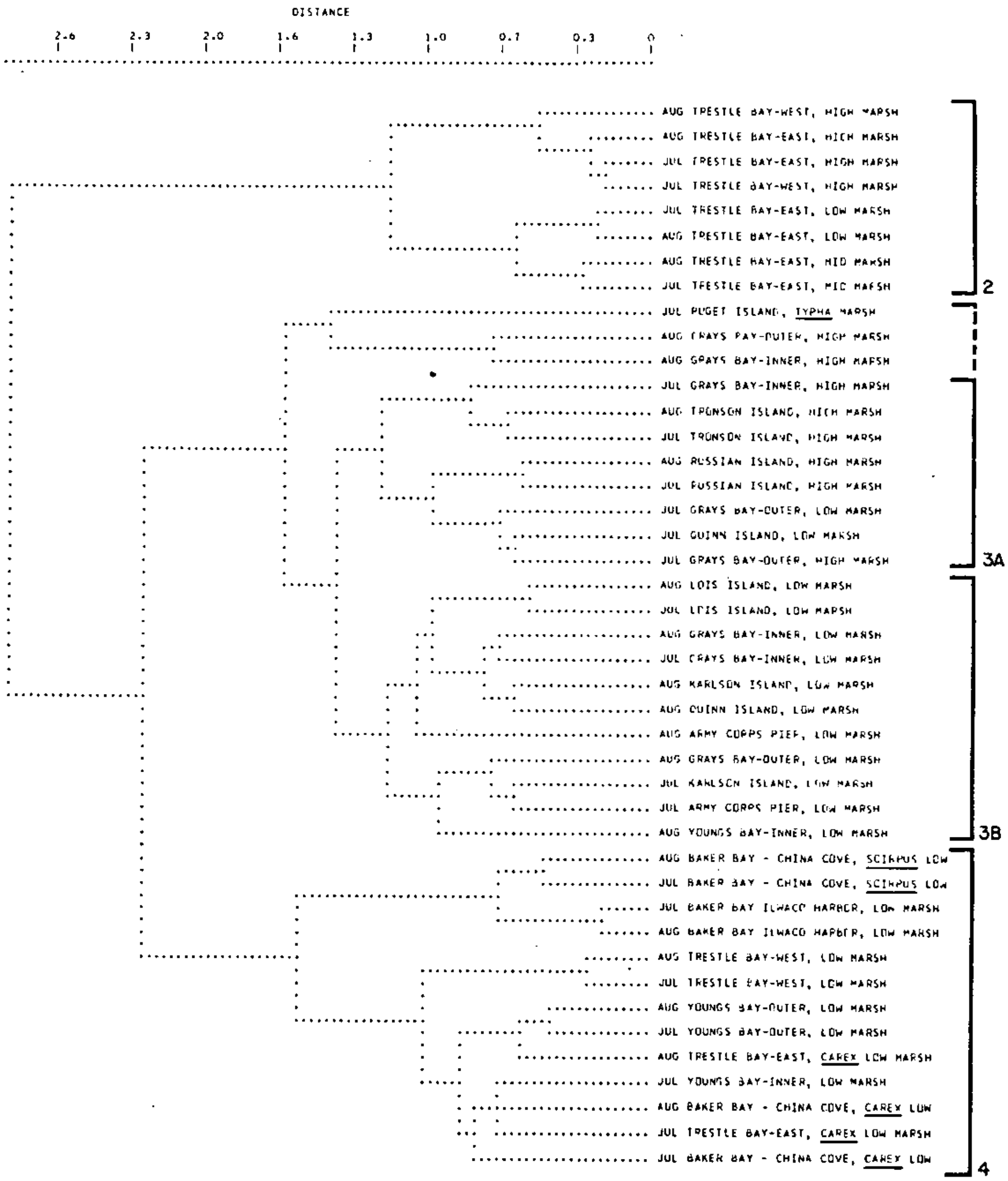


Figure 12. Q-Mode (Study Site) Dendrogram Based on ZAD Indices Calculated from Combined Species Percent Cover Data, July 1980 and August 1981. (Numbered brackets identify study site clusters.)

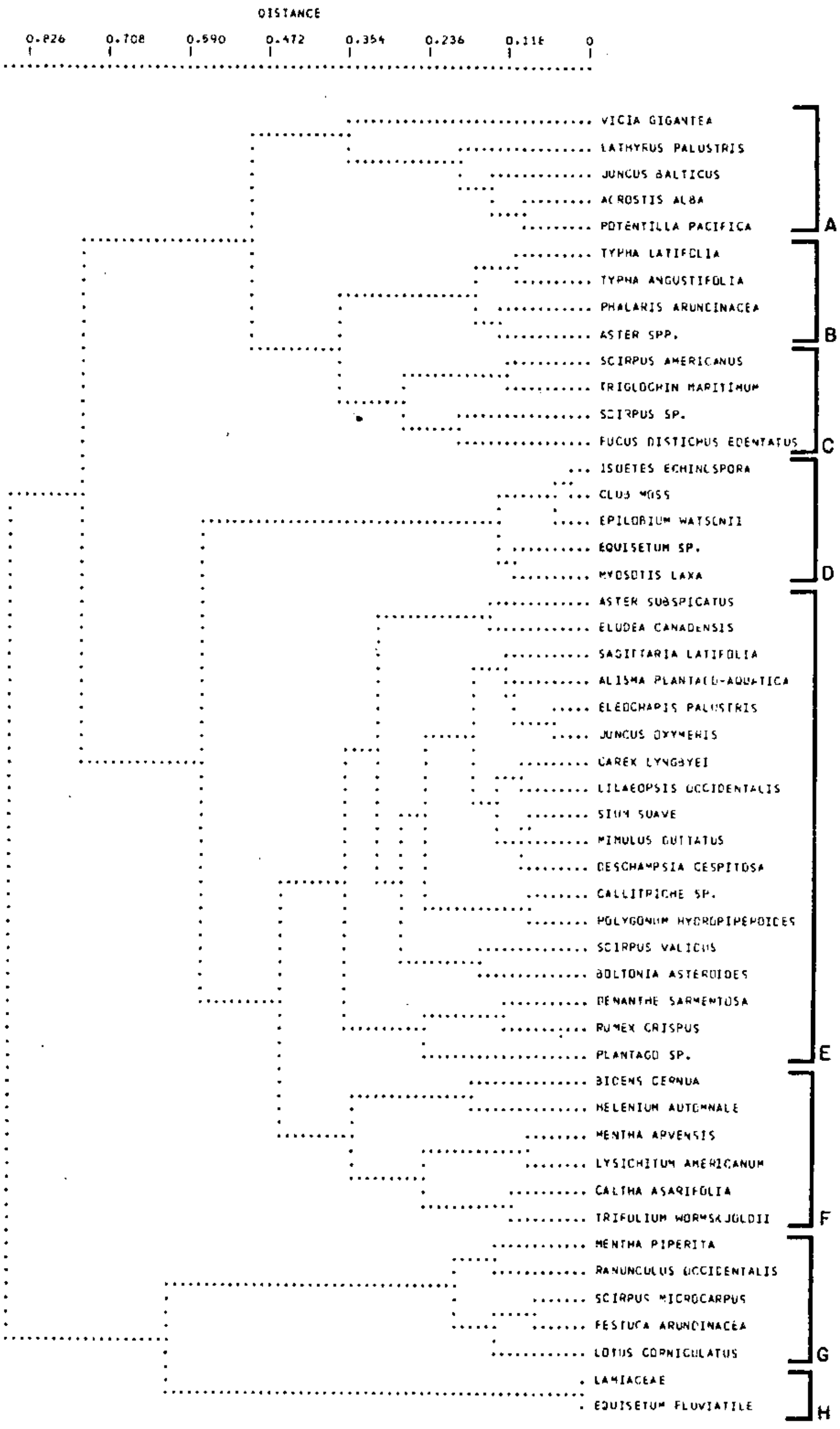


Figure 13. R-Mode (Species) Dendrogram Based on Bray-Curtis Indices Calculated from Combined Species Percent Cover Data, July 1980 and August 1981. (Lettered brackets identify species clusters; Lamiaceae = <u>Mentha</u> sp.)

SPECIES\STUDY SITES	2 (12345678)	901	3A (23456789)	3B (0123456789 0)	4 (1234567890123)	Group
VICIA GIGANTEA	-					
LATHYRUS PALUSTRIS	-+- --					
JUNCUS BALTICUS	+-+-..	.	*			
AGROSTIS ALBA	********		-- .	. .	-- -.	
POTENTILLA PACIFICA	****--+-	-	+--	.	.	A
TYPHA LATIFOLIA		+ .				
TYPHA ANGUSTIFOLIA		+.		. -	+*	
PHALARIS ARUNDINACEA		+	.	+ - -		
ASTER SPP.	---	*-.	-. - .	- -.		B
SCIRPUS AMERICANUS		-	. .	-	**++ - .	
TRIGLOCHIN MARITIMUM	.			.	+.*+++ .	
SCIRPUS SP.					- - +	
FUCUS DISTICHUS EDENTATUS					- +	C
ISOETES ECHINOSPORA			-	. +		
CLUB MOSS			-	+		
EPILOBIUM WATSONII			.-	+		
EQUISETUM SP.		--		+ -		
MYOSOTIS LAXA		.	.+-	+		D
ASTER SUBSPICATUS			*+*	.		
ELODEA CANADENSIS			+ +	.- -		
SAGITTARIA LATIFOLIA		.	- -+	++**-+. .		
ALISMA PLANTAGO-AQUATICA		*	- .	*++ --. .++	.	
ELEOCHARIS PALUSTRIS		.	-. -.	+*+ ---++++		
JUNCUS OXYMERIS		.	---.--.	*++++++++--		
CAREX LYNGBYEI	...----+	.-	--+++-++	.-.--++++++	-++++++++++	
LILAEOPSIS OCCIDENTALIS			++..+-	+- .. * *.	++ .+	
SIUM SUAVE		.	+.*++++*	+ +-. .		
MIMULUS GUTTATUS			++*+*...	-.+. .		
DESCHAMPSIA CESPITOSA	.	-	-++--+--	+++ --		
CALLITRICHE SP.			-	- * -		
POLYGONUM HYDROPIPEROIDES			-	+ + +.-+		
SCIRPUS VALIDUS				+++. -+ -	. .-	
BOLTONIA ASTEROIDES				. +		
OENANTHE SARMENTOSA	.	--	- +-	*	. +	
RUMEX CRISPUS	.	.	. +*	.		
PLANTAGO SP.			-	+		E
BIDENS CERNUA			+	+* .		
HELENIUM AUTOMNALE			*	-		
MENTHA ARVENSIS			++--			
LYSICHITUM AMERICANUM			-+.			
CALTHA ASARIFOLIA		+	*--. .			
TRIFOLIUM WORMSKJOLDII			++.			F
MENTHA PIPERITA		+	.			
RANUNCULUS OCCIDENTALIS		++	- .			
SCIRPUS MICROCARPUS		*+	.	.		
FESTUCA ARUNDINACEA	..	++				
LOTUS CORNICULATUS		+-	-			G
LAMIACEAE			-			
EQUISETUM FLUVIATILE			-			H

12345678901234567890123456789012345678901 23

Figure 14. Two Way Table: Distribution and Relative Abundance of Species Occurrences Among Study Sites, July 1980 and August 1981 Combined Data Sets. [Relative abundances standardized by species means (x) as follows: (.) <0.5x; (-) 0.5 to 1.0x; (+) = 1.0 to 2.0x; (*) >2.0x; blanks indicate absence.] Lamiaceae = Mentha sp.

palustris and Juncus balticus, is almost entirely responsible for separating the East Trestle Bay brackish high marsh sites from all other localities. Brackish low marsh sites (Cluster 4) are similarly uniquely defined by the presence of species Cluster C -- Scirpus americanus, Scirpus sp., Triglochin maritimum, and Fucus distichus.

A large group of species (Cluster E) is shared by many of the freshwater marshes, however the addition of species in Clusters F and G separates the freshwater high marsh sites, from those at lower elevations.

3.3 STANDING CROP MEASUREMENTS

No standing crop measurements, nor primary production estimates, were available from Columbia River Estuary tidal marshes prior to the initiation of this study. Two primary work unit goals therefore were to:

1. Measure seasonal changes in the abundance and distribution of tidal marsh plant biomass (grams dry weight/m^2) throughout the estuary.

2. Utilize the seasonal biomass data to estimate net annual primary production rates (g dry wt/m^2/year) for the estuary marshes.

Our preliminary marsh reconnaissance, as well as published studies and personal experience at other salt marsh sites, suggested that our estuary-wide sampling program also be designed to address the following questions:

1. Are there statistically significant (i.e., $p<0.05$) differences between standing crop and primary production values obtained from tidal marshes at high verses low intertidal elevations?

2. Are there statistically significant (i.e., $p<0.05$) differences between standing crop and primary production values obtained from tidal marshes at the same elevation, at upstream verses downstream locations?

3. Do seasonal patterns of above- and belowground marsh plant standing crop exhibit inverse relationships?

4. Do any trends in standing crop and primary production values among different marsh sites show significant correlations with environmental gradients documented within the estuary (e.g., salinity, tidal range)?

3.3.1 Aboveground Marsh Plant Biomass

Values for the net aboveground standing crop of marsh plants harvested from each study site, during each sampling period (April, May, June, July and October 1980, and August 1981) are presented in

Tables 7 through 12, respectively. All values represent plant biomass as grams dry weight/m^2, the most widely used units for published studies of marsh plant standing crop and primary production. Means ± standard deviations (n=9) are presented for three different components of the aboveground plant biomass: live shoots, attached standing dead material (defined as dead material attached to live plants and being of the same season's growth), and unattached dead plant litter, found lying on the marsh surface.

Precision Analysis

To gain a better understanding of the error (i.e. sampling variability) associated with the estimated mean biomass values, preliminary records for July 1980 total standing crop (i.e. live shoots plus attached standing dead material) were subjected to precision analysis (Elliott 1971). The results are summarized in Table 13 and more fully described in SAI/WCC(1981).

The calculated precision levels for the July 1980 nine-quadrat means at each study site ranged from 0.09 to 0.265, with an average of approximately 0.15. These numbers represent the error present in the estimated mean values. Interestingly, low marsh study sites yielded somewhat higher precision levels (mean, 0.17) than high marsh sites (mean, 0.11), suggesting that the later were more uniform and easier to sample with greater accuracy.

Table 13 also indicates estimated numbers of sample replicates required to change precision levels. In order to increase the precision levels of the means (i.e., reduce the error from 0.15 to 0.10, for example) the number of replicate clip-quadrats harvested would have had to be increased, on average, from nine to 22 (range, from zero to 54).

Percent Cover and 1980-1981 Biomass Relationships

The scatter plot presented in Figure 15 shows the relationship between mean absolute plant cover (estimated as a percentage of sample quadrat area) and the mean net aboveground live marsh plant biomass, recorded at each of the 22 study sites in July 1980. There is no obvious relationship between the two estimates.

Figure 16 presents a scatter plot in which July 1980, aboveground live biomass records for each study site are plotted against August 1981, biomass values for the same sites. While not tested statistically, a general trend is more apparent here. Study sites yielding minimal aboveground biomass in July 1980, tended to do so again in August 1981. Similarly, sites with high biomass values during the 1980 growth season tended to yield high values again at the end of the following year's growth.

Estuary-wide Distribution Patterns

Net aboveground total (live plus standing dead) standing crop measurements (grams dry weight/m^2) taken near the peak of the 1980 growth season (July 1980), and again the following year (August 1981), were divided among the four tidal marsh vegetation types, and pooled.

Table 7. Aboveground Marsh Plant Biomass (g dry wt/m^2): Mean ± Standard Deviation (n=9) April, 1980 (L = Low, M = Middle, and H = High Marsh).

	Live	Attached Dead	Litter
Baker Bay:			
China Cove *Carex* (L)	68±19	5±2	32±16
China Cove *Scirpus* (L)	29±5	4±1	7±2
Ilwaco (L)	32±12	9±4	10±9
Trestle Bay:			
West Trestle (L)	191±41	18±4	56±15
West Trestle (H)	250±28	40±9	782±148
East Trestle *Carex* (L)	140±17	12±3	113±50
East Trestle (L)	101±18	9±9	1051±121
East Trestle (M)	429±33	41±8	680±31
East Trestle (H)	125±33	32±12	670±114
Young's Bay:			
Outer Young's (L)	136±64	14±5	79±43
Inner Young's (L)	136±42	10±3	135±80
Gray's Bay:			
Outer Gray's (L)	-	-	-
Outer Gray's (H)	126±33	8±2	24±12
Inner Gray's (L)	90±28	13±5	19±15
Inner Gray's (H)	171±29	5±2	244±69
Cathlamet Bay:			
Army Corps Dock (L)	48±9	10±5	107±28
Lois Island (L)	7±4	<1±<1	7±5
Russian Island (H)	26±9	1±<1	123±42
Karlson Island (L)	28±9	3±1	49±40
Tronson Island (H)	77±47	12±11	224±112
Fluvial Zone:			
Quinns Island (L)	30±5	2±1	42±11
Puget Island (H)	-	-	-

Table 8. Aboveground Marsh Plant Biomass (g dry wt/m^2): Mean ± Standard Deviation (n=9) May, 1980 (L = Low, M = Middle, and H = High Marsh).

	Live	Attached Dead	Litter
Baker Bay:			
China Cove Carex (L)	575±307	26±21	1±3
China Cove Scirpus (L)	340±69	2±3	0±0
Ilwaco (L)	622±218	8±9	2±4
Trestle Bay:			
West Trestle (L)	645±227	0±0	0±0
West Trestle (H)	509±184	12±7	808±121
East Trestle Carex (L)	479±126	19±11	0±0
East Trestle (L)	320±192	0±0	379±246
East Trestle (M)	540±114	6±8	756±133
East Trestle (H)	445±130	0±0	715±180
Young's Bay:			
Outer Young's (L)	924±301	100±33	0±0
Inner Young's (L)	433±281	23±23	28±34
Gray's Bay:			
Outer Gray's (L)	317±153	4±4	1±4
Outer Gray's (H)	470±130	0±0	27±36
Inner Gray's (L)	476±142	3±7	9±23
Inner Gray's (H)	573±266	9±20	80±150
Cathlamet Bay:			
Army Corps Dock (L)	536±228	0±0	7±6
Lois Island (L)	204±62	0±0	0±0
Russian Island (H)	419±84	0±0	88±51
Karlson Island (L)	114±83	2±5	14±20
Tronson Island (H)	295±147	13±23	52±47
Fluvial Zone:			
Quinns Island (L)	342±124	20±16	23±20
Puget Island (H)	-	-	-

Table 9. Aboveground Marsh Plant Biomass (g dry wt/m²): Mean ± Standard Deviation (n=9) June, 1980 (L - Low, M = Middle, and H = High Marsh).

	Live	Attached Dead	Litter
Baker Bay:			
China Cove *Carex* (L)	821±241	52±23	9±13
China Cove *Scirpus* (L)	386±139	36±15	0±0
Ilwaco (L)	597±374	29±22	25±99
Trestle Bay:			
West Trestle (L)	794±423	49±22	6±10
West Trestle (H)	782±327	43±23	668±205
East Trestle *Carex* (L)	1089±412	48±14	2±5
East Trestle (L)	706±238	28±9	619±191
East Trestle (M)	279±283	26±25	517±324
East Trestle (H)	551±173	24±20	391±146
Young's Bay:			
Outer Young's (L)	2358±434	170±83	42±74
Inner Young's (L)	718±446	113±58	36±25
Gray's Bay:			
Outer Gray's (L)	416±303	28±19	0±0
Outer Gray's (H)	971±361	26±14	94±44
Inner Gray's (L)	319±152	16±10	8±8
Inner Gray's (H)	1021±247	83±37	298±185
Cathlamet Bay:			
Army Corps Dock (L)	595±181	32±18	30±14
Lois Island (L)	331±112	33±18	13±14
Russian Island (H)	819±151	53±13	53±29
Karlson Island (L)	547±265	20±18	13±19
Tronson Island (H)	712±288	56±16	96±57
Fluvial Zone:			
Quinns Island (L)	624±162	49±19	10±20
Puget Island (H)	-	-	-

Table 10. Aboveground Marsh Plant Biomass (g dry wt/m^2): Mean ± Standard Deviation (n=9) July, 1980 (L = Low, M = Middle, and H = High Marsh).

	Live	Attached Dead	Litter
Baker Bay:			
China Cove <u>Carex</u> (L)	523±179	108±76	14±21
China Cove <u>Scirpus</u> (L)	356±221	117±72	2±7
Ilwaco (L)	717±182	128±99	33±39
Trestle Bay:			
West Trestle (L)	545±235	55±35	23±28
West Trestle (H)	730±180	87±26	474±205
East Trestle <u>Carex</u> (L)	1417±480	313±174	17±34
East Trestle (L)	679±271	102±62	691±318
East Trestle (M)	816±304	84±48	712±300
East Trestle (H)	639±210	132±68	704±171
Young's Bay:			
Outer Young's (L)	1646±905	323±135	66±133
Inner Young's (L)	772±404	209±139	48±46
Gray's Bay:			
Outer Gray's (L)	555±317	86±75	28±31
Outer Gray's (H)	700±317	120±131	34±17
Inner Gray's (L)	316±173	75±56	7±18
Inner Gray's (H)	839±316	54±39	144±61
Cathlamet Bay:			
Army Corps Dock (L)	822±516	80±60	83±200
Lois Island (L)	274±202	36±50	100±24
Russian Island (H)	959±258	134±61	101±80
Karlson Island (L)	527±246	49±29	31±31
Tronson Island (H)	539±274	53±33	101±32
Fluvial Zone:			
Quinns Island (L)	701±484	77±31	50±54
Puget Island (H)	1383±835	119±102	1074±893

Table 11. Aboveground Marsh Plant Biomass (g dry wt/m^2): Mean ± Standard Deviation (n=9) October, 1980 (M = Low, M = Middle, and H = High Marsh).

	Live	Attached Dead	Litter
Baker Bay:			
China Cove *Carex* (L)	226±98	382±136	75±86
China Cove *Scirpus* (L)	39±66	228±138	2±5
Ilwaco (L)	237±134	429±167	2±6
Trestle Bay:			
West Trestle (L)	196±91	224±117	6±8
West Trestle (H)	485±216	227±125	212±112
East Trestle *Carex* (L)	10±10	148±54	11±9
East Trestle (L)	460±253	179±149	380±139
East Trestle (M)	487±178	190±102	287±247
East Trestle (H)	176±43	229±96	236±71
Young's Bay:			
Outer Young's (L)	479±402	631±325	56±67
Inner Young's (L)	156±95	221±182	58±36
Gray's Bay:			
Outer Gray's (L)	186±94	48±37	43±23
Outer Gray's (H)	402±266	184±223	135±136
Inner Gray's (L)	290±246	95±92	66±64
Inner Gray's (H)	479±260	265±67	155±108
Cathlamet Bay:			
Army Corps Dock (L)	192±118	97±68	106±46
Lois Island (L)	28±40	16±19	45±24
Russian Island (H)	232±184	312±176	22±15
Karlson Island (L)	268±121	85±56	29±18
Tronson Island (H)	223±73	66±44	83±37
Fluvial Zone:			
Quinns Island (L)	153±72	47±31	198±65
Puget Island (H)	-	-	-

Table 12. Aboveground Marsh Plant Biomass (g dry wt/m^2): Mean ± Standard Deviation (n=9) August, 1981 (L = Low, M = Middle, and H = High Marsh).

	Live	Attached Dead	Litter
Baker Bay:			
China Cove *Carex* (L)	597±256	268±217	3±10
China Cove *Scirpus* (L)	288±113	180±76	1±2
Ilwaco (L)	896±370	167±143	0±0
Trestle Bay:			
West Trestle (L)	928±286	96±31	4±11
West Trestle (H)	883±367	184±85	286±262
East Trestle *Carex* (L)	721±175	138±80	0±0
East Trestle (L)	1172±549	60±37	203±122
East Trestle (M)	1033±184	294±258	294±119
East Trestle (H)	861±282	252±97	267±259
Young's Bay:			
Outer Young's (L)	1329±901	417±211	93±78
Inner Young's (L)	578±247	143±48	32±25
Gray's Bay:			
Outer Gray's (L)	260±228	10±7	37±25
Outer Gray's (H)	724±539	108±66	26±61
Inner Gray's (L)	470±188	60±71	19±26
Inner Gray's (H)	1568±1131	205±166	181±167
Cathlamet Bay:			
Army Corps Dock (L)	590±253	67±46	58±24
Lois Island (L)	290±155	24±31	63±22
Russian Island (H)	945±344	119±37	56±48
Karlson Island (L)	524±253	66±84	20±23
Tronson Island (H)	464±159	35±32	76±53
Fluvial Zone:			
Quinns Island (L)	643±207	74±20	24±28
Puget Island (H)	-	-	-

Table 13. Precision Level, Estimated Number of Quadrats for Selected Precision Levels, and Confidence Intervals for Data Collected During July 1980.

Study Site*	Precision Level* (%)	Estimated Number of Quadrats for Precision Levels** 0.10	0.20	Confidence Intevals† $\alpha = 0.10$	$\alpha = 0.20$
Baker Bay-China Cove, Carex Low Marsh	12	13.2	3.3	630.2 ± 141.9	630.2 ± 106.6
Baker Bay-China Cove, Scirpus Low Marsh	20	36.1	9.0	472.5 ± 176.0	472.5 ± 132.2
Baker Bay-Ilwaco, Low Marsh	10.5	10.0	2.5	845.7 ± 165.5	845.7 ± 124.3
West Trestle Bay, Low Marsh	14	18.5	4.6	600.5 ± 160.0	600.5 ± 120.1
West Trestle Bay, High Marsh	8	6.2	1.5	817.7 ± 125.9	817.7 ± 94.6
East Trestle Bay, Carex Low Marsh	12	12.1	3.0	1730.1 ± 373.1	1730.1 ± 280.2
East Trestle Bay, Low Marsh	13	16.1	4.0	781.3 ± 194.4	781.3 ± 146.0
East Trestle Bay, Middle Marsh	12	13.0	3.3	899.9 ± 201.3	899.9 ± 151.2
East Trestle Bay, High Marsh	10	8.8	2.2	771.5 ± 142.1	771.5 ± 106.7
Outer Young's Bay, Low Marsh	17	27.1	6.8	1969.1 ± 635.9	1969.1 ± 477.6
Inner Young's Bay, Low Marsh	18	27.5	6.9	991.4 ± 323.5	991.4 ± 242.9
Outer Gray's Bay, Low Marsh	18	28.3	7.1	640.9 ± 211.5	640.9 ± 158.8
Outer Gray's Bay, High Marsh	11	10.2	2.6	820.4 ± 162.4	820.4 ± 122.0
Inner Gray's Bay, Low Marsh	18	28.3	7.1	391.4 ± 129.1	391.4 ± 97.0
Inner Gray's Bay, High Marsh	12	12.5	3.1	892.6 ± 195.7	892.6 ± 147.0
Army Corps Dock, Low Marsh	20	36.4	9.1	902.2 ± 337.6	902.2 ± 253.6
Lois Island, Low Marsh	26.5	63.3	15.8	310.8 ± 153.3	310.8 ± 115.1
Russian Island, High Marsh	9	6.8	1.7	1094.0 ± 176.3	1094.9 ± 132.4
Karlson Island, Low Marsh	15	20.8	5.2	576.4 ± 162.9	576.4 ± 122.4
Tronson Island, High Marsh	16	23.6	5.9	591.1 ± 178.0	591.1 ± 133.7
Quinns Island, Low Marsh	20	36.3	9.1	777.7 ± 290.3	777.7 ± 218.1
Puget Island, Typha, Low Marsh	19	32.1	8.0	1501.5 ± 527.7	1501.5 ± 396.3

* Precision level $D = \frac{\text{standard error}}{\text{mean}}$ (Elliott 1971).

** Number of quadrats (n) estimated from following formula (Elliott 1979): $n = \frac{S^2}{D^2 X^2}$

† Confidence intervals calculated using following formula: $\bar{x} \pm t_{\alpha(2),\nu} S_{\bar{x}}$

$\nu = 8$; at $\alpha = 0.10$, $t = 1.860$, at $\alpha = 0.20$, $t = 1.397$

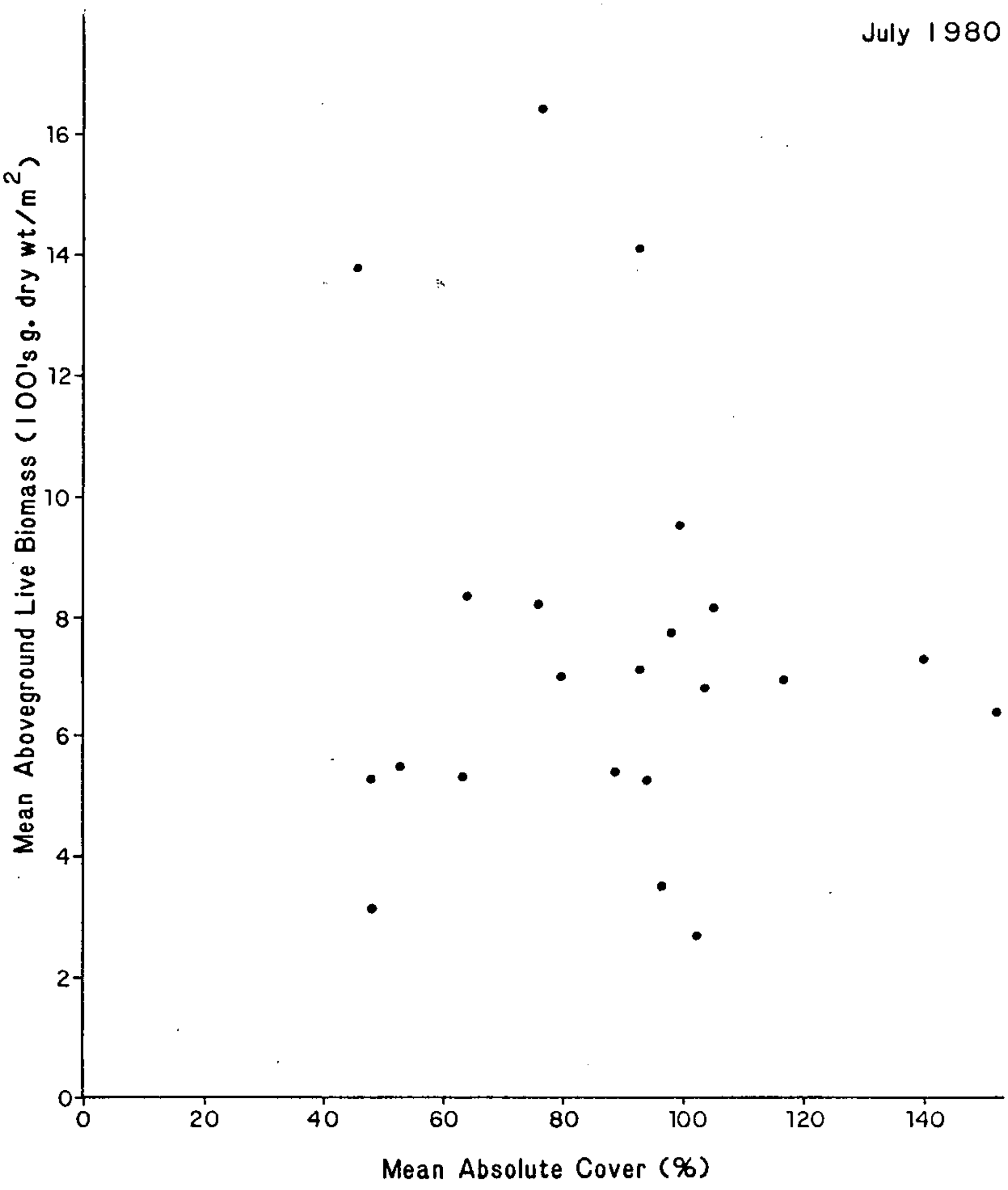


Figure 15. Scatter Plot Showing Relationship Between Mean Absolute Plant Cover (Percent) and Mean Net Aboveground Live Biomass at each Tidal Marsh Study Site, July 1980.

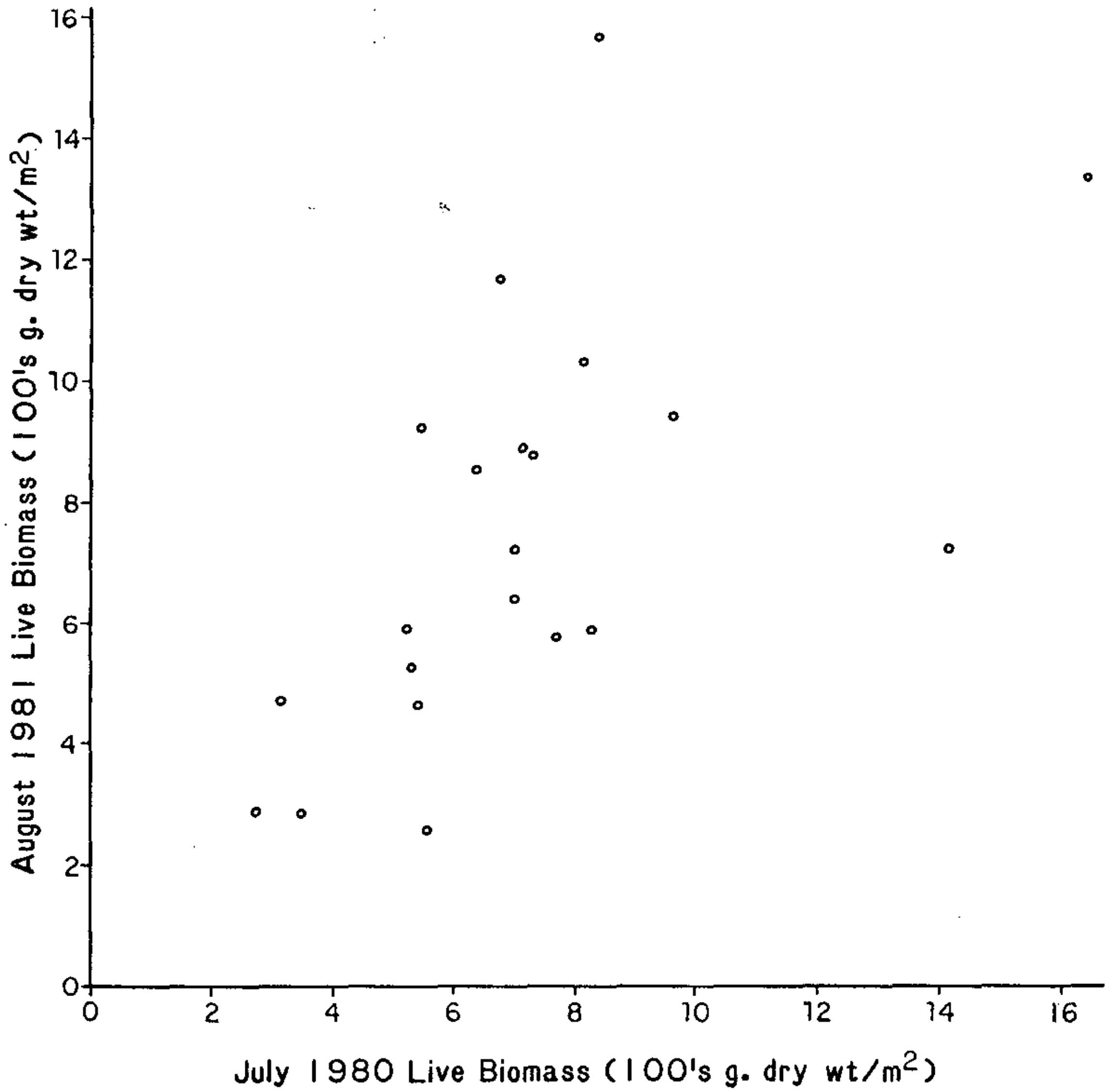


Figure 16. Scatter Plot Showing Relationship Between July 1980 and August 1981 Net Aboveground Live Biomass Means at each Tidal Marsh Study Site.

Summary statistics (mean ± standard deviation, standard error, and range) were then calculated separately for all of the quadrat records within each marsh type (n=27 to 72), and for all marshes combined (n=189 and 198), for both the 1980 and 1981 growth seasons. These summary statistics are presented in Table 14.

Analysis of variance tests (Schefler 1969) were performed separately on the July 1980 and August 1981 net aboveground total standing crop measurements, for the four different groups of tidal marshes (Table 14). Analysis of the July 1980 data yielded a statistically non-significant F-value ($F_{3,194dof} = 0.57$, $p > 0.05$). Standing crop differences among the four marsh groups, in July 1980 at least, can be satisfactorily explained by random variation. A different result was obtained from the August 1981 data, however. Here the analysis of variance F-value was statistically significant ($F_{3,185dof} = 12.44$ $p < 0.01$), implying real differences between total standing crop values among the four marsh categories. Data inspection confirms that in August 1981, standing crop values from the freshwater low marshes were substantially lower than those from the other three marsh groups (Table 14).

The changing rank order of standing crop means among different marsh categories (Table 14), as well as the 1980 to 1981 change in statistical significance, confirm the natural variability and sampling problems associated with tidal marsh standing crop measurements.

3.3.2 Belowground Live Root Biomass

Data describing the net belowground standing crop of live root material (grams dry weight/m^2) contained in replicate (n=2) soil cores, collected from the same locations as aboveground clip-quadrat harvests, are shown in Table 15. Raw data values, as well as means ± standard deviations, are tabulated for soil core samples collected in April, June, July, and October 1980, respectively.

Mean live root biomass estimates were extrapolated from sediment core values (soil core cross sectional area = 50.265 cm^2 x 198.8) to a per square-meter basis (Table 16).

The relationship between seasonal changes in the abundance of aboveground and belowground live biomass of the tidal marsh vegetation is discussed a later section.

3.3.3 Wet Weight-Dry Weight-Ash Free Dry Weight Relationships

As noted above, the majority of published studies describing standing crop data or primary production estimates for marsh vegetation express plant biomass units as grams dry weight/m^2. Wet weight and ash-free dry weight (i.e. organic matter content) values are also sometimes useful however. The Columbia River Estuary Wildlife Work Unit (Dunn et al., 1984), for example, expressed food requirements for several key estuary area mammals in terms of wet weights of marsh plants.

Table 14. Columbia River Estuary Tidal Marshes: Data Summary for Net Aboveground Total Standing Crop Measurements for July 1980 and August 1981. [Values represent grams dry weight/m^2, live tissue plus attached dead plant material of current year's growth.]

Marsh Type	(n)	Mean±S.D.	(Standard Error)	Range
Brackish Tidal Marsh				
Low Marsh - July 1980	(72)	1001±707	(±83)	83-3609
August 1981	(72)	997±576	(±68)	265-3822
High Marsh - July 1980	(27)	830±253	(±49)	492-1259
August 1981	(27)	1169±344	(±66)	341-1815
Freshwater Tidal Marsh				
Low Marsh - July 1980	(54)	600±406	(±55)	102-2009
August 1981	(54)	513±271	(±37)	98-1167
High Marsh - July 1980	(45)	980±537	(±80)	202-3656
August 1981	(36)	1042±844	(±141)	330-5158
All Marshes Combined				
July 1980	(198)	864±571	(±41)	83-3656
August 1981	(189)	892±597	(±43)	98-5158

Table 15. Grams Dry Weight of Live Root Material (raw data, mean ± standard deviation) Contained in Marsh Study Site Soil Cores. 1980. Core Diameter 8 cm, Length 20 cm, and Cross Sectional Area 50.265 cm^2.

	April		June		July		October	
	Raw Data	Mean ± SD	Raw Data	Mean ± SD	Raw Data	Mean ± SD	Raw Data	Mean ± SD
Baker Bay:								
China Cove *Carex* (L)	12.46 14.01	13.24 ± 1.10	14.16 15.13	14.64 ± 0.69	11.96 16.84	14.40 ± 3.45	18.48 19.39	18.94 ± 0.64
China Cove *Scirpus* (L)	10.60 13.17	11.88 ± 1.82	4.86 5.78	5.32 ± 0.65	- -		12.11 16.22	14.16 ± 2.91
Ilwaco (L)	14.84 16.11	15.48 ± 0.90	7.81 15.81	11.81 ± 5.66	12.40 16.94	14.67 ± 3.21	10.39 14.20	12.30 ± 2.69
Trestle Bay:								
West Trestle (L)	15.00 18.16	16.58 ± 2.23	13.06 13.24	13.15 ± 0.13	14.48 14.80	14.64 ± 0.23	12.08 18.71	15.40 ± 4.69
West Trestle (H)	- -		2.12 6.56	4.34 ± 3.14	6.42 7.37	6.90 ± 0.67	5.11 9.92	7.52 ± 3.40
East Trestle *Carex* (L)	- -		9.84 10.39	10.12 ± 0.39	8.16 10.12	9.14 ± 1.39	12.31 17.94	15.12 ± 3.98
East Trestle (L)	- -		0.58 1.56	1.07 ± 0.69	4.36 10.12	7.24 ± 4.07	3.03 5.69	4.36 ± 1.88
East Trestle (M)	- -		6.48 10.99	8.74 ± 3.19	1.52 1.95	1.74 ± 0.30	3.11 4.51	3.81 ± 0.99
East Trestle (H)	2.74 4.36	3.80 ± 1.50	7.06 8.32	7.69 ± 0.89	3.91 5.49	4.70 ± 1.12	6.51 8.62	7.56 ± 1.49
Young's Bay:								
Outer Young's (L)	7.13 25.78	16.46 ±13.19	4.02 9.52	6.77 ± 3.89	3.91 11.51	7.71 ± 5.37	10.39 19.19	14.79 ± 6.22
Inner Young's (L)	6.62 8.84	7.73 ± 1.57	2.89 6.87	4.88 ± 2.81	7.29 10.62	8.96 ± 2.35	4.49 17.45	10.97 ± 9.16

Table 15. (Continued).

	April		June		July		October	
	Raw Data	Mean ± SD	Raw Data	Mean ± SD	Raw Data	Mean ± SD	Raw Data	Mean ± SD
Gray's Bay:								
Outer Gray's (L)	- -		2.60 4.22	3.41 ± 1.15	0.91 3.24	2.08 ± 1.65	3.65 9.40	6.52 ± 4.66
Outer Gray's (H)	7.02 16.86	11.94 ± 6.96	5.30 5.77	5.45 ± 0.33	11.30 16.84	14.07 ± 3.92	5.13 13.68	9.40 ± 6.05
Inner Gray's (L)	4.67 6.10	5.38 ± 1.01	1.58 5.45	3.52 ± 2.74	3.54 5.48	4.51 ± 1.37	1.16 2.52	1.84 ± 0.96
Inner Gray's (H)	8.31 10.00	9.16 ± 1.20	6.30 8.18	7.24 ± 1.33	6.17 11.28	8.72 ± 3.61	7.94 13.55	10.74 ± 3.97
Cathlamet Bay:								
Army Corps Dock (L)	11.84 13.97	12.90 ± 1.51	3.34 10.13	6.74 ± 4.80	3.16 5.02	4.09 ± 1.32	5.42 6.17	5.80 ± 0.53
Lois Island (L)	6.60 7.13	6.86 ± 0.37	0.90 0.95	0.92 ± 0.04	3.96 5.41	4.68 ± 1.03	2.18 3.80	2.99 ± 1.15
Russian Island (H)	15.11 17.14	16.12 ± 1.44	11.48 14.82	13.15 ± 2.36	13.69 15.29	14.49 ± 1.13	1.16 8.29	4.72 ± 5.04
Karlson Island (L)	5.78 11.89	8.84 ± 4.32	6.74 7.28	6.98 ± 0.35	6.87 7.35	7.11 ± 0.34	1.30 1.36	1.33 ± 0.04
Tronson Island (H)	14.66 20.63	17.64 ± 4.22	- -		8.11 8.54	8.32 ± 0.30	4.22 5.26	4.74 ± 0.74
Fluvial Zone:								
Quinns Island (L)	4.43 8.89	6.66 ± 3.15	3.28 5.91	4.60 ± 1.86	5.95 10.20	8.08 ± 3.01	3.66 7.14	5.40 ± 2.46
Puget Island (H)	- -		- -		7.34 9.61	8.48 ± 1.61	- -	

Table 16. Mean Dry Weight of Live Root Material (g dry wt/m^2) Extrapolated (x198.8) From Soil Core Data .

	April	June	July	October
Baker Bay:				
China Cove Carex (L)	2632	2910	2863	3765
China Cove Scirpus (L)	2362	1058	-	2815
Ilwaco (L)	3077	2348	2916	2445
Trestle Bay:				
West Trestle (L)	3296	2614	2910	3062
West Trestle (H)	-	863	1372	1495
East Trestle Carex (L)	-	2012	1817	3006
East Trestle (L)	-	213	1439	867
East Trestle (M)	-	1738	346	757
East Trestle (H)	755	1529	934	1503
Young's Bay:				
Outer Young's (L)	3272	1346	1533	2940
Inner Young's (L)	1537	970	1781	2181
Gray's Bay:				
Outer Gray's (L)	-	678	414	1296
Outer Gray's (H)	2374	1101	2797	1869
Inner Gray's (L)	1070	700	897	366
Inner Gray's (H)	1821	1439	1734	2135
Cathlamet Bay:				
Army Corps Dock (L)	2565	1340	813	1153
Lois Island (L)	1364	183	930	594
Russian Island (H)	3205	2614	2881	938
Karlson Island (L)	1757	1388	1413	264
Tronson Island (H)	3507	-	1654	942
Fluvial Zone:				
Quinns Island (L)	1324	914	1606	1074
Puget Island (H)	-	-	1686	-

Dry weight measurements, as a percentage of the wet weight of freshly harvested marsh plants, were determined for several species at various locations around the estuary. Table 17 presents data for aerial shoots of nine species collected at five of the estuary study sites. Table 18 includes wet weight, dry weight, and ash-free dry weight determinations for mixed-species assemblages of both live root material and aboveground marsh vegetation. The later represent ash-free dry weights for aboveground "whole marsh" assemblages and contain subsamples of the entire species assemblage represented at each study site indicated. In all cases the data are presented as means ± standard deviations.

Additional data describing ash-free dry weights as a percentage of dry weights for aerial shoots of key tidal marsh species, are presented in Tables 19 and 20. Table 19 presents values for Carex lyngbyei and Potentilla pacifica sampled from several estuary sites, in both May 1980 and August 1981. Considerable variation is apparent, but no consistent trends among ash-free weight/dry weight relationships were noted.

3.4 PRIMARY PRODUCTION ESTIMATES

3.4.1 Smalley Net Aboveground Production

The Marsh Plant Primary Production Work Unit, as previously noted under Methods (Section 2.4), relied on sequential replicate (n=9) harvesting of net aboveground standing crop (grams dry weight/m^2) to estimate net annual primary production (grams dry weight/m^2/year). While a number of different methods are available that approximate actual net production with varying levels of accuracy, the method chosen here was that of Smalley (1958). The principal reason for our choice was that Smalley's method offers the most cost-effective balance between accuracy of production estimates and field labor requirements. (Clip-quadrat harvesting of nine 0.1m^2 replicate samples, at each of 21 estuary locations, typically took a field party of four "clippers" and one supervisor between two and three full days to complete.) Smalley's method is probably also the most commonly used estimation procedure among the numerous published studies of marsh production.

Table 21 summarizes individual study site mean net aboveground biomass data from successive harvests in April, May, June, July, and October 1980; shows the Smalley net production calculations; and lists the completed estimates of tidal marsh, net annual aboveground primary production (as grams dry weight/m^2/year). Note that since only a single harvest (July 1980) was completed at Puget Island, that site's net production estimate is based on end of growing season total standing crop.

3.4.2 Other Production Estimates

A number of other approximations of 1980 net production at the different estuary study sites are presented in Table 22. Actual peak live biomass and peak total biomass values were recorded in either late June or late July, depending on location. Maximum minus minimum

Table 17. Dry Weight as a Percentage of Wet Weight, for Aerial Shoots of Tidal Marsh Plants Collected at Selected Study Sites, During 1980 (Mean ± standard deviation).

Collection Site	Collection Date (1980)			
Species	May (n=2)	July (n=5)	August (n=10)	October (n=5)
Baker Bay-Ilwaco				
Triglochin maritimum	-	13.7±1.1	-	-
East Trestle Bay				
Agrostis alba	26.7±3.2	-	-	-
Carex lyngbyei	16.7±0.5	22.1±1.2	25.6±0.8	46.9±1.9
Juncus balticus	35.1±0.1	-	-	-
Potentilla pacifica	19.6±0.2	-	16.5±0.9	31.2±0.9
Inner Grays Bay				
Aster sp.	-	-	-	61.1±2.9
Carex lyngbyei	-	23.2±2.3	-	-
Deschampsia caespitosa	-	27.6±1.1	-	-
Festuca arundinacea	-	-	-	47.9±2.2
Scirpus validus	-	-	-	26.0±1.1
Russian Island				
Carex lyngbyei	16.0±0.1	-	-	-
Potentilla pacifica	16.6±1.2	-	-	-
Quinns Island				
Scirpus validus	12.2±1.0	-	-	-

Table 18. Wet Weight, Dry Weight, and Ash Free Dry Weight (AFDW) Relationships For Mixed Species Samples of Marsh Plant Live Root Material and Aerial Shoots Collected from Selected Study Sites, May 1980 (Mean ± standard deviation).

Study Site	Root Material: Dry Weight as % of Wet Wt. (n=2)	Root Material: AFDW as % of Dry Wt. (n=3)	Aerial Shoots: AFDW as % of Dry Wt. (n=3)
Baker Bay:			
China Cove *Carex* (L)	28.2±7.8	-	-
China Cove *Scirpus* (L)	26.3±4.9	42.9±4.3	-
Ilwaco (L)	26.5±4.9	-	86.8±0.2
Trestle Bay:			
West Trestle (L)	27.4±6.5	64.8±1.1	-
West Trestle (H)	25.7±4.1	78.0±1.3	89.6±0.4
East Trestle *Carex* (L)	-	-	-
East Trestle (L)	-	-	89.2±0.2
East Trestle (M)	25.4±4.6	-	85.9±0.2
East Trestle (H)	26.7±5.6	-	-
Young's Bay:			
Outer Young's (L)	25.9±5.2	-	86.3±0.4
Inner Young's (L)	26.6±6.5	76.8±0.2	-
Gray's Bay:			
Outer Gray's (L)	32.1±11.0	55.9±3.6	88.2±0.2
Outer Gray's (H)	26.4±5.0	49.9±1.4	89.9±0.5
Inner Gray's (L)	25.3±5.0	-	-
Inner Gray's (H)	27.4±6.1	-	-
Cathlamet Bay:			
Army Crops Dock (L)	-	-	-
Lois Island (L)	26.3±4.9	-	89.2±0.3
Russian Island (H)	26.5±5.5	-	-
Karlson Island (L)	26.4±5.3	75.5±0.5	90.6±0.3
Tronson Island (H)	27.3±6.3	-	76.4±0.3
Fluvial Zone:			
Quinns Island (L)	25.5±4.3	-	-
Puget Island (H)	-	-	-
All Data, Pooled:	27.4±6.1 (n=38)	63.2±13.9 (n=19)	87.1±4.1 (n=29)

Table 19. Ash-Free Dry Weight as a Percentage of Dry Weight, for Aerial Shoots of *Carex lyngbyei* and *Potentilla pacifica* at Selected Study Sites, May 1980 and August 1981 (Mean ± standard deviation, n=3; *n=2).

Study Site	*Carex lyngbyei* May 1980	*Carex lyngbyei* August 1981
Baker Bay, China Cove-*Carex* Low Marsh	89.0 ± 0.6	79.8 ± 0.1
West Trestle Bay, High Marsh	91.5 ± 0.4	91.0 ± 0.6
Inner Young's Bay, Low Marsh	78.1 ± 0.1	89.7 ± 0.4
Inner Gray's Bay, High Marsh	91.7 ± 0.3	94.1 ± 0.6
Russian Island, High Marsh	84.7 ± 0.3	91.5 ± 0.4

Study Site	*Potentilla pacifica* May 1980	*Potentilla pacifica* August 1981
West Trestle Bay, High Marsh	85.6 ± 0.5	88.9 ± 0.5
Inner Gray's Bay, High Marsh*	73.8 ± 0.3	89.4 ± 0.4
Tronson Island, High Marsh*	78.2 ± 0.8	76.9 ± 0.1

Table 20. Ash-Free Dry Weight (AFDW) as a Percentage of Dry Weight, for Aerial Shoots of Tidal Marsh Plants Collected August 1981 (Mean ± standard deviation; n=3).

Species	AFDW (% of Dry Wt.)
Agrostis alba	89.2 ± 0.1
Aster subspicatus	88.1 ± 0.4
Deschampsia caespitosa	82.3 ± 0.6
Eleocharis palustris	86.6 ± 0.1
Equisetum sp.	84.0 ± 0.3
Festuca arundinacea	89.7 ± 1.1
Juncus balticus	95.2 ± 0.2
Juncus oxymeris	92.3 ± 0.1
Lysichitum americanum	59.3 ± 1.7
Oenanthe sarmentosa	87.1 ± 0.2
Scirpus americanus	81.7 ± 0.4
Scirpus microcarpus	93.1 ± 0.3
Scirpus validus	91.7 ± 0.2
Triglochin maritimum	76.5 ± 0.5
Typha angustifolia	91.1 ± 0.3
Average Species Mean Value (n=15).	85.9 ± 8.9

Table 21. Mean (n=9) Live and Attached Dead Marsh Plant Aboveground Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	LIVE	DEAD	LIVE	DEAD	LIVE	DEAD	LIVE	DEAD	LIVE	DEAD	CALCULATION	NAPP
Baker Bay:												
China Cove *Carex* (L)	68	5	575	26	821	52	523	108	226	382	73+528+272	873
China Cove *Scirpus* (L)	29	4	340	2	386	36	356	117	39	228	33+311+80+51	475
Ilwaco (L)	32	9	622	8	597	29	717	128	237	429	41+590+219	850
Trestle Bay:												
West Trestle (L)	191	18	645	0	794	49	545	55	196	224	209+454+198	861
West Trestle (H)	250	40	509	12	782	43	730	87	485	227	290+259+304	853
East Trestle *Carex* (L)	140	12	479	19	1089	48	1417	313	10	148	152+346+639+593	1730
East Trestle (L)	101	9	320	0	706	28	679	102	460	179	110+219+414+47	790
East Trestle (M)	429	41	540	6	279	26	816	84	487	190	470+111+595	1176
East Trestle (H)	125	32	445	0	551	24	639	132	176	229	157+320+130+196	803
Young's Bay:												
Outer Young's (L)	136	14	924	100	2358	170	1646	323	479	631	150+874+1504	2528
Inner Young's (L)	136	10	433	23	718	113	772	209	156	221	146+310+375+150	981
Gray's Bay:												
Outer Gray's (L)	-	-	317	4	416	28	555	86	186	48	321+123+197	641
Outer Gray's (H)	126	8	470	0	971	26	700	120	402	184	134+344+527	1005
Inner Gray's (L)	90	13	476	3	319	16	316	75	290	95	103+386+56	545
Inner Gray's (H)	171	5	573	9	1021	83	839	54	479	265	176+406+522	1104
Cathlamet Bay:												
Army Corps Dock (L)	48	10	536	0	595	32	822	80	192	97	58+488+91+275	912
Lois Island (L)	7	<1	204	0	331	33	274	36	28	16	7+197+160	364
Russian Island (H)	26	1	419	0	819	53	959	134	232	312	27+393+453+221	1094
Karlson Island (L)	28	3	114	2	547	20	527	49	268	85	31+86+451+9	577
Tronson Island (H)	77	12	295	13	712	56	539	53	223	66	89+219+460	768
Fluvial Zone:												
Quinns Island (L)	30	2	342	20	624	49	701	77	153	47	32+330+331+105	778
Puget Island (H)	-	-	-	-	-	-	1383	119	-	-	1383+119	1502*

* End of Season Total Standing Crop.

Table 22. Columbia River Estuary: Summary of Tidal Marsh Plant Net Aboveground Standing Crop Measurements (g dry wt/m^2) and Primary Production Estimates (g dry wt/m^2/yr), 1980.

Study Site	Net Standing Crop			Net Primary Production		
	Peak Live[1]	Peak Total[1]	Max-Min. [Peak-April]	Smalley	Smalley Spp. Peak	Species Peak Carex
Baker Bay:						
China Cove Carex (L)	821*	873*	800	873	1667	1115
China Cove Scirpus (L)	386*	473	440	475	580	154
Ilwaco (L)	717	845	804	850	918	670
Trestle Bay:						
West Trestle (L)	794*	843*	634	861	1286	831
West Trestle (H)	782*	825*	535	853	1108	121
East Trestle Carex (L)	1417	1730	1578	1730	1796	1715
East Trestle (L)	706*	781	671	790	1271	531
East Trestle (M)	816	900	430	1176	1511	629
East Trestle (H)	639	771	614	803	977	20
Young's Bay:						
Outer Young's (L)	2358*	2528*	2378	2528	2706	1816
Inner Young's (L)	772	981	835	981	1082	901
Gray's Bay:						
Outer Gray's (L)	555	641	641[2]	641	833	207
Outer Gray's (H)	971*	997*	863	1005	1680	612
Inner Gray's (L)	319*	391	293	545	754	193
Inner Gray's (H)	1021*	1104*	928	1104	1437	658
Cathlamet Bay:						
Army Corps Dock (L)	822	902	844	912	1204	368
Lois Island (L)	331*	364*	356	364	490	37
Russian Island (H)	959	1093	1066	1094	1193	699
Karlson Island (L)	547*	576	545	577	710	299
Tronson Island (H)	712*	768*	679	768	871	114
Fluvial Zone:						
Quinns Island (L)	701	778	746	778	1157	613
Puget Island (H)	1383	1501	1501[2]	-	-	51

[1]Asterisks indicate July 1980 data; other values June 1980.
[2]Peak total only; no April 1980 measurements.

standing crop (taken as peak total, minus April total biomass) allows for the presence of "overwintering" shoots generated during the previous (1979) growth season. Either the peak live biomass, or the maximum minus minimum total biomass, method usually yielded the lowest net aboveground production estimate at each study site.

Since the Smalley species peak procedure sums net production, calculated separately for each species, its production estimates (490 to 2,706 grams dry weight/m^2/year, net aboveground) were consistently the highest of those calculated. The regular Smalley calculation considers all species together so individual species peaks are averaged out. In contrast, the species peak procedure identifies these peak values and then sums them.

3.4.3 Net Aboveground Production By Marsh Type

Smalley net annual aboveground plant production estimates from the different estuary study sites (Table 21, NAPP), were sorted among the four major tidal marsh types, and pooled. Numbers of production estimates per tidal marsh category varied from three to eight. Summary statistics (mean ± standard deviation, standard error, and range) for net production estimates, by marsh category, and for all marshes combined, are presented in Table 23.

An analysis of variance (Schefler 1969) performed on net production estimates from the four different groups of tidal marshes (Table 23) yielded a statistically non-significant F-value ($F_{3,18dof} = 1.59$ $p > 0.05$). This indicates that production differences among the four groups of marshes can be satisfactorily explained by random variation.

For estuary-wide data integration and planning purposes therefore, it can be assumed that all marsh types are equally productive. The mean estimated net annual aboveground marsh production value (based on all 22 study sites) of 964 grams dry weight/m^2/year, can be assumed representative of all tidal marshes in the Columbia River Esutary. The additional potential contribution of scrub-shrub, and forested wetland (swamp) habitats still remains to be investigated.

The absence of statistically significant differences among primary production estimates from the four major tidal marsh types at least partly reflects the high site-to-site variability noted within each marsh catagory. This variability certainly might be real, or it may be an artifact of inadequate sampling. If differences do exist among the marshes, then it would be useful to persue the question of what environmental variables correlate with productivity estimates from individual study sites.

3.4.4 Smalley Marsh Production and Environmental Variables

The influence of specific environmental variables upon the species composition and primary production of tidal marshes is only partly understood, however several key parameters have been identified. These include:

Table 23. Columbia River Estuary Tidal Marshes: Data Summary for Estimated Net Annual Aboveground Plant Production. [Calculated from 1980 plant biomass data using the Smalley (1958) Method; values represent grams dry weight/m^2/year.]

Marsh Type	(n)	Mean±S.D.	(Standard Error)	Range
Brackish Tidal Marsh				
Low Marsh	(8)	1136±665	(±236)	475-2528
High Marsh	(3)	944±202	(±117)	803-1175
Freshwater Tidal Marsh				
Low Marsh	(6)	636±191	(±78)	364-912
High Marsh	(5)	1095±265	(±119)	768-1502
All Marshes Combined	(22)	964±469	(±100)	364-2528

1. Frequency and duration of tidal submergence (influenced by: local topography, relative elevation within the intertidal zone, local tidal patterns, interaction of ocean tides and river outflow);

2. Salinity regimes of interstitial soil water (soil salinity) and tidal flood waters (particularly spatial and temporal patterns of salinity extremes and variability of soil salinity at increasing intertidal elevations);

3. Substrate type (which influences cohesion and stability, water-retaining capacity, soil oxygen conditions, nutrient and organic matter availability);

4. Availability and abundance of dissolved nutrients (particularly nitrate and phosphate);

5. Climate and local weather conditions that might influence plant growth (temperature, frost-free days, precipitation).

Direct field measurements of these types of variables at each of the tidal marsh study sites was beyond the scope of this project. Study site values for physical variables available from maps and published records (see Methods, Section 2.6) were therefore used as indirect indicators of the types of parameters listed above. These variables included, study site distance from the estuary mouth (km), mean diurnal tidal range (ft), and mean surface salinities (ppt) under conditions of both high freshwater river outflow and low river outflow. In addition, specific study site elevation measurements (ft), relative to MLLW or its local equivalent, were provided by CREDDP staff and the U.S. Army Corps of Engineers. Values for these selected physical variables are presented for each study site in Table 24.

Statistical Analyses

Correlation coefficients calculated among all possible pairs of the five environmental variables noted above indicated significant ($p < 0.03$) negative correlations of all variables with increasing distance upriver; and positive correlations ($p < 0.02$) between study site elevations and surface salinity values, under both high and low river flow conditions. This precluded their use as "independent variables" in standard multiple regression procedures to examine relationships with dependant variables such as marsh standing crop or estimated production.

This difficulty was partially overcome by using an R-square procedure (SAS 1982) that rapidly calculated 1000 separate regression models, accounting for all possible numbers and combinations of the physical variables against the Smalley net annual aboveground primary production estimates. The original variables and $(\text{variable})^2$-transforms were used, to allow for both linear and non-linear regression models. The variables from the five-variable model with the highest R-square value and minimum duplication of variables were then substituted in a standard multiple regression procedure. The resulting

Table 24. Selected Physical Variables at Columbia River Estuary Marsh Study Sites. See Text for Additional Explanation.

	Distance From River Mouth (km)[1]	Elevation Above MLLW (ft)[2]	Mean Diurnal Tidal Range (ft)	Mean Surface Salinity[3]	
				High Flow	Low Flow
Baker Bay:					
China Cove *Carex* (L)	7.4	6.00	8.0	5.0	16.8
China Cove *Scirpus* (L)	7.4	6.10	8.0	5.0	16.8
Ilwaco (L)	7.8	6.50	8.0	5.0	16.8
Trestle Bay:					
West Trestle (L)	8.5	7.37	8.1	3.9	13.0
West Trestle (H)	8.5	8.50	8.1	3.9	13.0
East Trestle *Carex* (L)	9.5	7.17	8.2	3.3	11.5
East Trestle (L)	9.5	7.85	8.2	3.3	11.5
East Trestle (M)	9.5	8.43	8.2	3.3	11.5
East Trestle (H)	9.5	8.83	8.2	3.3	11.5
Young's Bay:					
Outer Young's (L)	17.0	6.40	8.6	0.3	5.0
Inner Young's (L)	20.0	6.76	8.7	0.1	4.0
Gray's Bay:					
Outer Gray's (L)	31.2	2.90	8.1	0.0	0.5
Outer Gray's (H)	31.2	5.90	8.1	0.0	0.5
Inner Gray's (L)	31.6	3.81	8.1	0.0	0.5
Inner Gray's (H)	31.6	8.31	8.1	0.0	0.5
Cathlamet Bay:					
Army Corps Dock (L)	26.4	5.35	8.5	0.0	0.5
Lois Island (L)	28.4	4.99	8.5	0.0	0.5
Russian Island (H)	34.0	6.14	8.1	0.0	0.0
Karlson Island (L)	35.5	2.87	8.1	0.0	0.0
Tronson Island (H)	42.7	6.26	7.6	0.0	0.0
Fluvial Zone:					
Quinns Island (L)	44.2	4.35	7.6	0.0	0.0
Puget Island (H)	60.1	6.85	6.6	0.0	0.0

[1]Minimum study site to rivermouth (i.e., midpoint of line joining seaward ends of north and south Jetties) distance, measured at water level (i.e., around islands, headlands, etc.).

[2]Elevation at specific sampling location.

[3]Mean surface salinity values (ppt) under conditions of high and low river flow, respectively.

five-variable regression model projected study site net production estimates with statistical significance ($F_{20dof} = 4.448$, $p<0.008$). Negative regressions with both study site distance upriver, and surface salinity values under high river flow conditions, were the most significant terms in the regression model.

The statistical significance of the multiple regression model (physical variables against net production) increased substantially (F value $p<0.0004$) when only two environmental variables -- surface salinities under conditions of high (negative regression) and low (positive regression) river flow, respectively -- were included.

A stepwise regression procedure that ignored interaction terms between the "independent" environmental variables was also used to predict net aboveground production values at the various study sites. Again, all possible combinations of environmental variables were tested. No one- or two-variable regression models proved to be statistically significant. The three-variable regression including study site elevation (positive regression) and surface salinities under high river flow (negative regression) and low river flow (positive regression) conditions, was statistically significant (F20dof = 4.78, $p<0.014$)
however.

A four-variable stepwise regression model that included distance upriver (negative regression), tidal range (negative regression), and surface salinities under high (negative regression) and low (positive regression) river flow conditions, predicted net annual aboveground primary production values with slightly greater significance ($p=0.01$).

Principal Components Analysis, applied to the same variables as discussed above, failed to produce significant ($p>0.20$) results, apparently because of the high site-to-site variability in net aboveground primary production estimates. Axis selection again hinted however, that surface salinity values were the most important environmental variables affecting net production.

Conclusions

When taken together, the results of the various statistical analyses outlined above suggest the following conclusions:

1. Prediction of primary production (or standing crop) values at specific estuary sites, on the basis of the mostly indirect environmental measurements available, is very difficult -- principally because of the great site-to-site variability in net production (or standing crop) that exists.

2. Indirect measurements of environmental variables, such as used here, were a less useful substitute for site specific physical data than expected.

3. Among the five indirect environmental variables tested, surface salinity regimes yielded the most significant regressions against estimated net annual aboveground primary

production in the tidal marshes. Site elevations were also important.

4. While the relationships are clearly not simple ones, tidal marsh net aboveground primary production exhibits statistically significant trends -- increasing both upriver from the estuary mouth and at higher intertidal elevations.

3.5 MARSH PLANT DECOMPOSITION RATES

Decomposition and loss rates of plant material from the marsh surface were measured during three litter bag experiments, as described in Section 2.5. Initiated in May 1980, July 1980, and October 1980, respectively, the three experiments were each designed to measure loss rates for different plant types, marsh elevations, and estuary locations.

The litterbag experiments were initially designed to address two questions:

1. Do marsh plant species decompose more quickly in low marsh than high marsh habitats?

2. Do less "fiberous" marsh plants decompose more quickly than more "fiberous" species at similar intertidal elevations?

Preliminary data from the initial experiment suggested a modification of the experimental design to address a third question:

3. Do similar species, at similar intertidal elevations, decompose more quickly at upstream verses downstream locations?

The distribution of litterbags during the three experiments is shown in Figure 17. Experimental results for each separate test period -- tabulated as percentages of dry weight material lost, after varying numbers of weeks of litterbag exposure in the field -- are shown in Tables 25, 26, and 27, respectively. The same data are plotted graphically (as percentages of the initial dry weight equivalent of litterbag material still remaining/against exposure time, in weeks) for Experiment One in Figures 18 and 19; for Experiment Two in Figure 20; and for Experiment Three in Figures 21, 22, and 23. Note that decomposition rates are often quite rapid for the first month or two, but then slow substantially.

In all, decomposition rates for nine species -- *Agrostis*, *Aster*, *Carex*, *Deschampsia*, *Festuca*, *Juncus*, *Potentilla*, *Scirpus*, and *Triglochin* -- at high and low marsh sites in Baker and East Trestle Bays downriver, and Gray's Bay, Russian and Quinns Island upriver, were measured.

Analysis of covariance tests indicate that within each separate experiment the slopes of the decomposition curves for different species and locations (i.e. the decomposition rates) are not all equal ($p<0.05$). Student-Newman-Kuels tests were used to identify

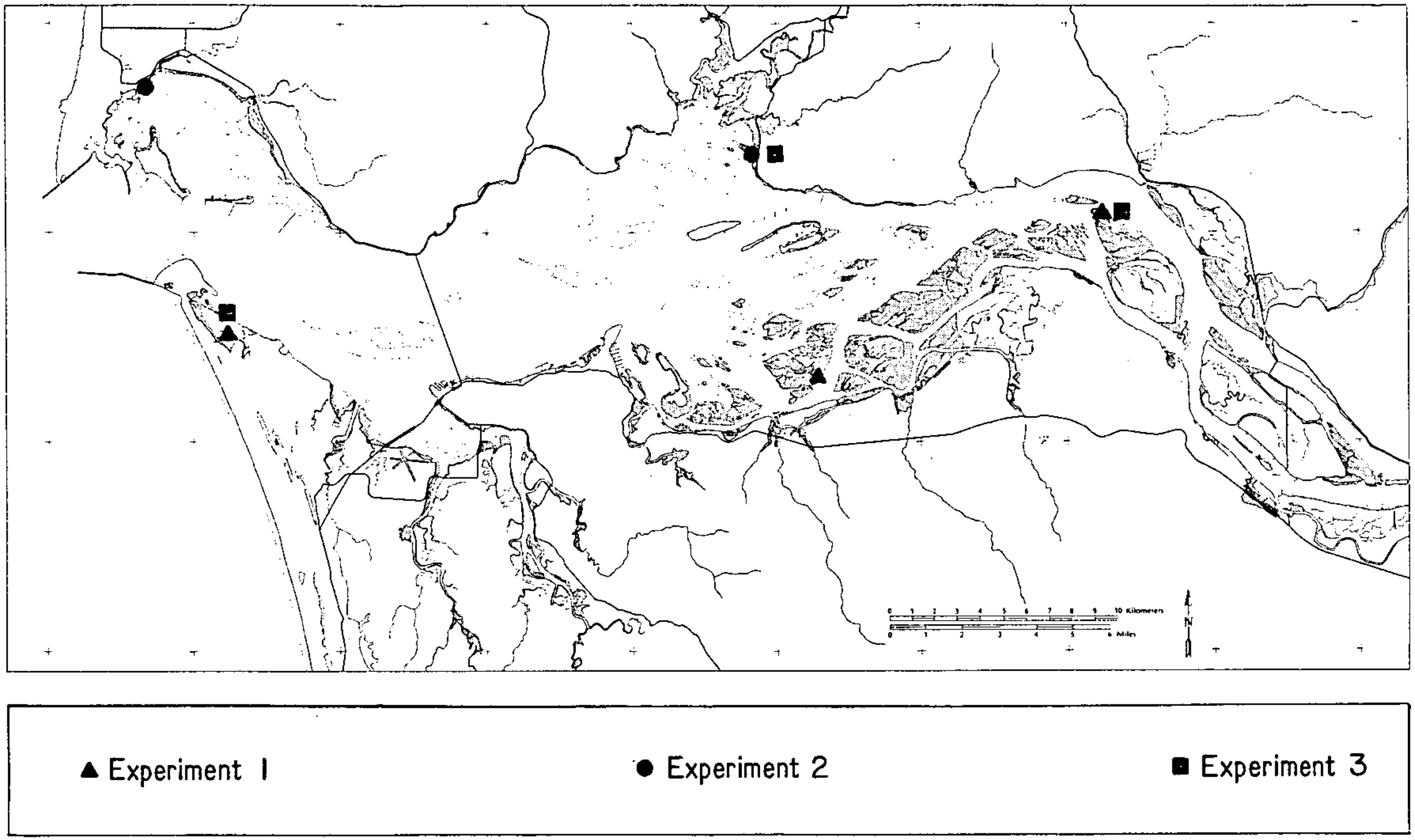


Figure 17. Study Site Locations for the Columbia River Estuary Litterbag Experiments.

Table 25. Litterbag Experiment One: Duration 33 Weeks, May 1980 Through January 1981. (Values represent percentages of initial dry weight equivalent of plant material lost after various numbers of weeks in the field.)

Location Elevation	Species*	Percent Dry Weight Material Lost After: 4 Weeks	9 Weeks	22 Weeks	33 Weeks
East Trestle Bay					
Low Marsh	*Carex lyngbyei*	30	38	49	72
	Agrostis alba	35	43	54	76
High Marsh	*Carex lyngbyei*	25	35	59	67
	Potentilla pacifica	27	23	44	61
	Juncus balticus	14	25	45	60
Russian Island					
High Marsh	*Carex lyngbyei*	12	61	88	99.4
	Potentilla pacifica	13	57	94	99.3
Quinn's Island					
Low Marsh	*Carex lyngbyei*	29	63	86	96
	Scirpus validus	62	84	90	97

* East Trestle Bay material collected on site; all other material collected from Grays Bay.

Table 26. Litterbag Experiment Two: Duration 28 Weeks, July 1980 Through January 1981. (Values represent percentages of initial dry weight equivalent of plant material lost after various numbers of weeks in the field.)

Location Elevation	Species	Percent Dry Weight Material Lost After: 4 Weeks	10 Weeks	17 Weeks	28 Weeks
Baker Bay - Ilwaco Harbor					
Low Marsh	*Carex lyngbyei**	12	32	36	61
	Triglochin maritimum	43	68	66	86
Inner Grays Bay					
Low Marsh	*Carex lyngbyei*	29	59	71	86
	Deschampsia caespitosa	35	65	63	86

* Collected from East Trestle Bay.

All other meterial collected on site.

Table 27. Litterbag Experiment Three: Duration 38 Weeks, October 1980 through July 1981. (Values represent percentages of initial dry weight equivalent of plant material lost after various numbers of weeks in the field.)

Location		Percent Dry Weight Material Lost After:				
Elevation	Species	6 Weeks	12 Weeks	20 Weeks	28 Weeks	38 Weeks
East Trestle Bay						
Low Marsh	*Carex lyngbyei*	23	33	52	60	66
	Scirpus validus	24	41	55	60	68
High Marsh	*Festuca arundinacea*	12	28	32	44	50
	Potentilla pacifica	42	51	57	60	71
	Aster sp.	30	44	47	49	72
Inner Grays Bay						
Low Marsh	*Carex lyngbyei*	31	48	71	91	94
	Scirpus validus	32	38	58	87	93
High Marsh	*Festuca arundinacea*	0	7	17	52	56
	Potentilla pacifica	12	42	48	69	83
	Aster sp.	22	47	49	60	65
Quinn's Island						
Low Marsh	*Carex lyngbyei*	35	47	71	95	96
	Scirpus validus	33	44	59	90	92
High Marsh	*Festuca arundinacea*	0	24	52	72	80
	Potentilla pacifica	0	25	67	90	93
	Aster sp.	24	51	64	72	87

All *Carex* and *Potentilla* collected from East Trestle Bay.

All *Scirpus*, *Festuca* and *Aster* collected from Inner Grays Bay.

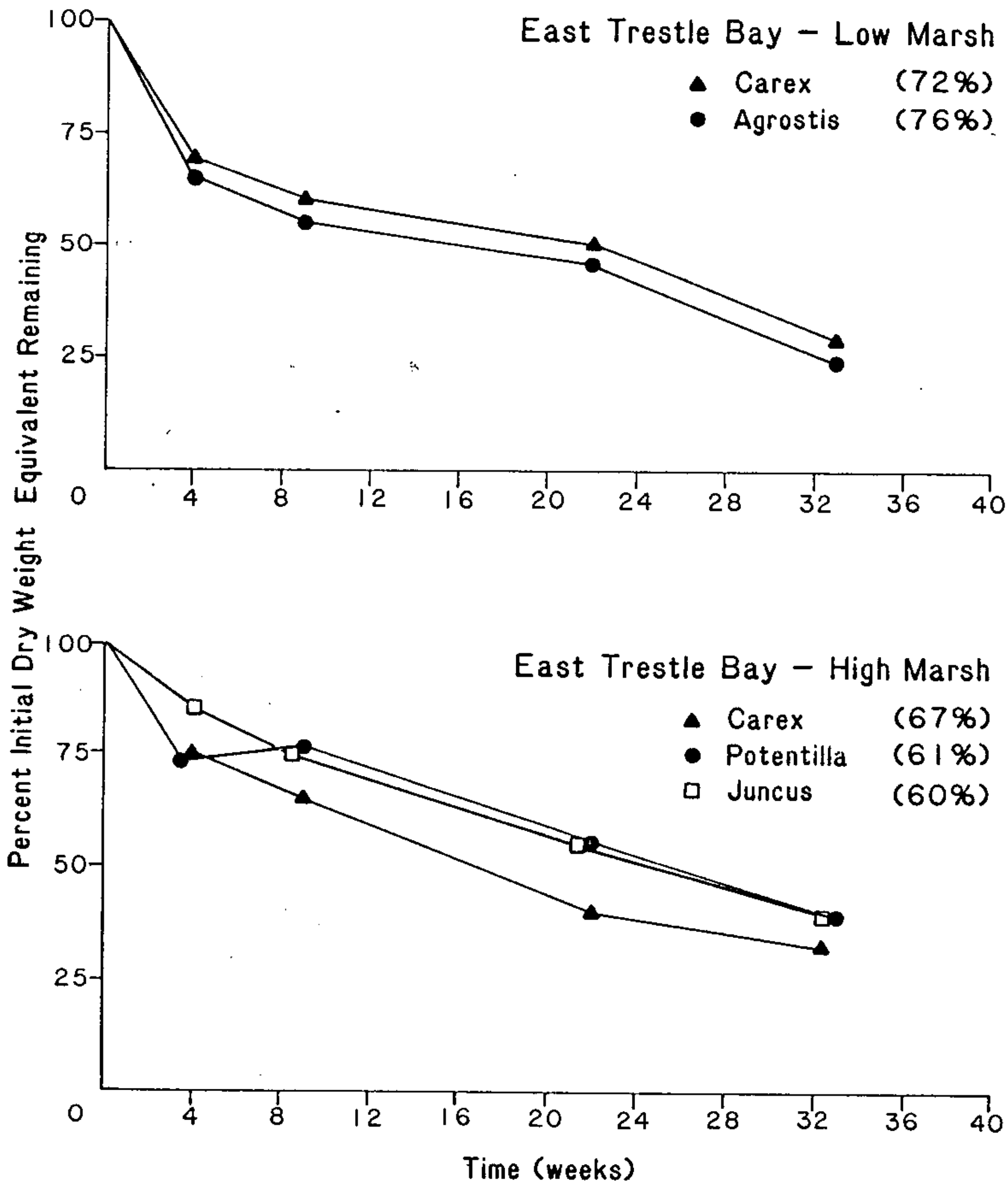


Figure 18. Decomposition Rates of Selected Tidal Marsh Plants, Columbia River Estuary. Experiment One; litterbags set out May 30, 1980.

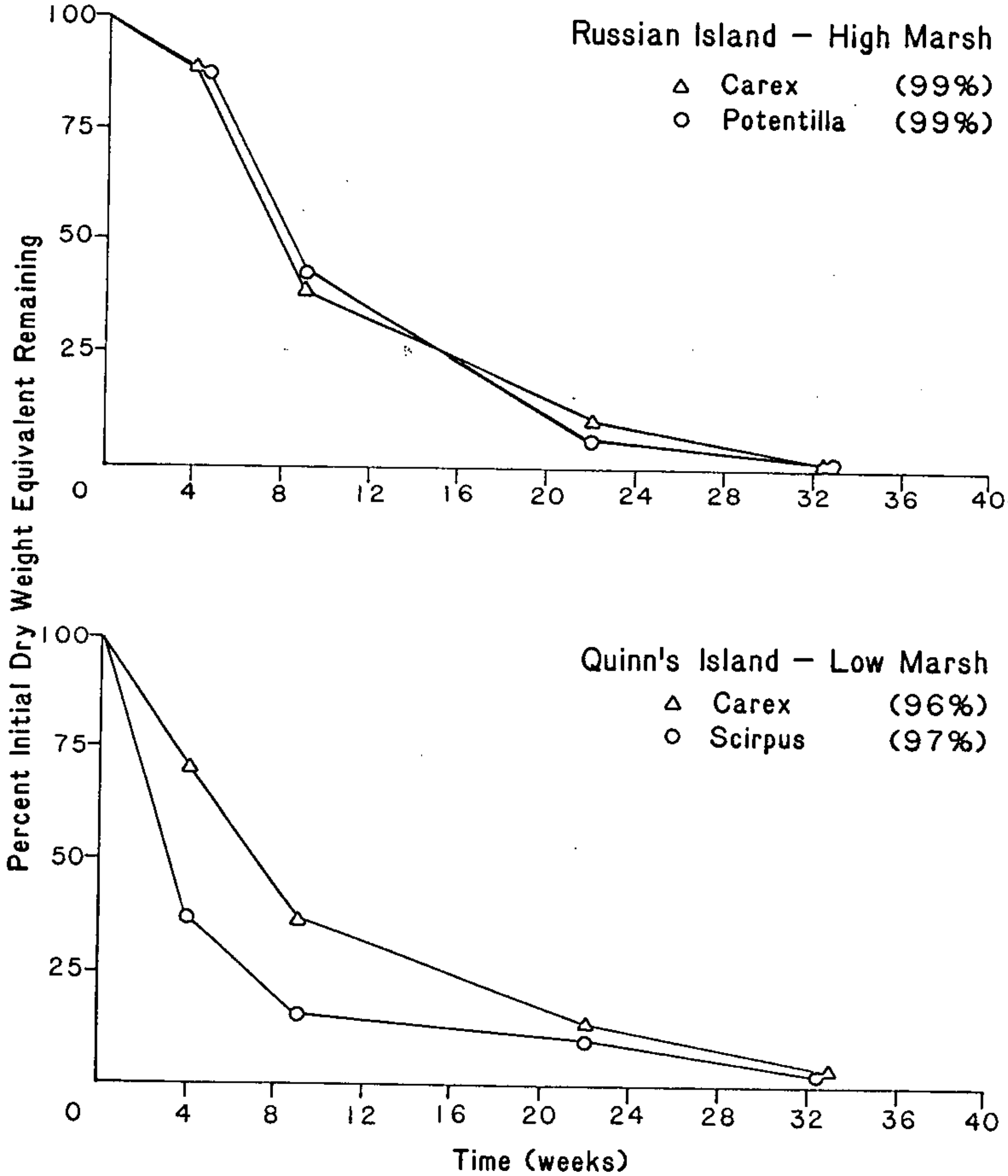


Figure 19. Decomposition Rates of Selected Tidal Marsh Plants, Columbia River Estuary. Experiment One; litterbags set out May 30, 1980.

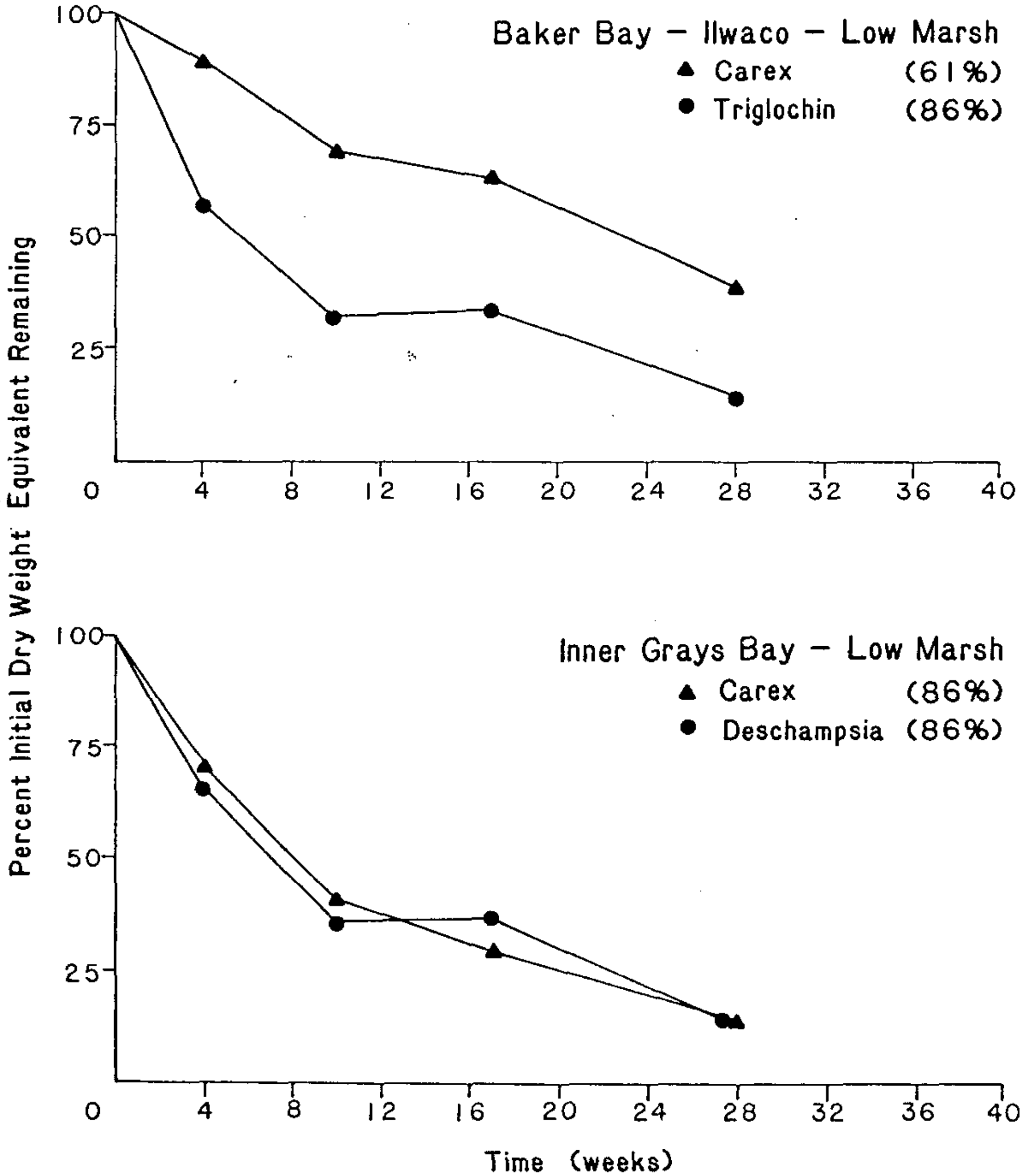


Figure 20. Decomposition Rates of Selected Tidal Marsh Plants, Columbia River Estuary. Experiment Two; litterbags set out July 2, 1980.

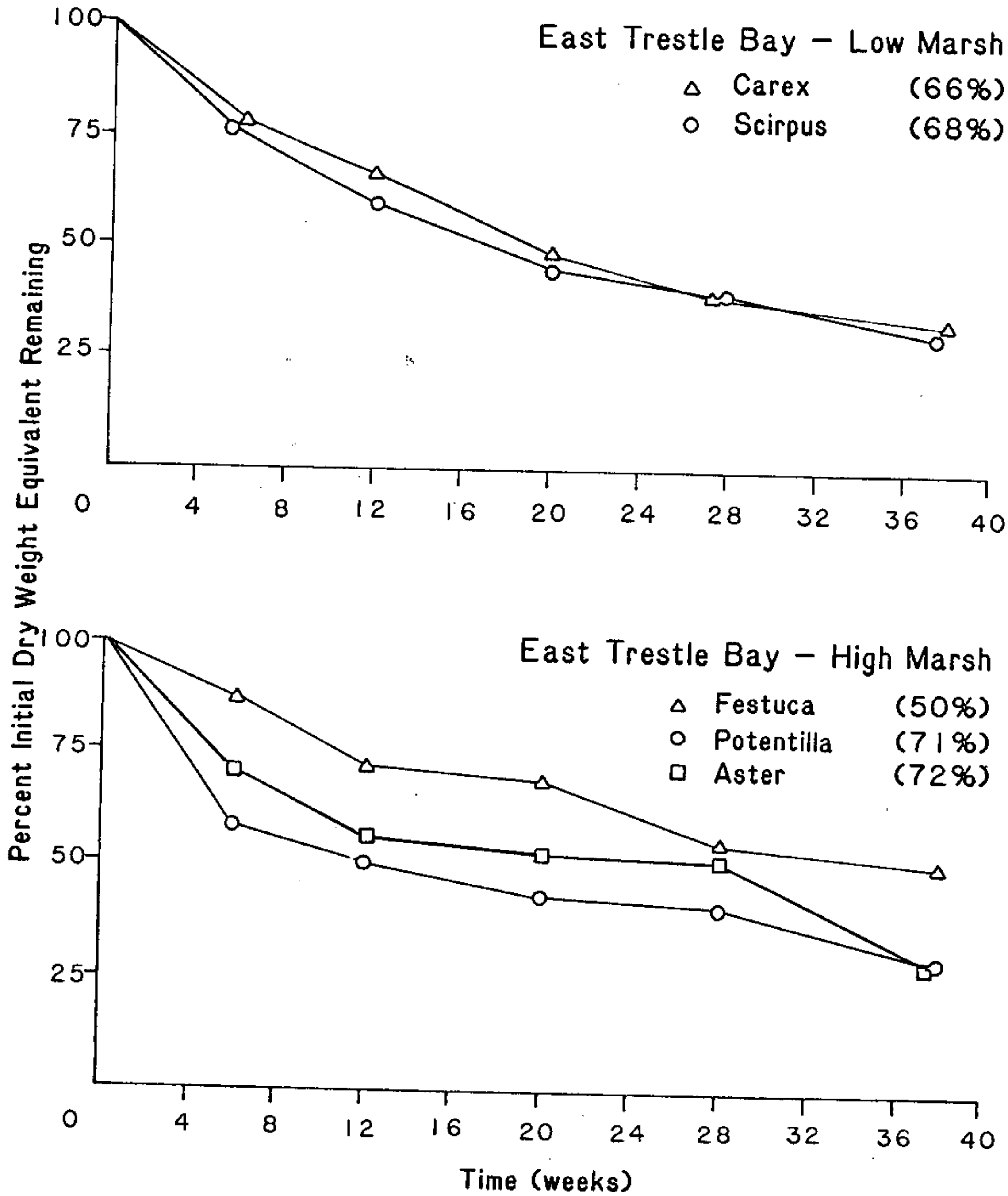


Figure 21. Decomposition Rates of Selected Tidal Marsh Plants, Columbia River Estuary. Experiment Three; litterbags set out October 24, 1980.

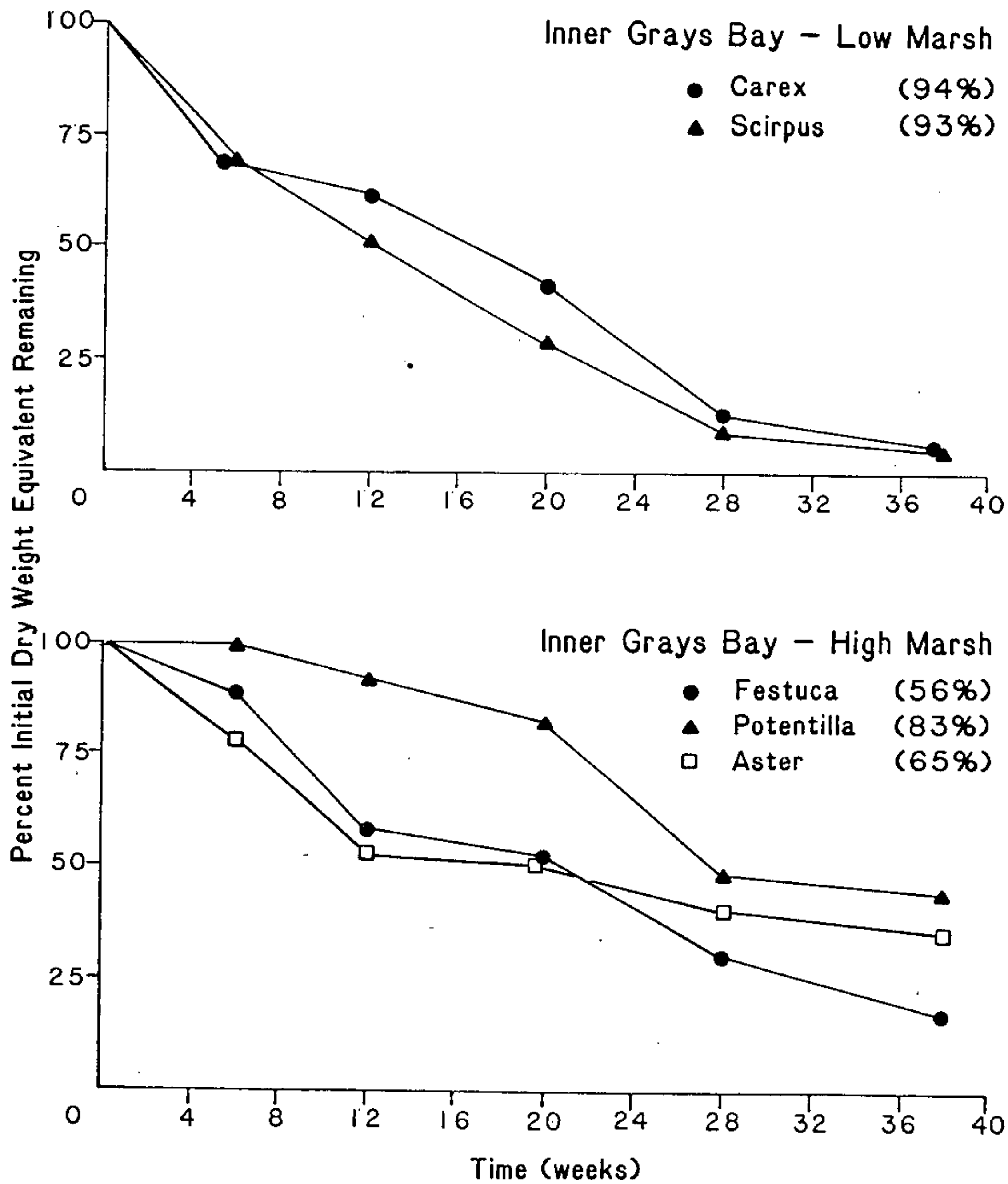


Figure 22. Decomposition Rates of Selected Tidal Marsh Plants, Columbia River Estuary. Experiment Three; litterbags set out October 24, 1980.

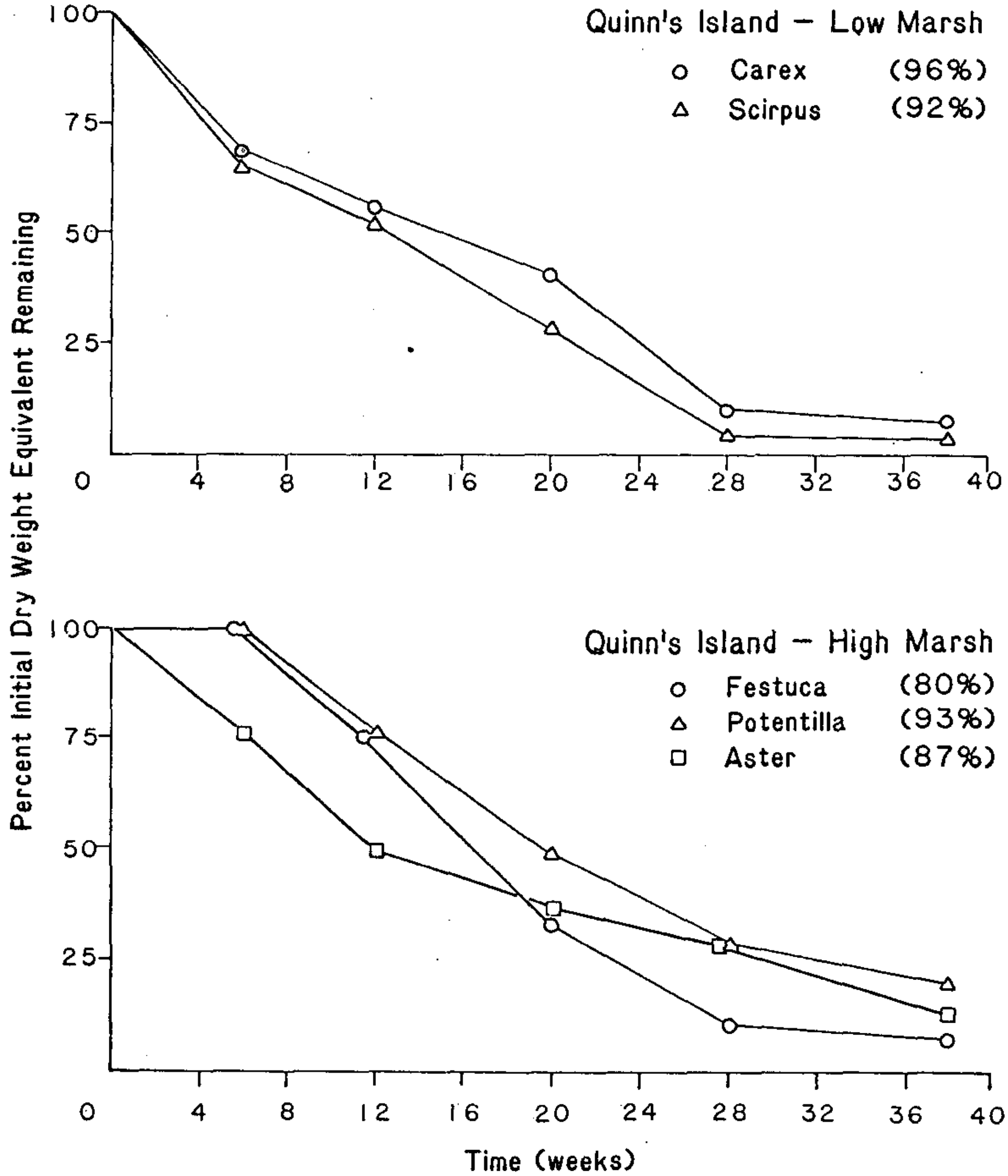


Figure 23. Decomposition Rates of Selected Tidal Marsh Plants, Columbia River Estuary. Experiment Three; litterbags set out October 24, 1980.

significantly different ($p<0.05$) decomposition rates (i.e. slopes) among all possible species-location pairs within each experiment (Figure 24).

Experiment One

Observed differences in species decomposition rates (slopes; Table 25, Figures 18 and 19) between upstream (Russian Island, Quinns Island) and downstream (East Trestle Bay) study sites are significant ($p<0.05$). Differences between elevations at East Trestle Bay are not significant ($p>0.05$). Of particular interest is the wide difference in decomposition rates noted for Carex lyngbyei. Upstream, between 96.0 and 99.4 percent of initial dry weights of Carex disappeared during the experiment (33 weeks), whereas only between 67.0 and 72.0 percent of initial dry weight disappeared at the downstream station (East Trestle Bay). The same pattern is also evident for Potentilla pacifica between East Trestle Bay high marsh and Russian Island high marsh. Downstream, 61.0 percent of the initial dry weight of Potentilla had disappeared after 33 weeks, while upstream 99.3 percent had disappeared.

Experiment Two

Observed differences in decomposition rates (slopes; Table 26, Figure 20) between Carex lyngbyei at Baker Bay and the remaining species are significant ($p<0.05$). This conforms to the pattern observed in Experiment One; plant species generally decompose at a faster rate at upstream locations than at downstream locations.

Triglochin maritimum initially appears to be an exception to the general trend. Triglochin however, is a succulent grass-like species and its observed rapid decomposition is not surprising considering the apparent reduction in supporting tissue. Triglochin will decompose rapidly regardless of location or elevation; these, and other factors responsible for the observed differences with other species, are clearly overridden by the softness of Triglochin tissues.

Experiment Three

Experiment Three was perhaps the most informative in that the same five species (Carex, Scirpus, Festuca, Potentilla, and Aster) were set out at each of the study locations (Table 27, Figures 21, 22, and 23). Again, the same pattern seen in Experiments One and Two is evident in Experiment Three. The same species at upstream locations (Gray's Bay and Quinns Island) generally decompose significantly faster ($p<0.05$) than downstream at East Trestle Bay.

There are two exceptions however, Festuca and Aster, both of which decompose slowly. (The East Trestle Bay Festuca sample yielded the slowest decomposition rate of any measured; 50 percent of the original material still remaining after 38 weeks in the field.) Decomposition rates for Festuca and Aster placed in Grays Bay were not significantly different ($p>0.05$) from rates of other plant species at East Trestle Bay, the downstream station. This may reflect a higher percentage of

PLANT DECOMPOSITION RATES

Analysis of Covariance test confirmed statistically significant differences ($p<0.05$) within each decomposition rate data set. Statistically significant pair-wise comparisons, using Student-Newman-Kuels Tests ($\alpha=0.05$), indicated with asterisk.

EXPERIMENT ONE

	A	B	C	D	E	F	G	H	I
A									
B									
C									
D									
E									
F	*	*	*	*	*				
G	*	*	*	*	*				
H	*	*	*	*	*				
I	*	*	*	*	*				

A *Potentilla* - E. Trestle Bay, High Marsh
B *Juncus* - East Trestle Bay, High Marsh
C *Carex* - East Trestle Bay, High Marsh
D *Carex* - East Trestle Bay, Low Marsh
E *Agrostis* - East Trestle Bay, Low Marsh
F *Scripus* - Quinn's Is., Low Marsh
G *Carex* - Quinn's Island, Low Marsh
H *Potentilla* - Russian Is., High Marsh
I *Carex* Russian Is., High Marsh

EXPERIMENT TWO

	A	B	C	D
A				
B	*			
C	*			
D	*			

A *Carex* - Baker Bay, Ilwaco Low Marsh
B *Triglochin* - Baker Bay, Ilwaco Low Marsh
C *Carex* - Gray's Bay, Low Marsh
D *Deschampsia* - Gray's Bay, Low Marsh

EXPERIMENT THREE

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
A															
B															
C															
D	*														
E	*														
F	*														
G	*														
H	*	*	*	*	*	*	*								
I	*	*	*	*	*	*	*								
J	*	*	*	*	*	*	*								
K	*	*	*	*	*	*	*	*	*						
L	*	*	*	*	*	*	*	*	*	*					
M	*	*	*	*	*	*	*	*	*	*					
N	*	*	*	*	*	*	*	*	*	*					
O	*	*	*	*	*	*	*	*	*	*	*				

A *Festuca* - E. Trestle Bay, High Marsh
B *Festuca* - Grays Bay, High Marsh
C *Aster* - E. Trestle Bay, High Marsh
D *Aster* - Gray's Bay, High Marsh
E *Potentilla* - E. Trestle Bay, High Msh.
F *Carex* - E. Trestle Bay, Low Marsh
G *Scirpus* - E. Trestle Bay, Low Marsh
H *Festuca* Quinn's Is., High Marsh
I *Potentilla* - Grays Bay, High Marsh
J *Aster* - Quinn's Is., High Marsh
K *Scirpus* - Quinn's Is., Low Marsh
L *Scirpus* - Gray's Bay, Low Marsh
M *Potentilla* - Quinn's Is., Low Marsh
N *Carex* - Gray's Bay, Low Marsh
O *Carex* - Quinn's Is., Low Marsh

Figure 24. Litterbag Experiments: Statistically Significant ($\alpha=0.05$) Pair-Wise Comparisons Among Species Decomposition Rates, Estuary Location, and Marsh Elevation.

tough, supportive tissue in these two species which overrides other factors normally responsible for upstream-downstream decomposition rate differences.

Summary

The results of the litterbag experiments described above provide answers to each of the three questions posed about decomposition rates of tidal marsh plants in the Columbia River Estuary.

1. Do marsh plant species decompose more quickly in low marsh than high marsh habitats?

Experiment one was designed to address this question by comparing decomposition rates for a single species, Carex lyngbyei, among several stations at high and low intertidal elevations. Marsh elevation was found to have no significant effect (i.e., $p>0.05$) upon decomposition rates.

2. Do less "fiberous" marsh plants decompose more quickly than more "fiberous species at similar intertidal elevations?

Some significant differences ($p<0.05$) were noted among decomposition rates for different plant types. Triglochin, a succulent species, decomposes faster than Carex at the same location. Similarly, Carex and Scirpus both decompose faster than more fiberous species such as Aster and Festuca.

3. Do similar species, at similar intertidal elevations, decompose more quickly at upstream verses downstream locations?

The most striking differences are seen between decomposition rates of all species at upriver freshwater marshes, verses downriver brackish water marsh locations. Almost every possible upriver-downriver species comparison yielded statistically significant ($p<0.05$) decomposition rate differences.

Pooled, total percentage dry weight loss figures from upriver sites (irrespective of experimental period, marsh elevation, or species) yield a mean and standard deviation of 88 ± 12 percent loss ($n=16$). Similarly pooled downriver values yield 68 ± 9 percent loss ($n=12$). Although the reasons remain to be explored, marsh plants at upriver freshwater sites decompose substantially faster and more completely, than the same species at brackish water sites nearer the estuary mouth.

Reasons for the observed decomposition rate differences remain unknown. They might reflect physical differences in current velocities or flushing action; perhaps the plant tissues are more suseptable to mechanical breakdown; or possibly the decomposer community (bacteria, fungii, insect larvae, etc.) are either more abundant or more active under freshwater than brackish conditions.

4. DISCUSSION

4.1 MARSH VEGETATION COMPOSITION

The species composition and relative abundance characteristics of Columbia River Estuary tidal marshes have been investigated using several different approaches. Both Duncan Thomas (1980a, In Press) and ourselves, visited a wide variety of estuary marsh sites throughout one or more growing seasons and developed subjective descriptions and classifications of floristically distinct marsh types.

The quantitative species percent cover data collected over two successive years during this program, have also been analysed using different multivariate methods. David McIntire used these data to define marsh groups on the basis of divisive clustering and canonical discriminant analysis, while we used agglomerative cluster analysis procedures to achieve a similar goal.

The most striking feature of these various approaches and analyses is that they have all yielded closely similar floristic groupings of tidal marshes around the Columbia River Estuary. The major subdivision is clearly between freshwater tidal marshes east (upriver) of Tongue Point, and brackish water tidal marshes from Tongue Point west to the eatuary mouth. The second important division, though not quite as clear as the first, is between marshes that occupy higher verses lower elevations within the intertidal zone. The various analytical approaches used to separate these four major tidal marsh types, also shared broad agreement on groups of species that characterized each type.

As pointed out by Thomas (Thomas 1980a, In Press), and reiterated here, the marsh vegetation types found in brackish water areas of the Columbia River Estuary can be readily matched with salt marsh community descriptions (Jefferson 1974, Eilers 1975) from Oregon's Pacific Coast bays and estuaries. The estuary's tidal freshwater marshes however, represent an unusual and scarce habitat along the Pacific Coast. Further studies of these marsh assemblages are certainly warranted. The shrub and forested swamps of the estuary also deserve attention, for the potential contributions of these extensive habitats to the estuary ecosystem remains to be documented.

4.2 BIOMASS AND NET PRODUCTION DISTRIBUTIONS

4.2.1 Regional Distribution Patterns

Despite an extensive quantitative sampling program, no obvious or striking regional trends are apparent among aboveground biomass measurements, or net production estimates, for Columbia River Estuary tidal marshes. Indeed in all but one case, statistical comparisons of standing crop and production data failed to identify significant ($p<0.05$) differences among the four floristically distinct tidal marsh types. The exception was freshwater low marshes, which in August 1981 yielded significantly lower aboveground standing crop values than the other marsh types.

Initially this lack of statistical differences might suggest that any marsh type, at any estuary location, has an equal chance of being as productive as any other. Data inspection certainly confirms the great variability in net production and biomass values from marsh to marsh (see Table 22, for example).

Multiple regression procedures used to examine potential interactions among environmental variables and primary production estimates however, revealed that statistically significant ($p<0.05$) regional productivity trends do exist among the estuary marshes. While the relationships are not simple ones, tidal marsh net aboveground production shows trends of increasing upriver from the estuary mouth, and from lower to higher intertidal elevations.

These trends are very likely non-linear and probably reflect the interactive affects of a number of environmental variables in addition to the "key" parameters chosen for testing. Because of the highly variable responses noted among different marsh sites, a more elaborate program of *in situ* environmental data collection -- possibly over a greater number of sites, or with greater numbers of samples per site, or conducted over a longer period of time -- will probably be needed to resolve these trends more clearly.

4.2.2 Seasonal Distribution Patterns

Since the various above- and belowground mean standing crop values obtained from the four marsh types sampled are not statistically different ($p<0.05$), an estuary-wide overview of seasonal changes was obtained by averaging all tidal marsh biomass samples on a month-to-month basis. Figure 25 shows these month-to-month net mean values (± standard error of the mean) for aboveground live, aboveground attached standing dead, and belowground live root biomass, as well as for dead plant litter.

Mean net aboveground live standing crop on the marshes throughout the estuary was at its lowest in April (112 ± 22 g dry wt/m^2), climbed rapidly through the end of June (735 ± 95 g dry wt/m^2), and held steady through August. By mid-October however, estuary-wide marsh biomass had declined substantially again (257 ± 34 g dry wt/m^2).

Attached standing dead plant material of the 1980 growth season was virtually absent in April (12 ± 5 g dry wit/m^2) and as would be expected showed a steady increase through mid-October (205 ± 32 g dry wt/m^2).

Despite field observations suggesting that the majority of detached plant litter is removed from the tidal marshes each winter, litter biomass measurements showed little overall variation from month-to-month. The highest mean value was recorded in April 1980 (223 ± 69 g dry wt/m^2), apparently reflecting the presence of dead plant material remaining from the previous season's (1979) growth. The mean value declined to 105 ± 23 g dry wt/m^2 by October 1980. In August 1981, at the end of the following years growth season, the mean litter value was the lowest recorded, 83 ± 22 g dry wt/m^2. Except for the April 1980

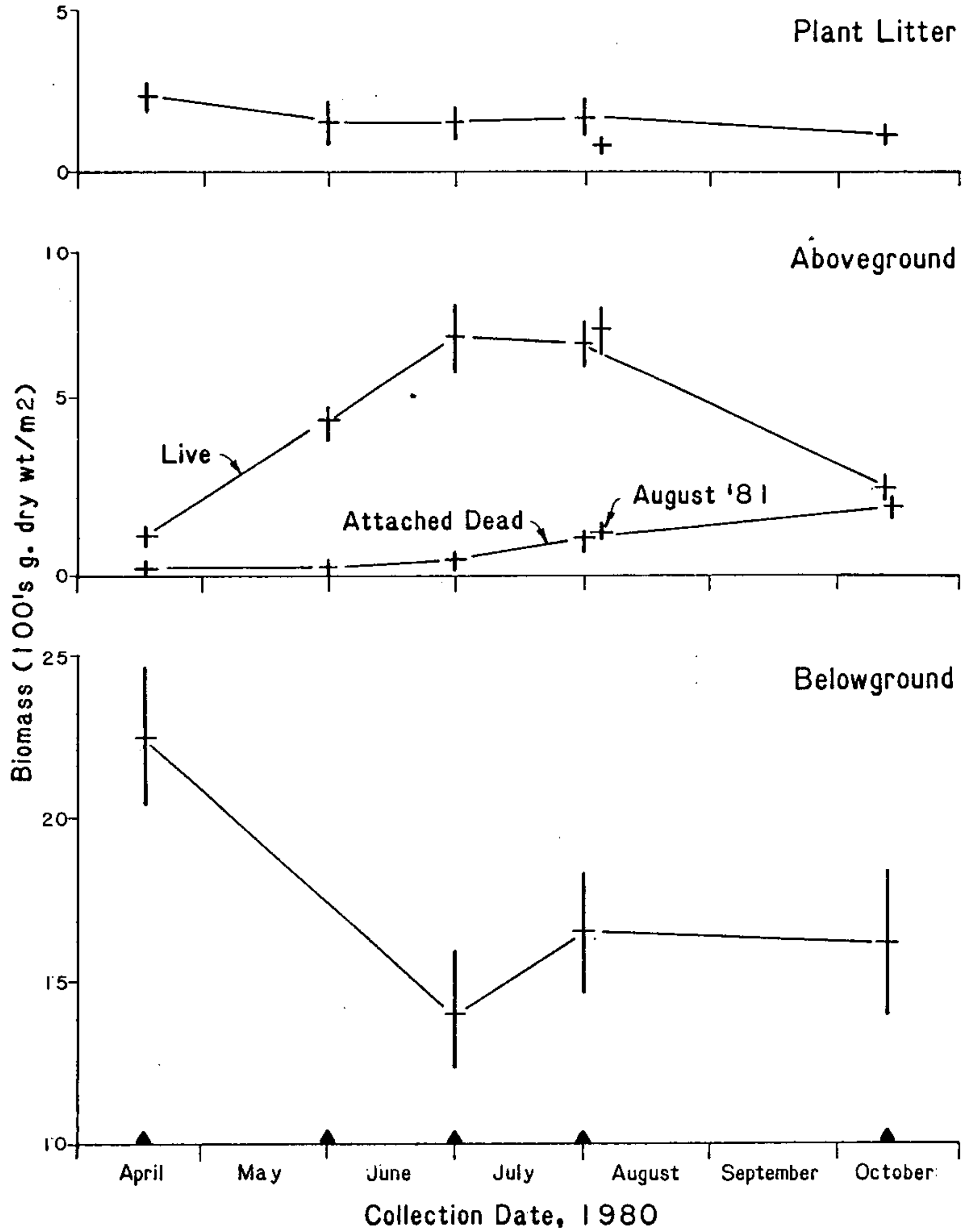


Figure 25. Mean Abundance of Live and Dead Marsh Plan Material Averaged over all Columbia River Estuary Study Sites by 1980 Collection Dates. Vertical bars indicate ± standard error of means. (Puget Is. data excluded. Results for August 1981 also shown for comparison.)

sampling period when marsh plant growth was just getting underway, these litter values represented only a small proportion of the total (live and attached dead) marsh plant biomass (Figure 25).

Net belowground live root biomass data were less complete than aboveground standing crop components, even so two obvious features stand out: First, the belowground live biomass (roots) is always substantially higher than the aboveground live plant biomass. Second, seasonal patterns of root biomass abundance are the opposite of aboveground biomass trends. Root biomass was highest in April (20 times greater than aboveground biomass), lowest at the end of June (less than double aboveground biomass values), and was on an uptrend again in July and October.

The reciprocal relationship between changes in above and belowground plant biomass supports the concept that late in the growing season some perennial species (such as Carex lyngbyei, for example) translocate biomass and nutrients from aerial shoots to overwintering root systems. Subsequently this stored material supports and accelerates the spring burst of growth typical of many marsh plants in cooler latitudes (Gallagher and Kibby 1981, Kistritz et al. 1983).

4.3 MARSH PRODUCTION DYNAMICS

The Marsh Plant Primary Production Work Unit of CREDDP focused on describing vegetation composition, measuring biomass, and estimating net annual primary production. The resulting somewhat static picture is deceptive, for as illustrated in Figure 26, "net production" really represents a dynamic balance among several ongoing processes that account for the difference between true total, or "gross" production of marsh plants and the residual, "net" production estimated in this Work-Unit. In the sections that follow some of these processes are briefly reviewed and tentatively quantified.

4.3.1 Carbon Contributions From Plant Decomposition

Plant litter on the marshes stayed relatively constant, yet attached dead material showed a steady increase throughout the growing season and probably into the fall and winter. This suggests an increasing rate of plant decomposition and carbon release during the growing season. Maximum release probably occurs during late winter and spring river flood flows, when standing dead plants remaining on the marsh surface are "swept" away.

Besides the temporal changes in carbon release rates suggested above, the litterbag experiments confirm significant regional differences in carbon release rates also. The upstream mean decomposition rate (Quinns Island) from Experiment Three (Table 27) is approximately 2.36 percent dry wt/week, while the downstream mean rate (East Trestle Bay) is approximately 1.72 percent dry wt/week.

Assuming an estuary-wide average abundance of attached standing dead plant material of 100 grams dry wt/m^2 and 175 grams dry wt/m^2 of plant litter, then during the growing season approximately 275 grams

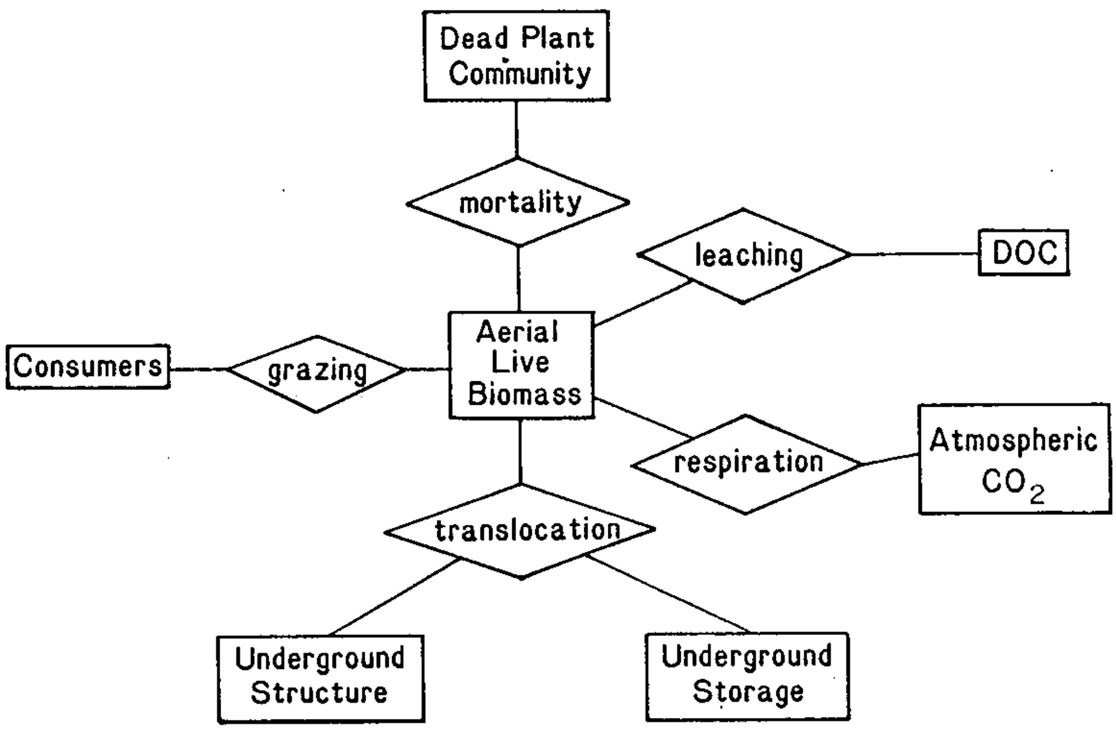


Figure 26. Possible Pathways of Biomass Loss From Aerial Portions of Tidal Marsh Plants. (DOC-dissolved organic carbon; after Gallagher and Kibby 1981).

dry wt/m^2 of dead plant material is available for decomposition and removal. Using the decomposition rates from Experiment Three, this calculates out at a downstream loss of 4.73 grams dry wt/m^2/week, compared with 6.49 gram dry wt/m^2/week lost from upstream marshes.

Kistritz and Yesaki (1979) determined the Carbon content of standing dead Carex lyngbyei as a percentage of dry weight. The mean value was 30.2 ± 8.1 percent Carbon, with a range from 18.4 percent (August) to 40.6 percent (December). Assuming the same mean value for Columbia River Estuary plants, then the weekly loss of Carbon from downstream marshes during the growing season would be 1.43 grams Carbon/g. dry wt/m^2 and from upstream marshes 1.96 grams Carbon/grams dry wt/m^2.

4.3.2 Translocation and Detrital Export

Studies of almost pure Carex lyngbyei stands in the Fraser River estuary (Kistritz and Yesaki 1979, Kistritz et al. 1983) suggest that aboveground biomass losses from July to September primarily reflect translocation into root and rhizome storage, rather than the death, decomposition and export of aerial plant parts (also see Gallagher and Kibby 1981). Potential end of growing season export would therefore be more closely represented by aboveground standing crop remaining on the marshes in September.

Extrapolation to the mixed Carex assemblages of the Columbia River Estuary can only be approximate, however our nearest comparable measurements would be July 1980 mean aboveground total standing crop of 833 grams dry wt/m^2 declining to an October 1980 mean value of 462 grams dry st/m^2. Losses from aerial plant parts through translocation to roots would thus be approximately 371 grams dry wt/m^2, about 38.5 percent of the average annual estuary-wide aboveground net production. (964 grams dry wt/m^2/year). The October value would indicate a minimum end of season detrital export of 462 grams dry wt/m^2 48 percent of average annual net production.

4.3.3 Leaching of Dissolved Organic Matter

Several studies have demonstrated that dissolved organic matter (DOM) can be leached from the aerial shoots of live, healthy marsh plants when they are submerged. Kistritz et al. (1983) provide measurements of DOM leaching rates for Carex lyngbyei. Values were found to vary with the frequency and duration of tidal submergence, length of growing season, etc.; when integrated for these variables over the entire growing season a value of 39 grams Carbon/m^2/year was obtained.

Kistritz and Yesaki (1979) provide a mean carbon content from dry weight live Carex material of 39.4 percent; range 37.2 percent (January) to 43.1 percent (September). Using this conversion factor, the dry weight equivalent of DOM leaching over an entire growing season would be approximately 99 grams dry wt/m^2/year, more than 10 percent of the Columbia River Estuary tidal marsh average annual aboveground net production (964 grams dry wt/m^2/year). This value may be too high as an average for Columbia River marshes, for they are mostly mixed species stands rather than pure Carex.

4.3.4 Marsh Herbivory

Herbivory by several groups of organisms -- mammals, ducks and geese, invertebrates especially insects -- may be a significant pathway for carbon transport out of the tidal marshes. Quantitative data are scarce however; only potential utilization by non-marine mammals has been well documented.

Dunn et al. (1981) identified 10 non-marine mammal species key to Columbia River Estuary mammalian relationships. Three of these species: Nutria (Myocastor coypus), Muskrat (Ondatra zibethica), and Beaver (Castor canadensis), rely extensively upon tidal marsh and swamp habitats for both denning and feeding. Three additional species: Columbian white-tailed deer (Odocoileus virginianus leucarus, an endangered subspecies) Columbian black-tailed deer (Odocoileus hemionus colubmianus), and Townsend's vole (Microtus townsendii), utilize tidal marsh habitats to a lesser extent but their overall impact remains unclear.

Trophic requirements for the three key marsh-dependant species are outlined in Table 28. Potential total annual marsh plant consumption (aerial shoots and roots) can be estimated by: (1) assuming 100 percent dependence by nutria and muskrat, 50 percent by beaver, and (2) using the mid-points of annual estuary-wide food consumption ranges. The resulting figure of approximately 21,200 MT (23,320 tons) wet weight-/year of marsh vegetation is impressive. Assuming a wet weight to dry weight conversion of 25 percent, yields 5,300 MT (5,830 tons) dry wt/year.

Extrapolating the estuary-wide mean net annual aboveground primary production estimate of 964 g dry wt marsh plants/m^2/year, over the 3,718 ha of estuary marshes, yields a total net annual marsh production of 35,840 MT (39,430 tons) dry weight/year. Herbivory (under the various assumptions noted) would be equivalent of 14.8 percent of this total. Reduced to a per square-meter basis -- nutria, muskrat, and beaver together -- could be consuming the equivalent of 143 g dry wt of marsh plants/m^2/year. This number would increase substantially if the upper ends of the ranges noted in Table 28 were used.

4.3.5 Summary

In the course of this study several major componants of tidal marsh production have been identified and quantified, some rigorously, others more tentatively. Many of these estimates are already expressed in common units (grams dry weight/m^2/year) and a plant dry weight: Carbon ratio can be used to convert them to grams Carbon/m^2/year. A widely used conversion factor for Carbon in plant tissues is 45 percent, however Kistritz and Yesaki's (1979) measured value for Carex lyngbyei of 39.4 percent, is somewhat lower. We have chosen to use 40 percent for the conversions that follow in Table 29.

Table 28. Columbia River Estuary Wetland-Dependant Mammals: Food Requirements and Estimated Consumption Rates (after Washington Department Game 1983).

	NUTRIA	MUSKRAT	BEAVER
Habitats Occupied	Tidal Marsh/Swamp Mid/Upper Estuary	Tidal Marsh/Swamp All Areas	Swamp
Preferred Feeding Areas	Low>High Marsh>Swamp Yearround	Low Marsh Yearround	High Marsh Spring-Summer
Preferred Foods	Marsh Plants: Aerial Shoots, Roots (*Carex*, *Scirpus*)	Marsh Plants: Aerial Shoots, Roots (*Sium suave*)	Mostly *Carex*
Body Weight (juvenile- adult male)	2.0-5.9 kg	0.7-1.0 kg	13.0-27.0 kg
Population Density	2.5-20.8/ha	0.8-6.6/ha	0.28/ha
Food Consumption[1]			
Daily, individual	0.5-1.5 kg/day	0.24-0.34 kg/day	0.6-0.7 kg/day
Daily, estuary-wide	10,900-90,600 kg/day	1,400-12,200 kg/day	480-550 kg/day
Annual, estuary-wide	4,000-33,000 MT/year[2]	500-4,450 MT/year	180-200 MT/year

[1] All Estimates as Wet Weights
[2] 1,000 Kilograms = Metric Ton (MT)

Table 29. Columbia River Estuary Tidal Marshes: Quantitative Estimates for some of the Key Processes Controlling Net Annual Primary Production.

PROCESS/VARIABLE	(grams/m^2) DRY WEIGHT	CARBON
Yearround Average Aboveground Total Biomass	535	214
Yearround Average Belowground Total Biomass	1,730	692
Mean Net Annual Aboveground Primary Production	965/yr	386/yr
Herbivory	145/yr	58/yr
Leaching of Dissolved Organic Matter	100/yr	40/yr
Translocation to Roots (Fall)	370/yr	148/yr
Minimum Detrital Export	460/yr	184/yr

5. CONCLUSIONS

The Columbia River Estuary is one of only four major estuaries along the entire Pacific Coast of North America receiving sufficient freshwater outflow to maintain extensive areas of both brackish (marine-estuarine) and freshwater tidal marshes. This report describes the species composition, standing crop, and primary production dynamics of the tidal marsh vegetation found within the Columbia River Estuary. Major conclusions reached during the study are summarized in a series of numbered paragraphs presented below.

1. An estuary-wide field reconnaissance conducted in October 1979 confirmed the floristic diversity of Columbia River Estuary tidal marshes and suggested that their species composition reflected: (a) Salinity changes from the marine estuary mouth to upstream freshwater conditions; and (b) low marsh to high marsh elevation changes at any specific location. Twenty-two broadly representative tidal marsh study sites, located to examine these two environmental gradients, were selected for intensive study.

2. Percent species cover and aboveground biomass data sets, collected from the 22 tidal marsh study sites in both July 1980 and August 1981, yielded 67 different plant species. An additional 15 species were collected nearby but did not occur within the sample quadrats. Despite this diversity, the great majority of plant cover and biomass within the marshes was composed of a smaller subset -- some 20 species -- of the total 82 species recorded. Lyngby's sedge (*Carex lyngbyei*) was by far the most abundant and widespread species throughout the estuary tidal marshes.

3. Inspection of the species composition data, as well as our own field observations, confirmed that the most striking differences among tidal marsh types within the estuary are between marshes developed under freshwater verses brackish water conditions, and higher verses lower intertidal elevations.

4. The species percent cover data from July 1980 and August 1981 were examined more objectively using both divisive clustering combined with cannonical discriminant analysis, and agglomerative cluster analysis. Both procedures yielded results in good agreement with the subjective four-fold subdivision of estuary tidal marsh types already noted above. The four major tidal marsh types are each characterized by distinctive groups of species and relative abundance patterns, as described in Section 3.1.2 of the text.

5. Brackish low marshes (567 hectares/1,400 acres) fringe much of the shoreline of Baker, Trestle and Young's Bay. Brackish high marsh (316 hectares/780 acres) is also best developed in Trestle and Young's Bays. Freshwater tidal marshes extend upriver from Tongue Point (RM-18). Low marsh habitats (2,268 hectares/5,600 acres) are widespread throughout the islands of Cathlamet Bay,

fringe much of Gray's Bay, and occur on the downstream portions of Tronson, Quinns, Grassy, and Fitzpatrick Islands, near Aldrich Point (RM-30). Freshwater high marshes (576 hectares/1,400 acres) are present along the eastern shores of Gray's Bay and are more broadly developed across portions of Marsh, Horseshoe and Welsh Islands.

Additional wetland habitats within the estuary include brackish shrub swamp (53 hectares) and freshwater shrub/forested swamp (2,357 hectares) that were excluded from this study.

6. Seasonal patterns of net aboveground marsh plant standing crop were established from replicate clip-quadrats harvested at each study site during April, May, June, July and October 1980, and August 1981. Biomass data for live shoots, attached standing dead material, and unattached plant litter, were treated separately.

Mean net aboveground total standing crop (live plus standing dead) values, measured near the peak of the 1980 growing season, indicated no statistically significant differences among the four tidal marsh categories. The overall mean value (± standard error) for all marsh sites was 864 ± 41 g dry wt/m^2. Comparable data collected near the 1981 growth season peak indicated that standing crop values from the freshwater low marshes were significantly ($p<0.01$) lower than those from the other three marsh groups. The overall mean value for all marsh sites was 892 ± 43 g dry wt/m^2.

7. An estuary-wide overview of seasonal biomass changes was obtained by averaging all tidal marsh standing crop samples on a month-to-month basis. Mean net aboveground live standing crop (± standard error) was at its lowest in April (112 ± 22 g dry wt/m^2), climbed rapidly through the end of June (735 ± 95 g dry wt/m^2), and held steady through August. By mid-October however, estuary-wide marsh biomass had declined substantially again (257 ± 34 g dry wt/m^2). Attached standing dead plant material was virtually absent in April (12 ± 5 g dry wt/m^2) but showed a steady increase through mid-October (205 ± 32 g dry wt/m^2).

Detached plant litter biomass measurements showed little overall variation from month-to-month. The highest mean value was recorded in April 1980 (223 ± 69 g dry wt/m^2). Except for the April 1980 sampling period when marsh plant growth was just getting underway, these litter values represented only a small portion of the total (live and attached dead) marsh plant biomass.

8. Net belowground live root biomass data were collected from replicate soil cores taken at each study site in April, June, July and October 1980. Two obvious features stand out: First, live root biomass is always substantially higher than the aboveground live plant biomass. Second, seasonal patterns of root biomass abundance are the opposite of aboveground biomass trends. Root

biomass was highest in April (20 times greater than aboveground biomass), lowest at the end of June (less than double aboveground biomass values), and was on an uptrend again in July and October.

9. The reciprocal relationship between changes in above and belowground plant biomass supports the concept that late in the growing season some perennial species (Carex lyngbyei, for example) translocate biomass and nutrients from aerial shoots to overwintering root systems. Subsequently this stored material supports and accelerates the spring burst of growth typical of many marsh plants in cooler latitudes.

10. Net annual aboveground primary production estimates for each marsh site were calculated from the 1980 sequential standing crop harvests using the Smalley Method. Values ranged from a low of 364 g dry wt/m^2/year at Lois Island low marsh, to a high of 1,730 g dry wt/m^2/yr for low marsh Carex stands at East Trestle Bay.

When production estimates were sorted among the four major tidal marsh types and pooled, no statistically significant differences were found. This suggests that all marsh types are equally productive, with an overall mean estimated net annual aboveground production value (± standard error) of 964 ± 100 g dry wt/m^2/yr.

11. The general absence of significant differences among biomass measurements and primary production estimates from the various marshes may be real. It could also reflect sampling problems associated with high within- and between-marsh variability.

Among five indirect environmental variables tested, surface salinity regimes yielded the most significant regressions against estimated net annual aboveground primary production values from the different tidal marshes; site elevation was also important. While the relationships are clearly not simple ones, tidal marsh net aboveground primary production does exhibit significant trends -- increasing both upriver from the estuary mouth and at higher intertidal elevations.

12. Decomposition and loss rates of plant material from the marsh surface were measured during three litter bag experiments initiated in May, July, and October 1980, respectively. The experiments were each designed to measure loss rates for different plant types, marsh elevations, and estuary locations. The overall results of the experiments suggest marsh elevation has no significant effect ($p>0.05$) upon decomposition rates. Some significant differences ($p<0.05$) were noted among decomposition rates for different plant types, more succulent species decomposing faster than more fiberous species at the same location. The most striking difference however, was that marsh plants at upriver freshwater sites decomposed substantially faster and more completely, than the same species at brackish water sites nearer the estuary mouth.

13. Net tidal marsh production represents a dynamic balance among several ongoing processes that account for the difference between true total, or "gross" production and the residual, "net" production estimated here (964 g dry wt/m^2/year, aboveground). Some of these processes have been tentatively quantified as follows:

a. leaching of dissolved organic matter from live plants, 200 g dry wt/m^2/yr,

b. utilization by herbivores (nutria, muskrat, and beaver), 145 g dry wt/m^2/yr,

c. translocation to plant roots in the fall 370 g dry wt/m^2/yr, and

d. minimum detrital export, 460 g dry wt/m^2/yr.

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APPENDIX A

Columbia River Estuary: Quantitative Species Composition Data for Tidal Marsh Vegetation at Twenty-Two Intensive Study Sites, July 1980 and August 1981.

Species composition presented as mean cover (percent; n=5) and mean above-ground live biomass (percent; n=9; units, grams dry weight/m^2).

Table A-1. Baker Bay-China Cove, *Carex* Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980		August 1981	
	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Agrostis alba	*		0.1	0.7
Carex lyngbyei	76.5	53.3	87.0	90.0
Fucus distichus edentatus	18.1		4.4	
Lilaeopsis occidentalis			1.5	
Orthocarpus castillejoides	*			
Scirpus americanus	**	35.9	2.8	1.7
Scirpus validus	5.3	3.4	4.1	7.7
Triglochin maritimum	0.1	7.3		
Mean Absolute Cover (%)	94		75	
Mean Total Live Biomass (g dry wt/m^2)		523		597

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-2. Baker Bay-China Cove, *Scirpus* Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Carex lyngbyei	22.9	33.5	*	6.7
Scirpus americanus	77.1	65.9	98.2	93.3
Triglochin maritimum	**		1.8	
Other grasses		0.6		
Mean Absolute Cover (%)	96		60	
Mean Total Live Biomass (g dry wt/m^2)		356		288

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-3. Baker Bay-Ilwaco Harbor, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Aster subspicatus	*			
Carex lyngbyei	63.4	76.0	82.7	87.8
Cotula coronopifolia	*			
Eleocharis palustris	*	0.7		
Festuca arundinacea	*			
Lotus corniculatus	*			
Scirpus americanus	33.3	18.5	14.5	8.0
Scirpus sp.	*			
Triglochin maritimum	3.2	4.7	2.7	4.2
Zannichellia palustris	**			
Mean Absolute Cover (%)	93		83	
Mean Total Live Biomass (g dry wt/m^2)		717		896

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-4. West Trestle Bay, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980		August 1981	
	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Agrostis alba	5.6	16.5	5.1	12.6
Carex lyngbyei	91.0	77.6	88.5	82.5
Lilaeopsis occidentalis	2.2	1.1	2.3	
Potentilla pacifica	*		1.3	2.2
Triglochin maritimum	1.1	5.0	2.6	2.6
Mean Absolute Cover (%)	89		86	
Mean Total Live Biomass (g dry wt/m^2)		545		928

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-5. West Trestle Bay, High Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980		August 1981	
	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Agrostis alba	37.7	47.8	31.3	45.3
Aster sp.	4.6			
Carex lyngbyei	13.8	15.1	0.8	10.7
Festuca arundinacea	*		0.8	
Juncus balticus	4.6	10.4	17.5	13.9
Lathyrus palustris	6.1			
Oenanthe sarmentosa			0.8	
Potentilla pacifica	33.1	16.4	32.6	22.1
Rumex crispus			0.1	
Vicia gigantea			14.8	
Other grasses		0.7		
Other herbs		9.6		8.0
Mean Absolute Cover (%)	140		144	
Mean Total Live Biomass (g dry wt/m^2)		730		883

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-6. East Trestle Bay, *Carex* Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Agrostis alba	*	0.5	*	1.8
Carex lyngbyei	100.0	99.0	100.0	91.8
Deschampsia caespitosa	*			
Eleocharis palustris			*	0.2
Lilaeopsis occidentalis	*	0.5		
Scirpus sp.	*			
Triglochin maritimum			*	5.7
Other grasses				0.5
Mean Absolute Cover (%)	93		87	
Mean Total Live Biomass (g dry wt/m^2)		1417		721

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-7. East Trestle Bay, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Agrostis alba	79.7	61.3	79.9	86.1
Carex lyngbyei	16.3	32.4	15.2	5.9
Deschampsia caespitosa	1.0			
Hordeum brachyantherum	*			
Juncus balticus	1.0	3.5	1.3	3.1
Potentilla pacifica	1.9	1.0	3.5	4.9
Trifolium wormskjoldii	*	1.8	0.1	
Triglochin maritimum	*			
cf. Vallisneria americana	*			
Zannichellia palustris	*			
Mean Absolute Cover (%)	104		94	
Mean Total Live Biomass (g dry wt/m^2)		679		1172

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-8. East Trestle Bay, Middle Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980		August 1981	
	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Achillea millefolium	*			
Agrostis alba	39.0	37.0	57.8	47.4
Carex lyngbyei	50.5	39.7	26.7	19.5
Elymus glaucus	*			
Festuca arundinacea	*	7.6		
Juncus balticus	*	1.5		
Lathyrus palustris	8.6		6.2	
Oenanthe sarmentosa	*			
Potentilla pacifica	1.9	12.5	9.2	23.7
Other herbs		1.7		1.9
Other grasses				7.5
Mean Absolute Cover (%)	105		101	
Mean Total Live Biomass (g dry wt/m^2)		816		1033

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-9. East Trestle Bay, High Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

	July 1980		August 1981	
Species	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
<u>Agrostis alba</u>	26.8	16.0	36.1	41.3
<u>Aster</u> sp.	7.2		4.5	
<u>Carex lyngbyei</u>	2.0	3.0	2.7	6.8
<u>Festuca arundinacea</u>			1.8	
<u>Juncus balticus</u>	7.8	11.6	3.6	10.3
<u>Lathyrus palustris</u>	15.0		8.6	
<u>Potentilla pacifica</u>	41.1	40.8	42.7	26.4
Other grasses		9.2		6.5
Other herbs		19.4		8.8
Mean Absolute Cover (%)	153		119	
Mean Total Live Biomass (g dry wt/m^2)		639		862

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-10. Outer Young's Bay, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980		August 1981	
	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Carex lyngbyei	81.8	86.7	91.3	65.0
Eleocharis palustris				0.9
Lilaeopsis occidentalis	*			
Oenanthe sarmentosa			0.1	
Potentilla pacifica	*			
Scirpus validus	1.3	1.4	1.5	10.4
Typha angustifolia	16.9	11.9	7.1	23.7
Mean Absolute Cover (%)	77		85	
Mean Total Live Biomass (g dry wt/m^2)		1646		1330

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-11. Inner Youngs' Bay, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Agrostis alba	4.1		*	0.8
Alisma plantago-aquatica	**		3.6	
Carex lyngbyei	86.6	89.6	44.3	67.5
Eleocharis palustris	*	0.1	13.7	2.6
Equisetum sp.	*			
Lilaeopsis occidentalis	**		0.1	0.2
Oenanthe sarmentosa	6.1	6.6	35.4	18.8
Potentilla pacifica			*	
Rumex conglomeratus	*			
Rumex crispus			0.1	
Scirpus microcarpus			0.1	
Scirpus sp.	1.0			
Scirpus validus	1.0	0.4	2.6	10.0
Trifolium wormskjoldii	*			
Triglochin maritimum			0.1	
Typha sp.			*	
Other grasses		3.2		
Mean Absolute Cover (%)	98		87	
Mean Total Live Biomass (g dry wt/m^2)		772		578

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-12. Outer Grays Bay, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Alisma plantago-aquatica			*	
Aster sp.			7.3	
Aster subspicatus	9.4		*	
Carex lyngbyei	20.6	21.9	46.9	20.3
Deschampsia caespitosa	11.4	17.6	7.1	37.0
Eleocharis palustris	3.8	2.7	12.1	10.4
Elodea canadensis	13.1	2.2		
Juncus balticus	31.9	2.9		
Juncus oxymeris	1.9	2.9	7.8	13.6
Lilaeopsis occidentalis	3.8		12.6	1.9
Mimulus guttatus	**			
Plantago sp.			0.5	
Polygonum hydropiperoides			0.7	
Sagittaria latifolia	*			
Scirpus americanus	**	1.1	2.5	6.7
Scirpus validus			2.5	
Sium suave	3.8			
Other grasses		11.7		
Other herbs		37.1		10.1
Mean Absolute Cover (%)	53		46	
Mean Total Live Biomass (g dry wt/m^2)		555		260

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-13. Outer Grays Bay, High Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

	July 1980		August 1981	
Species	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Agrostis alba			*	
Alisma plantago-aquatica			5.9	
Aster sp.	0.9		4.9	
Aster subspicatus	6.0			
Caltha asarifolia	**	0.6	*	0.1
Carex lyngbyei	58.0	70.0	9.9	47.6
Deschampsia caespitosa	6.8	5.9	3.6	11.8
Eleocharis palustris	*	0.1	1.3	0.2
Elodea canadensis	19.6	0.1		
Equisetum fluviatile			2.7	
Festuca arundinacea	*	1.1	25.1	
Fontinalis sp.			*	0.5
Habenaria dilatata	*			
Juncus balticus	*	0.3		
Juncus oxymeris	0.1	0.9	0.2	0.3
Lotus corniculatus	*		21.5	
Mimulus guttatus	0.1			
Oenanthe sarmentosa	*	1.4	5.0	
Plantago lanceolata	*	0.1		
Ranunculus sp.			1.3	
Rumex crispus			0.1	
Scirpus americanus	**		5.1	2.4
Scirpus microcarpus			13.0	1.4
Scirpus validus	*			
Sium suave	8.5		0.1	
Typha latifolia			0.1	2.2
Other grasses				25.8
Other herbs		19.4		7.7
Mean Absolute Cover (%)	117		95	
Mean Total Live Biomass (g dry wt/m^2)		700		724

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-14. Inner Grays Bay, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
<u>Alisma plantago-aquatica</u>			2.0	
<u>Aster subspicatus</u>			5.5	
<u>Carex lyngbyei</u>	35.3	37.0	2.2	8.1
<u>Deschampsia caespitosa</u>	12.5	1.3	20.8	12.5
<u>Eleocharis palustris</u>	*	2.2	10.6	
<u>Elodea canadensis</u>	8.3	0.6		
<u>Festuca arundinacea</u>		0.3		
<u>Fontinalis</u> sp.			*	2.0
<u>Isoetes echinospora</u>			0.2	
<u>Juncus oxymeris</u>	8.3	14.6	17.7	16.4
<u>Littorella</u> sp.			*	
<u>Mimulus guttatus</u>	**		1.9	
<u>Polygonum hydropiperoides</u>			1.9	
<u>Sagittaria latifolia</u>	16.6	10.8	17.7	
<u>Scirpus validus</u>	18.7	33.2	17.5	40.6
<u>Sium suave</u>			1.9	
Other herbs				20.3
Mean Absolute Cover (%)	48		57	
Mean Total Live Biomass (g dry wt/m^2)		316		470

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-15. Inner Grays Bay, High Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m²) Species Composition Data Summary.

Species	July 1980		August 1981	
	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Agrostis alba	3.1		*	
Aster sp.	3.1		1.3	
Caltha asarifolia	7.8	0.6	3.7	**
Carex lyngbyei	29.5	54.5	42.0	41.7
Deschampsia caespitosa	6.4	1.2		
Eleocharis palustris	*	0.2		
Equisetum fluviatile	4.7	9.3	3.9	3.9
Festuca arundinacea	*	1.7	25.1	
Galium cymosum	*			
Habenaria dilitata	**			
Heracleum lanatum	*			
Hypericum formosum	*			
Juncus balticus			0.1	
Juncus cf. *nevadensis*			*	
Iris sp.	*			
Juncus oxymeris	*	0.1		
Lamiaceae	24.9			
Lotus corniculatus	6.2		7.2	
Lysichitum americanum	*			
Mentha piperia			5.9	
Mimulus guttatus	1.6			
Myosotis laxa	**		0.2	
Oenanthe sarmentosa	3.1	1.5	3.8	
Potentilla pacifica	6.2	1.1	1.5	0.9
Ranunculus sp.			1.2	
Rumex crispus	**			
Scirpus microcarpus	**		3.7	2.3
Trifolium wormskjoldii	3.1			
Typha latifolia			0.1	
Other grasses				37.3
Other herbs		29.8		14.0
Mean Absolute Cover (%)	64		92	
Mean Total Live Biomass (g dry wt/m²)		839		1569

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-16. Army Crops Dock, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Agrostis alba			0.1	
Alisma plantago-aquatica	1.4		0.2	
Aster subspicatus	*		0.1	
Bidens cernua			0.1	
Callitriche sp.			0.1	
Carex lyngbyei	73.5	38.1	45.3	44.6
Eleocharis palustris	11.8	3.0	4.3	4.3
Epilobium watsonii			1.0	
Equisetum sp.	2.6	10.7	16.5	35.5
Fontinalis sp.			0.2	0.1
Helenium automnale			0.1	
Isoetes echinospora			11.4	
Juncus oxymeris	2.6	0.9	8.0	6.0
Lilaeopsis occidentalis	6.6	0.5		
Littorella sp.			*	
Lotus corniculatus	*			
Mimulus guttatus	*		0.1	
Myosotis laxa	*		9.5	
Phalaris arundinacea	*		0.2	
Polygonum hydropiperoides			0.3	
Potentilla pacifica	*		0.9	
Rumex conglomeratus			*	
Sagittaria latifolia			0.1	
Sium suave	**		0.4	
Typha angustifolia	1.3	44.8	0.2	7.1
Other grasses		0.5		1.0
Other herbs		1.5		1.5
Mean Absolute Cover (%)	76		117	
Mean Total Live Biomass (g dry wt/m^2)		822		590

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-17. Lois Island, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

	July 1980		August 1981	
Species	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Agrostis alba			0.1	
Alisma plantago-aquatica	2.0		5.1	
Bidens cernua	2.9		1.7	
Boltonia asteroides			0.1	
Callitriche sp.			0.1	
Carex lyngbyei	11.8	10.6	3.3	21.6
Ceratophyllum sp.			*	
Eleocharis palustris	51.9	24.1	32.6	25.6
Elodea canadensis	8.8	0.7	1.7	
Gratiola neglecta			*	
Juncus oxymeris	15.7	27.4	48.8	36.4
Lilaeopsis occidentalis	1.0	0.4	2.0	0.2
Limosella aquatica			*	
Littorella sp.			*	
Mimulus guttatus	**		0.4	
Myosotis laxa	*			
Najas sp.	**			
Oenanthe sarmentosa		6.2		
Phalaris arundinacea	1.0			
Polygonum hydropiperoides			0.7	
Sagittaria latifolia	3.9		1.9	
Sium suave	*			
Tillaea aquatica			*	
Other grasses		27.7		3.6
Other herbs		2.9		12.6
Mean Absolute Cover (%)	102		70	
Mean Total Live Biomass (g dry wt/m^2)		274		290

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.
* Plant present nearby but absent from sample quadrats.

Table A-18. Russian Island, High Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Agrostis alba	**			
Alisma plantago-aquatica	**		*	
Aster modesta	**		6.2	
Callitriche sp.			0.1	
Caltha asarifolia			0.1	
Carex lyngbyei	81.6	60.5	62.4	59.1
Deschampsia caespitosa	2.0	12.7	6.5	7.9
Epilobium watsonii	*		0.4	
Festuca arundinacea		2.6		
Fontinalis sp.			0.1	0.6
Habenaria dilitata	*		*	
Helenium automnale	*			
Isoetes echinospora			1.6	
Juncus oxymeris	1.1	13.7	2.1	7.3
Lilaeopsis occidentalis	0.1		0.3	
Lysichitum americanum	*	1.6	1.6	1.5
Mentha arvensis	1.0		0.4	
Mimulus guttatus	3.0		1.9	
Oenanthe sarmentosa	2.0		5.1	
Plantago sp.			0.1	
Polygonum hydropiperoides			0.3	
Ranunculus sp.	**			
Rumex crispus	2.0		1.9	
Sagittaria latifolia	2.0		0.3	
Senecio triangularis	*			
Sium suave	5.0		8.1	
Other grasses		0.1		1.6
Other herbs		8.9		21.9
Mean Absolute Cover (%)	99		69	
Mean Total Live Biomass (g dry wt/m^2)		959		945

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-19. Karlson Island, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980		August 1981	
	Percent Cover	Percent Live Biomass	Percent Cover	Percent Live Biomass
Alisma plantago-aquatica	**		0.4	
Aster modestus	*			
Aster sp.	**			
Boltonia asteroides			4.9	
Callitriche sp.			0.9	
Carex lyngbyei	66.5	51.1	26.2	40.0
Deschampsia caespitosa	4.2		19.6	6.3
Eleocharis palustris	8.3	8.6	7.1	14.7
Juncus oxymeris	2.1	4.6	11.6	0.6
Lilaeopsis occidentalis			0.2	
Phalaris arundinacea	*		0.6	
Polygonum hydropiperoides			0.6	
Sagittaria latifolia	**		0.6	
Scirpus validus	18.7	34.0	24.7	34.2
Sium suave	*		2.4	
Other herbs	**	1.7		4.2
Mean Absolute Cover (%)	48		47	
Mean Total Live Biomass (g dry wt/m^2)		527		524

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-20. Tronson Island, High Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Agrostis alba			4.6	
Alisma plantago-aquatica	*		0.3	
Aster sp.			1.5	
Bidens cernua			1.5	
Caltha asarifolia	1.6		1.8	0.3
Carex lyngbyei	42.6	54.3	28.6	41.6
Deschampsia caespitosa	7.9	2.0	20.2	1.7
Eleocharis palustris	1.7	3.3	6.2	3.4
Epilobium watsonii	**		*	
Galium sp.			*	
Habenaria dilitata	*			
Helenium automnale			1.5	
Helenium grandiflorum			*	
Juncus oxymeris	4.7	8.6	4.6	15.4
Lilaeopsis occidentalis	1.6	0.2	1.8	
Lupinus sp.	*			
Lysichitum americanum	26.8	5.0	9.1	13.3
Mentha arvensis	1.7		3.2	
Mentha piperita			0.3	
Mimulus guttatus	3.2		0.6	
Myosotis laxa	1.6		7.6	
Phalaris arundinacea			0.1	
Potentilla pacifica	4.7	0.9	2.0	1.2
Prunella vulgaris	*			
Ranunculus sp.	0.2			
Sagittaria latifolia			0.4	
Senecio triangularis	**			
Sium suave	**		1.7	
Trifolium wormskjoldii	**		1.7	
Veratrum californicum	*			
Other grasses		7.2		12.8
Other herbs		18.4		10.5
Mean Absolute Cover (%)	63		71	
Mean Total Live Biomass (g dry wt/m^2)		539		465

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-21. Quinn's Island, Low Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m^2) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Alisma plantago-aquatica			0.3	
Aster subspicatus	2.5			
Carex lyngbyei	84.8	56.6	72.9	70.2
Deschampsia caespitosa	2.5	4.7	*	2.2
Eleocharis palustris	1.2	1.9	5.7	6.7
Juncus oxymeris	5.0	5.1	16.0	7.1
Lilaeopsis occidentalis	1.2	0.4	0.3	0.3
Mimulus guttatus	**			
Polygonum hydropiperoides			0.1	
Sagittaria latifolia			1.6	
Scirpus validus			1.6	1.9
Sium sauve	2.5		1.6	
Other grasses		0.3		
Other herbs		31.0		11.7
Mean Absolute Cover (%)	80		76	
Mean Total Live Biomass (g dry wt/m^2)		701		643

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

Table A-22. Puget Island, High Marsh: Mean (n=5) Percent Cover and Mean (n=9) Percent Aboveground Live Biomass (g dry wt/m²) Species Composition Data Summary.

Species	July 1980 Percent Cover	July 1980 Percent Live Biomass	August 1981 Percent Cover	August 1981 Percent Live Biomass
Alisima plantago-aquatica	*			
Aster sp.	32.6			
Beckmannia syzigachne	*			
Carex lyngbyei	*	3.7		
Iris pseudacorus	**			
Juncus effusus	*			
Juncus oxymeris	*			
Lysichitum americanum	*			
Mimulus guttatus	*			
Phalaris arundinacea	2.2	5.1		
Plantago lanceolata	*	0.5		
Sagittaria latifolia	**			
Scirpus validus	*			
Typha angustifolia	10.9			
Typha latifolia	52.2	90.3		
Other grasses		0.4		
Mean Absolute Cover (%)	46		-	
Mean Total Live Biomass (g dry wt/m²)		1383		-

** Plant present in sample quadrat(s) but mean cover value <0.1 percent.

* Plant present nearby but absent from sample quadrats.

APPENDIX B

Columbia River Estuary: Mean Live and Attached Dead Net Aboveground Marsh Plant Biomass and Estimated Net Annual Primary Production Data from Twenty-Two Intensive Study Sites.

Plant biomass as grams dry weight/m^2 (n=9). Net annual production, as grams dry weight/m^2/year, estimated using the Smalley (1958) species peak method.

Table B-1. Baker Bay-China Cove, Carex Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	64	5	575	26	794	52	279	57	223	381	69+532+245+269	1115
Scirpus americanus							188	45				233
Scirpus validus	3	0	0	0	0	0	18	0			3+18	21
Triglochin maritimum					23	0	38	6	3	1	23+21	44
											TOTAL	1423

Table B-2. Baker Bay-China Cove, *Scirpus* Low Marsh: Mean (n=9) Live and Attached Net Dead Marsh Plant Aboveground Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Eleocharis palustris							119	31	34	120	150+4	154
Scirpus americanus	29	4	340	2	386	36	234	85	4	108	33+311+80	424
Other grasses							2	0				2
											TOTAL	580

Table B-3. Baker Bay-Ilwaco Harbor, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	31	9	472	8	518	25	546	123	236	426	40+441+63+126	670
Eleocharis palustris							5	0				5
Scirpus americanus			82	0	70	3	133	6			82+66	148
Triglochin maritimum			67	0	8	1	34	0	1	3	67+26	93
Lilaeopsis occidentalis					1	0						1
Other grasses	1	0										1
											TOTAL	918

Table B-4. West Trestle Bay, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY CALCULATION	NAPP
	L	D	L	D	L	D	L	D	L	D		
Carex lyngbyei	94	13	425	0	772	46	423	42	168	222	107+331+393	831
Agrostis alba	57	6	215	0	20	3	90	10	29	2	63+158+77	298
Elodea candensis	40	0	0	0	2	0					40+2	42
Triglochin maritimum			5	0	0	0	27	3			5+30	35
Lilaeopsis occidentalis							6	0				6
											TOTAL	1212

Table B-5. West Trestle Bay, High Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	7	0	20	0	53	1	110	11	9	31	7+13+34+67	121
Agrostis alba	129	11	222	12	276	21	349	49	383	55	140+94+63+101+40	438
Juncus balticus	109	28	150	0	163	0	76	0	26	24	137+41+13	191
Triglochin maritimum					12	0						12
Potentilla pacifica	3	0	52	0	161	21	120	26	28	96	3+49+130	182
Other grasses			42	0	0	0	5	0			42+5	47
Other herbs	4	0	23	0	117	0	70	1	40	21	4+19+94	117
											TOTAL	1108

Table B-6. East Trestle Bay, *Carex* Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	136	12	476	19	1030	48	1402	313	10	148	148+347+583+637	1715
Eleocharis palustris			1	0								1
Agrostis alba	4	1	0	0	0	0	7	0			5+7	12
Triglochin maritimum			1	0	59	1					1+59	60
Lilaeopsis occidentalis			1	0	0	0	7	0			1+7	8
											TOTAL	1796

Table B-7. East Trestle Bay, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei			97	0	520	11	220	32	1	11	97+434	531
Agrostis alba	101	9	168	0	181	17	417	68	459	168	110+67+30+287+142	636
Juncus balticus			23	0	0	0	24	0			23+24	47
Triglochin maritimum			6	0	0	0	12	2			6+14	20
Potentilla pacifica			25	0	0	0	7	1			25+8	33
Other herbs					4	0						4
											TOTAL	1271

Table B-8. East Trestle Bay, Middle Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	18	3	337	5	64	4	324	27	206	149	21+321+283+4	629
Agrostis alba	352	24	188	1	142	22	302	39	256	37	376+177	553
Festuca arundinacea							62	6				68
Juncus balticus	41	14	0	0	64	0	12	0	2	0	55+64	119
Potentilla pacifica	18	0	12	0	8	0	102	12	17	4	18+106	124
Other herbs			4	0	0	0	14	0	5	0	4+14	18
											TOTAL	1511

Table B-9. East Trestle Bay, High Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei			9	0	12	0	19	1	1	0	9+3+8	20
Agrostis alba	52	14	167	0	177	12	102	12	88	32	66+115+22+6	209
Juncus balticus	33	10	124	0	119	0	74	0	37	72	43+91+35	169
Potentilla pacifica	32	6	90	0	145	12	261	105	32	57	38+58+67+209	372
Other grasses	4	2	26	0	17	0	59	9	8	0	6+22+51	79
Other herbs	4	0	28	0	81	0	124	4	11	68	4+24+53+47	128
											TOTAL	977

Table B-10. Outer Youngs Bay, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	134	14	901	100	1699	117	1427	287	286	564	148+853+815	1816
Eleocharis plaustris					34	0						34
Scirpus microcarpus			23	0								23
Scirpus validus	1	0	0	0	538	53	23	0	15	16	1+590+8	599
Typha latifolia					87	0	196	37	177	52	87+146	233
Oenanthe sarmentosa	1	0									1	1
											TOTAL	2706

Table B-11. Inner Youngs Bay, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	115	10	334	22	642	103	692	209	78	200	125+231+389+156	901
Eleocharis palustris			18	0	20	0	1	0			18+2	20
Scirpus validus	3	0	21	0	0	0	3	0	0	2	3+18+3	24
Agrostis alba					4	0	0	0	16	2	4+18	22
Lilaeopsis occidentalis									1	0	1	1
Oenanthe sarmentosa	16	0	60	1	52	10	51	0	57	18	16+45+1+24	86
Other grasses	3	0	0	0	0	0	25	0	3	0	3+25	28
											TOTAL	1082

Table B-12. Outer Grays Bay, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei			134	4	185	22	122	51	8	30	138+69	207
Eleocharis palustris			6	0	10	0	15	0	3	0	6+4+5	15
Scirpus americanus							6	0	1	0	6	6
Deschampsia caespitosa			109	0	62	3	98	12	105	19	109+45+14	168
Elodea candensis			1	0	37	0	12	0			1+36	37
Juncus balticus					4	0	16	0			4+12	16
Juncus oxymeris			19	0	25	2	16	1	66	0	19+8+50	77
Typha latifolia							0	22				22
Lilaeopsis occidentalis			13	0	4	0	0	0	1	0	13+1	14
Other grasses							65	0				65
Other herbs			34	0	89	0	206	0	4	0	34+55+117	206
											TOTAL	833

Table B-13. Outer Grays Bay, High Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	88	6	295	0	379	17	490	116	53	74	94+207+101+210	612
Eleocharis palustris			3	0	14	0	1	0			3+11	14
Scirpus americanus			20	0	80	0	0	0	62	23	20+60+85	165
Scirpus microcarpus	2	0	23	0	59	2					2+21+38	61
Equisetum fluviatile	1	0	0	0	39	0					1+39	40
Deschampsia caespitosa			1	0	25	0	41	4	5	0	1+24+20	45
Festuca arundinacea							8	0			8	8
Elodea candensis	3	0	1	0	0	0	1	0			3+1	4
Juncus balticus							2	0			2	2
Juncus oxymeris	3	1	19	0	2	0	6	0	12	12	4+16+4+18	42
Plantago lanceolata							1	0			1	1
Caltha asarifolia	1	0	15	0	0	0	4	0			1+14+4	19
Potentilla pacifica									20	5	25	25
Typha latifolia					7	0					7	7
Oenanthe sarmentosa					4	0	10	0			4+6	10
Other grasses	3	1	0	0	39	0	0	0	220	70	4+36+251	291
Other herbs	25	0	93	0	326	8	136	0	30	0	25+68+241	334
											TOTAL	1680

Table B-14. Inner Grays Bay, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Sagittaria latifolia							34	3			37	37
Carex lyngbyei	73	13	144	1	131	11	117	61	66	57	86+71+36	193
Eleocharis palustris			5	0	0	0	7	2			5+9	14
Scirpus validus	8	0	61	0	54	2	105	6	117	16	8+53+55+22	138
Deschampsia caespitosa	5	0	101	2	47	3	4	0	63	13	5+98+72	175
Festuca arundinacea							1	0			1	1
Elodea candensis	1	0	0	0	4	0	2	0	1	0	1+4	5
Juncus oxymeris			50	0	53	0	46	3	24	9	50+3	53
Triglochin maritimum					7	0					7	7
Other grasses			3	0							3	3
Other herbs	2	0	110	0	23	0	0	0	18	0	2+108+18	128
											TOTAL	754

Table B-15. Inner Grays Bay, High Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	88	5	229	9	603	54	458	53	42	189	93+145+419	658
Eleocharis palustris							2	0			2	2
Scirpus microcarpus			41	0	56	4					41+19	60
Equisetum fluviatile	9	0	29	0	103	6	78	0	59	16	9+20+80	109
Deschampsia caespitosa							10	0			10	10
Festuca arundinacea							14	0			14	14
Elodea candensis					1	0						1
Juncus oxymeris			1	0	0	0	1	0	2	0	1+1+1	3
Caltha asarifolia	29	0	0	0	10	0	5	0			29+10	39
Potentilla pacifica	3	0	6	0	17	1	9	1			3+3+12	18
Oenanthe sarmentosa					26	2	13	0			28	28
Other grasses	7	0	68	0	63	10	0	0	46	35	7+61+5+8	81
Other herbs	35	1	200	0	142	4	250	0	329	26	36+165+108+105	414
											TOTAL	1437

Table B-16. Army Corps Dock, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	26	10	293	0	261	26	313	39	113	73	36+267+65	368
Eleocharis palustris			15	0	14	0	25	0	1	0	15+11	26
Scirpus validus	5	0									5	5
Equisetum fluviatile	11	0	178	0	190	0	88	0	25	4	11+167+12	190
Elodea candensis	4	0	0	0	4	0					4+4	8
Juncus oxymeris			41	0	100	6	7	1	37	12	41+65+41	147
Typha latifolia							368	40	12	4	408	408
Lilaeopsis occidentalis			7	0	11	0	4	0	1	0	7+4	11
Oenanthe sarmentosa					15	0	0	0	2	4	15+6	21
Other grasses	2	0	0	0	1	0	4	0	2	0	2+1+3	6
Other herbs			2	0	0	0	12	0			2+12	14
											TOTAL	1204

Table B-17. Lois Island, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	3	0	8	0	17	8	29	3			3+5+17+12	37
Eleocharis palustris			107	0	122	13	66	5	4	0	107+28	135
Scirpus validus	3	0									3	3
Elodea candensis							2	0			2	2
Juncus oxymeris			74	0	175	13	75	11	17	16	74+114	188
Lilaeopsis occidentalis	1	0	6	0	4	0	1	0	1	0	1+5	6
Oenanthe sarmentosa							17	0			17	17
Other grasses			9	0	9	0	76	18	2	0	9+85	94
Other herbs			1	0	3	0	8	0	3	0	1+2+5	8
											TOTAL	490

Table B-18. Russian Island, High Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Lysichitum americanum					44	2	15	2			46	46
Carex lyngbyei	10	1	328	0	601	45	580	118	162	310	11+318+318+52	699
Scirpus validus	6	0									6	6
Deschampsia caespitosa			21	0	45	3	122	9	11	2	21+27+83	131
Festuca arundinacea							25	0			25	25
Elodea candensis	2	0	1	0	5	0					2+4	6
Juncus oxymeris			33	0	17	1	131	5	21	0	33+118	151
Oenanthe sarmentosa									15	1	16	16
Other grasses	1	0	0	0	0	0	1	0	3	0	1+1+2	4
Other herbs	8	0	36	0	106	3	85	0	21	0	8+28+73	109
											TOTAL	1193

Table B-19. Karlson Island, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	27	3	46	2	207	10	269	29	52	56	30+19+169+81	299
Eleocharis palustris			17	0	42	0	45	5			7+25+8	50
Scirpus validus			47	0	274	9	179	16	173	21	47+236	283
Elodea candensis	1	0									1	1
Juncus oxymeris			4	0	7	0	24	0	44	8	4+3+17+28	52
Oenanthe sarmentosa					9	0					9	9
Other grasses					7	0					7	7
Other herbs					1	0	9	0			1+8	9
											TOTAL	710

Table B-20. Tronson Island, High Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Lysichitum americanum	39	1	95	0	98	15	27	5	6	0	40+56+18	114
Carex lyngbyei	8	1	79	5	327	24	292	43	113	57	9+75+267	351
Eleocharis palustris			12	0	37	0	18	0	12	4	12+25	37
Deschampsia caespitosa	28	10	35	8	0	0	11	5	3	0	38+7	45
Elodea candensis					1	0					1	1
Juncus oxymeris			27	0	37	2	46	0	22	5	27+12+7	46
Potentilla pacifica			3	0	1	0	5	0	1	0	3+4	7
Lilaeopsis occidentalis							1	0	1	0	1	1
Other grasses			39	0	155	15	39	0	11	0	39+131	170
Other herbs	2	0	6	0	55	0	99	0	53	0	2+4+49+44	99
											TOTAL	871

Table B-21. Quinn's Island, Low Marsh: Mean (n=9) Live and Attached Dead Net Aboveground Marsh Plant Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/yr), Calculated Using the Smalley (1958) Species Peak Method.

	APRIL		MAY		JUNE		JULY		OCTOBER		SMALLEY	
	L	D	L	D	L	D	L	D	L	D	CALCULATION	NAPP
Carex lyngbyei	26	2	155	19	565	48	396	60	41	19	28+146+439	613
Eleocharis palustris			1	0	17	0	13	0			1+16	17
Scripus validus	4	0									4	4
Deschampsia caespitosa			73	0	6	0	33	16	23	9	73+43	116
Juncus oxymeris			35	1	34	1	36	1	85	19	36+2+67	105
Lilaeopis occidentalis							3	0			3	3
Oenanthe sarmentosa					2	0					2	2
Other grasses							2	0	1	0	2	2
Other herbs			78	0	0	0	217	0	4	0	78+217	295
											TOTAL	1157

Table B-22. Puget Island, High Marsh: Mean (n=9) Live and Attached Dead Marsh Plant Aboveground Biomass (g dry wt/m^2) and Estimated Net Annual Primary Production (NAPP, g dry wt/m^2/year), Based on End of Season Total Standing Crop.

	APRIL		MAY		JUNE		JULY		OCTOBER		TOTAL	
	L	D	L	D	L	D	L	D	L	D	STANDING CROP	NAPP
Carex lyngbyei							51	0			51	51
Phalaris arundinacea							70	6			76	76
Plantago lanceolata							7	0			7	7
Typha latifolia							1249	112			1361	1361
Other grasses							6	0			6	6
											TOTAL	1501

APPENDIX C

Columbia River Estuary: Scientific and Common Names of Plant Species Found During Quantitative Vegetation Surveys of Twenty-Two Intensive Study Sites.

Table C-1. Scientific and Common Names of Plant Species Found During Quantitative Vegetation Surveys of Columbia River Estuary Tidal Marshes.

SPECIES NAME	COMMON NAME
Algae	
Fucus distichus var. edentatus	Rockweed
Moses	
Fontinalis sp.	Water moss
Flowering Plants, by Family:	
Alismataceae	
Alisma plantago-aquatica L.	Water plantain
Sagittaria latifolia Willd.	Wappato
Araceae	
Lysichitum americanum Hulten & St. John	Yellow skunk cabbage
Boraginaceae	
Myosotis laxa Lehm.	Smaller forget-me-not
Callitrichaceae	
Callitriche sp.	Water starwort
Ceratophyllaceae	
Ceratophyllum sp.	Hornwort
Compositae	
Achillea millefolium L.	Yarrow
Aster subspicatus Nees	Douglas' aster
Aster sp.	
Bidens cernua L.	Stick-tight
Boltonia asteroides (L.) L'Her.	Aster boltonia
Cotula coronopifolia L.	Brass buttons
Erigeron philadelphicus L.	Fleabane
Helenium autumnale L.	Sneezeweed
Helenium autumnale var. grandiflorum (Nutt.) T. & G.	
Senecio triangularis Hook.	Arrowleaf groundsel
Crassulaceae	
Tillaea aquatica L.	Pigmy-weed

Table C-1. (Continued)

SPECIES NAME	COMMON NAME
Cyperaceae	
Carex lyngbyei Hornem.	Lyngby's Sedge
Eleocharis palustris (L.) R. & S.	Creeping spike-rush
Scirpus americanus Pers.	Three-square bulrush
Scirpus microcarpus Presl.	Small-fruited bulrush
Scirpus validus Vahl.	Softstem bulrush
Scirpus sp.	
Equisetaceae	
Equisetum fluviatile L.	Swamp horsetail
Equisetum sp.	Horsetail
Gramineae	
Agrostis alba L.	Creeping bentgrass
Beckmannia syzigachne (Steud.) Fern.	Slough grass
Deschampsia caespitosa (L.)Greene	Tufted hairgrass
Elymus glaucus Buckl.	Western rye-grass
Festuca arundinacea Schreb.	Reed fescue
Hordeum brachyantherum Nevski	Meadow barley
Phalaris arundinacea L.	Reed canary-grass
Hydrocharitaceae	
Elodea canadensis Rich. in Michx.	Rocky Mountain waterweed
c.f. Vallisneria americana Michx.	Tapegrass
Hypericaceae	
Hypericum formosum H.B.K.	Western St. John's-wort
Iridaceae	
Iris pseudacorus L.	Yellow flag
Iris sp.	
Juncaceae	
Juncus balticus Willd.	Baltic rush
Juncus effusus var. pacificus Fern. & Wieg.	Common rush
Juncus nevadensis Wats.	Sierra rush
Juncus oxymeris Engelm.	Pointed rush

Table C-1. (Continued)

SPECIES NAME	COMMON NAME
Juncaginaceae	
<u>Triglochin</u> <u>maritimum</u> L.	Seaside arrow-grass
Labiatae	
<u>Mentha</u> <u>arvensis</u> L.	Field mint
<u>Mentha</u> <u>piperita</u> L.	Peppermint
<u>Mentha</u> sp.	
<u>Prunella</u> <u>vulgaris</u> L.	Heal-all
Leguminosae	
<u>Lathyrus</u> <u>palustris</u> L.	Marsh pea
<u>Lotus</u> <u>corniculatus</u> L.	Birdsfoot-trefoil
<u>Lupinus</u> sp.	Lupine
<u>Trifolium</u> <u>wormskjoldii</u> Lehm.	Springbank clover
<u>Vicia</u> <u>gigantea</u> Hook.	Giant vetch
Liliaceae	
<u>Veratrum</u> <u>californicum</u> Durand	California false hellebore
Najadaceae	
<u>Najas</u> sp.	Bushy pondweed
Onagraceae	
<u>Epilobium</u> <u>watsonii</u> Barbey	Watson's Willow-herb
Orchidaceae	
<u>Habenaria</u> <u>dilatata</u> (Pursh) Hook.	Boreal bog orchid
Plantaginaceae	
<u>Littorella</u> sp.	Plaintain
<u>Plantago</u> <u>lanceolata</u> L.	English plaintain
<u>Plantago</u> sp.	
Polygonaceae	
<u>Polygonum</u> <u>hydropiperoides</u> Michx.	Mild water pepper
<u>Rumex</u> <u>conglomeratus</u> Murr.	Clustered dock
<u>Rumex</u> <u>crispus</u> L.	Curlyleaved dock
Ranunculaceae	
<u>Caltha</u> <u>asarifolia</u> DC.	Yellow marsh marigold
<u>Ranunculus</u> <u>occidentalis</u> Nutt.	Western buttercup

Table C-1. (Continued)

SPECIES NAME	COMMON NAME
Rosaceae	
Potentilla pacifica Howell	Pacific silverweed
Rubiaceae	
Galium cymosum Wieg.	Pacific bedstraw
Galium sp.	
Scrophulariaceae	
Gratiola neglecta Torr.	Obscure hedge-hyssop
Limosella aquatica L.	Mudwort
Mimulus guttatus DC.	Common monkey-flower
Orthocarpus castillejoides Benth.	Paintbrush orthocarpus
Typhaceae	
Typha angustifolia L.	Lesser cattail
Typha latifolia L.	Common/Narrow-leaved cattail
Umbelliferae	
Heracleum lanatum Michx.	Cow parsnip
Lilaeopsis occidentalis Coult. & Rose.	Western lilaeopsis
Oenanthe sarmentosa Presl.	Pacific water-parsley
Sium suave Walt.	Hemlock water-parsnip
Zannichelliaceae	
Zannichellia palustris L.	Horned pondweed

APPENDIX D

Description of data files related to the Emergent Plant Primary Production work unit of CREDDP. Each file is accessible through the U.S. Army Corps of Engineers Portland District, Portland, Oregon. Contact the Portland District Planning Division for further information, or see:

Mercier, H.T. 1984. Index to CREDDP data. Astoria, OR: Columbia River Estuary Data Development Program.

This appendix is reprinted from Mercier (1984).

EMERGENT PLANT PRIMARY PRODUCTION

The study objectives for the Emergent Plant Primary Production work unit were to:

- o describe and map emergent plant biomass and primary productivity patterns;
- o relate marsh vegetation types and productivity to elevation, salinity, and other pertinent physical and chemical factors;
- o estimate the export of detritus from marshes; and
- o determine the emergent plant carbon budget.

Data were collected using well-tested standard methods which are described in the work unit final report (see below). Briefly, these methods involve the use of:

- o clip quadrats for measuring net aboveground biomass;
- o core samples for measuring belowground biomass; and
- o litterbag studies for measuring decomposition of selected species of emergent vegetation.

These were processed to produce four data sets: Aboveground Dry Weight, Aboveground Ash-free Dry Weight, Belowground Dry Weight, and Litterbag Dry Weight. The aboveground and belowground biomass measurements were used to make estimates of net annual production throughout the estuary for major emergent marsh plant associations, for different intertidal elevations, and for individual species common in the estuary. Ash-free dry weight data are an alternative method of recording biomass which represents an estimate of the organic matter content of the vegetation. Decomposition rate data from selected plant materials were used to estimate the potential export of (particulate) detritus from the marshes of the estuary.

Principal investigator for this work unit was Keith B. Macdonald of Woodward-Clyde Consultants. For further information see:

Macdonald, K.B.; Winfield, T.P. 1984. Tidal marsh plant production in the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

A.1 DATA SET: Emergent Plant Aboveground Dry Weight

Aboveground biomass was used in conjunction with belowground (root) biomass to estimate overall primary production values for emergent vegetation. Production values were used as a basis for estimating potential organic carbon contribution to the estuary from various regions and intertidal elevations.

a. Variables

Aboveground dry weight

b. Data Set Description

This data set is one of the files in the computer archive. The file contains 6,049 records, 80 bytes each. The data are sorted first by date, then by station. All records are identical in format as follows:

Columns	Format	Contents
2-7	3I2	Date: YYMMDD
9-18	3I3'N'	Latitude: DD MM SSN(orth)
20-29	3I3'W'	Longitude: DDD MM SSW(est)
31-36	I6	Station number
38	I1	Replicate number
40	I1	Living/dead (Table A1)
42-43	I2	Plant code*
45-71	A27	Plant name
72-80	F9.1	Dry weight (g/m^2)

c. Sampling

The data were collected roughly monthly from 15 April 1980 to 11 October 1980 and again on 17 August 1981. In all, 22 sites were sampled.

d. Processing

Data were recorded on data entry forms and keypunched. Data were reformatted via a computer program and date, longitude, latitude and plant name were inserted into the record.

e. Quality Control

Data listings were checked against data entry forms. Selected computer input and output records were compared.

f. Data Set Request Information: Tape 6 File 79*

g. Alternate Sources: None

*Tape 6 File 82 contains species codes.

A.2 DATA SET: Emergent Plant Aboveground Ash-free Dry Weight

Ash-free dry weight values were determined from dry weight samples. These measurements were important due to the presence of volcanic dust on plants which inflated actual dry weight values, especially for May and June 1980 samples.

a. Variables

Aboveground ash-free dry weight

b. Data Set Description

This data set is one of the files in the computer archive. The file comprises 327 records, each 80 bytes long. The records are sorted first by date, then by station. All records have the following format:

Columns	Format	Contents
2-7	3I2	Date: YYMMDD
9-18	3I3'N'	Latitude: DD MM SSN(orth)
20-29	3I3'W'	Longitude: DDD MM SSW(est)
31-36	I6	Station number
38	I1	Replicate number
40	I1	Living/dead (Table A1)
42-43	I2	Plant code*
45-71	A27	Plant name
72-80	F9.2	Ash-free dry weight (% of dry weight)

c. Sampling: Same as A.1.c

d. Processing: Same as A.1.d

e. Quality Control: Same as A.1.e

f. Data Set Request Information: Tape 6 File 78*

g. Alternate sources: None

*Tape 6 File 82 contains species codes.

A.3 DATA SET: Emergent Plant Belowground Dry Weight

Belowground (root) biomass data were used in combination with aboveground biomass data to develop estimates of overall primary production values for emergent vegetation. Production estimates served as a basis for estimating potential organic carbon (particulate) contribution to the estuary by region and by intertidal elevation.

a. Variables

Belowground dry weight

b. Data Set Description

This data set resides in the computer archive. It consists of 198 records, 80 bytes each. The records are sorted first by date, then by location. All records are formatted as follows:

Columns	Format	Contents
2-7	3I2	Date: YYMMDD

9-18	3I3'N'	Latitude: DD MM SSN(orth)
20-29	3I3'W'	Longitude: DDD MM SSW(est)
31-36	I6	Station number
38	I1	Replicate number
72-80	F9.1	Dry weight (g/m^2)

c. Sampling: Same as A.1.c

d. Processing

Processing was the same as for Data Set A.1 except that no plant names were inserted.

e. Quality Control: Same as A.1.e

f. Data Set Request Information: Tape 6 File 80

g. Alternate Sources: None

A.4 DATA SET: Emergent Plant Litterbag Dry Weight

Litterbags were used to measure decomposition rates of selected species of plants at various locations throughout the estuary and at low and high intertidal elevations. Decomposition rate estimates were used to approximate the potential export of detritus from the various marsh types found in the estuary. Results for Carex lyngbyei and Potentilla pacifica suggest that plants decompose at a higher rate upstream than downstream (near the mouth) and that at the same location plants decompose faster in the low intertidal zone than in the high intertidal.

a. Variables

Litterbag dry weight

b. Data Set Description

This data set is one of the files in the computer archive. The file comprises 492 records, each 80 bytes long. The data are sorted first by date, then by location. All records are identical in format as follows:

Columns	Format	Contents
2-7	3I2	Date: YYMMDD
9-18	3I3'N'	Latitude: DD MM SS N(orth)
20-29	3I3'W'	Longitude: DDD MM SS W(est)
31-36	I6	Station number
38	I1	Replicate number
42-43	I2	Plant code*
45-71	A27	Plant name
72-80	F9.2	Dry weight (g/bag)

c. Sampling

Samples were collected at eight sites.

d. Processing: Same as A.1.d

e. Quality control: Same as A.1.e

f. Data Set Request Information: Tape 6 File 81*

g. Alternate Sources: None

*Tape 6 File 82 contains species codes.

Table A1. Living/dead Codes

Code	Usage
0	Mixture
1	Living
2	Dead