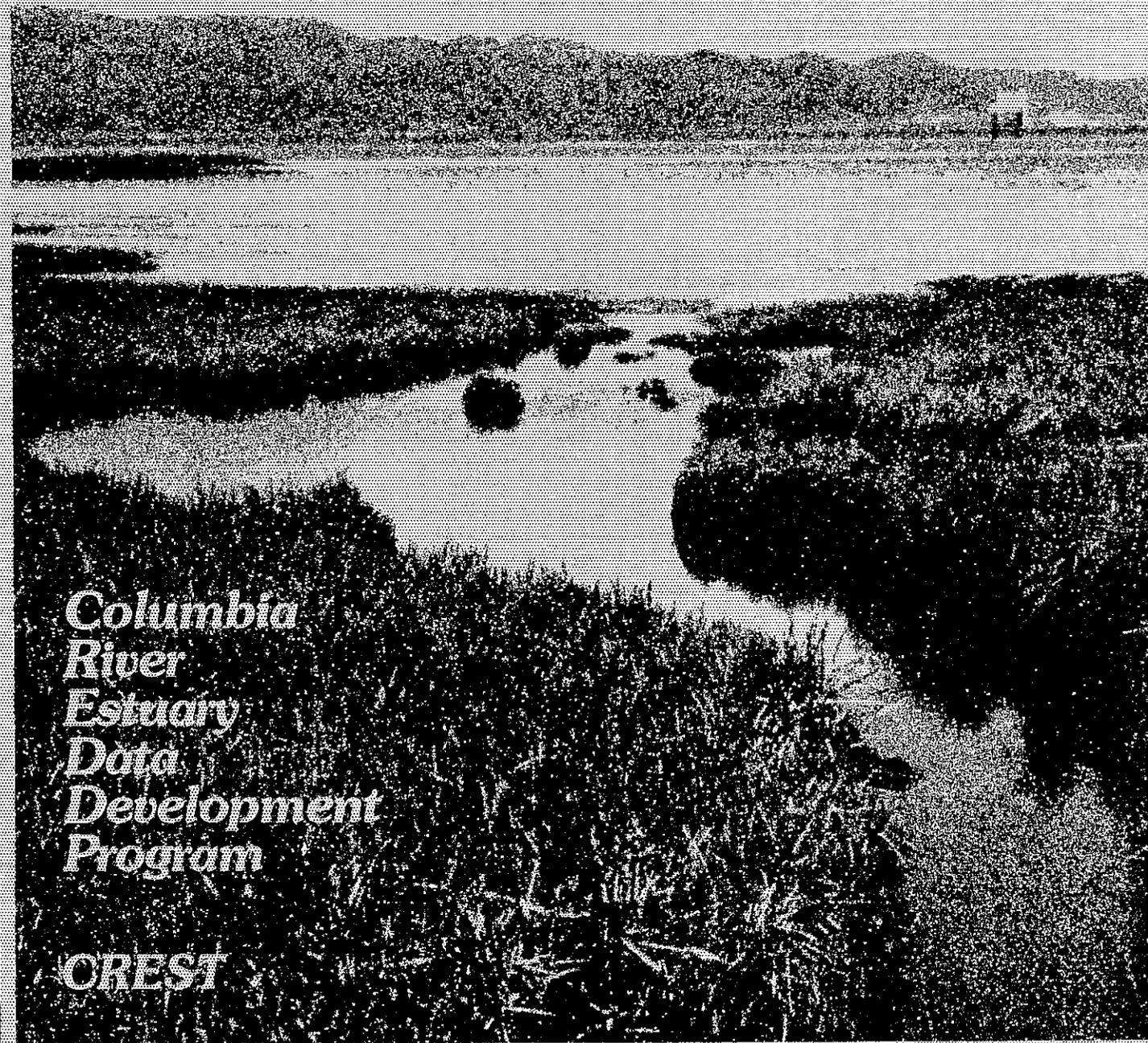


# BENTHIC INFAUNA OF THE COLUMBIA RIVER ESTUARY



*Columbia  
River  
Estuary  
Data  
Development  
Program*

**OREST**

Final Report on the Benthic Infauna Work Unit  
of the Columbia River Estuary Data Development Program

BENTHIC INFAUNA OF THE COLUMBIA RIVER ESTUARY

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## 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 hiatus 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 effects 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 these 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 has 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 report provides information on the benthic infauna of the Columbia River Estuary collected as part of the Columbia River Estuary Data Development Program (CREDDP). The studies were conducted by the Benthic Infauna Work Unit, Robert L. Holton, Principal Investigator, of the College of Oceanography, Oregon State University. In addition to funding provided through CREDDP, support was provided by the U.S. Army Corps of Engineers Portland District and by the College Work Study Program, which helped support part-time student aides. Sediment analyses were conducted by the Corps of Engineers, Portland State University and the School of Oceanography, University of Washington. Statistical advice was provided by Dr. Lyle D. Calvin, Department of Statistics, and Dr. Helen M. Berg, Survey Research Center, Oregon State University.

Several topics of research were investigated in this project, the results originally being assembled as separate research papers. The authors favored presenting these papers as separate chapters in the present report since this would maintain continuity of thought for each topic. However, format design characteristics required by CREDDP program management for final reports dictated that the various research papers be reassembled as integrated Introduction, Methods and Materials, Results and Discussion sections. The authors regret any loss of readability that the reorganization may have created.

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## EXECUTIVE SUMMARY

Distributional, life history and production ecology studies of the benthic infauna of the Columbia River Estuary were conducted as part of the Columbia River Estuary Data Development Program.

The vertical distribution of infauna was investigated by collecting 30 cm deep cores from intertidal sites in Grays Bay, Desdemona Sands, and Baker Bay. The cores were vertically sectioned and sieved on 4.0, 1.0, 0.5, 0.25, 0.125, and 0.063 mm mesh-size screens. In general, amphipods, polychaetes, and small bivalves were concentrated near the surface, nematodes and oligochaetes were broadly distributed and large bivalves were deeply placed. Corophium salmonis, a numerically and trophically important amphipod; was confined to the upper 15 cm of the Grays Bay core. Sieve retention data generally supported the commonly used 0.5 mm separation between meiofauna and macrofauna. However, nematodes, oligochaetes, harpacticoids, and insect larvae were retained on both macro- and meiofaunal size screens. In addition, some juvenile amphipods and bivalves passed through the 0.5 mm screen and were retained on 0.25 and 0.125 mm screens. The depth distribution and screen size retention information was utilized in planning other infaunal studies.

The infauna of a Baker Bay intertidal mudflat was intensively studied from August 1980 to September 1981. The substrate was composed of coarse silt and very fine sand with an oxygen depleted zone at about 7 cm, and was covered by a rich benthic diatom flora. The abundance of individual taxa changed dramatically during the year, but species richness and the relative dominance of surface deposit feeders were stable. Relative abundance of the species and species diversity were also stable except following a Hobsonia florida recruitment in June and July. Spawning periods of the dominant species were June to July for Macoma balthica, August for Pseudopolydora kempfi, and May to June and in September for Hobsonia florida. M. balthica dominated biomass density and produced 13.6 g ash-free dry weight (AFDW)/m<sup>2</sup>/yr. Hobsonia florida and Pseudopolydora kempfi followed at 1.4 g (AFDW)/m<sup>2</sup>/yr and 1.1 g (AFDW)/m<sup>2</sup>/yr, respectively. The remaining taxa together produced 2.3 g (AFDW)/m<sup>2</sup>/yr for a total community production rate of 18.3 g (AFDW)/m<sup>2</sup>/yr. This value is comparable to values published for the infauna of similar habitats in several other estuaries, although it is considerably lower than the highest values. The basis of secondary production by this deposit feeder dominated community is probably river-born detritus and benthic diatom production. This contrasts with the benthic systems of ocean-influenced estuaries in Europe and with salt-marsh dominated systems of the North American east coast.

Year-round studies of the benthic amphipod Corophium salmonis at Desdemona Sands and Grays Bay showed this species to have two generations per year. Spring generation juveniles were produced in May 1981 and grew throughout the summer, producing the fall generation in July and August. Fall juveniles became the overwintering population which then produced the next spring generation. Brood size (average about 15) and mature female lengths were both larger for the spring broods than for the fall broods. Declines in the male:female ratio at Grays Bay appeared attributable to higher predation on large males. At Desdemona Sands,

this ratio increased during the summer, possibly due to an increasing dominance by juveniles, since males can be identified at a smaller size than females. The Desdemona Sands population disappeared in September 1980 and reappeared in April 1981. Early colonists were adults and subadults, which at that time characterized the year-round Grays Bay population. The Desdemona Sands population increased dramatically during early summer 1981, reaching densities of 96,000/m<sup>2</sup> in August, and then declined rapidly. At Grays Bay, density increased steadily from 10,000/m<sup>2</sup> in August 1980 to 32,000/m<sup>2</sup> in February 1981. Density then declined steadily to a low of 4,000/m<sup>2</sup> in July 1981. The wintertime population increases were created by the immigration of adults and subadults. The different patterns of migration exhibited at the two sites appear attributable to higher fall salinities occurring at the Desdemona Sands site than at the Grays Bay site.

Infaunal community structure and secondary production were also investigated at the Desdemona Sands and Grays Bay study sites. Corophium salmonis dominated both biomass and production levels through the year. The species produced 13.1 g AFDW/m<sup>2</sup>/yr at Desdemona Sands and 8.2 g AFDW/m<sup>2</sup>/yr at Grays Bay. Respective production:biomass ratios were 12.3 and 5.5 on an annual basis, and 5.1 and 2.7 for the April to September period. At Grays Bay, biomass peaked in the winter due to immigration, while the Desdemona Sands biomass peaked in the summer followed by the fall depopulation. Size-specific growth rates by C. salmonis (maximum 0.10 mg/mg/day) were similar to values published for other Corophium species, although the production rates were higher than for these species.

Other taxa (e.g., Rhynchocoela, Nematoda, Oligochaeta, Neanthes limnicola) produced just 0.5 g AFDW/m<sup>2</sup>/yr at Desdemona Sands and 0.9 g AFDW/m<sup>2</sup>/yr at Grays Bay, for total community rates of 13.7 g AFDW/m<sup>2</sup>/yr and 9.1 g AFDW/m<sup>2</sup>/yr, which were somewhat lower than the production level at the Baker Bay site.

A survey to determine the estuary-wide distribution of sediment properties and the small macrofauna was conducted in September 1981. The survey utilized a stratified-random design based on 16 strata defined according to published salinity, substrate and depth contour information. Sand was the dominant textural grade (mean stratum silt and clay content usually <25%), and organic content was correspondingly low (about 1%). Biomass means were mostly <.5 g AFDW/m<sup>2</sup>. Dominant species were brackish water species common to other west coast estuaries, and included Macoma balthica, Neanthes limnicola, Hobsonia florida, Corophium salmonis, Eogammarus confervicolus and unidentified oligochaetes, rhynchocoelans and turbellarians. Near the estuary mouth was a sandy-habitat community dominated by Rhynchocoela, Paraphoxus milleri, Archaeomysis grebnitzkii, and Paraonella platybranchia, which gave way upriver to a Eogammarus confervicolus, Eohaustorius estuarius, Neanthes limnicola, Rhynchocoela community. Oligochaeta, Hobsonia florida, Macoma balthica and Neanthes limnicola were characteristic of both Baker Bay and Youngs Bay fine sediments. Pseudopolydora kemp and other polychaetes also in Baker Bay were replaced by Corophium salmonis in Youngs Bay. C. salmonis, oligochaetes, chironomid and heleid larvae and some freshwater molluscs formed a nearly ubiquitous upper-estuary fauna. The generally simple structure

of the estuary infauna is apparently a response to habitat instability in the form of strong currents; active sediments and high tidal and seasonal variability in salinity. A few euryhaline species with opportunistic life history patterns appear to dominate biomass and production rates over the estuary, and contribute very strongly to estuarine food chains.

## 1. INTRODUCTION

This report describes research conducted on the benthic infauna of the Columbia River Estuary (Figure 1). The work was supported primarily by the Columbia River Estuary Data Development Program (CREDDP), and proceeded, with interruptions, from the fall of 1979 to November 1983. Topics of investigation included community structure and distribution and their relationship to environmental properties, species life history and production ecology, and vertical distribution within the sediment.

The CREDDP plan of study considered the Columbia River Estuary as an integrated system and emphasized the need for elucidating food chain processes and the physical-chemical factors which influence them. Key species were defined as those species which fill important roles in food chains, respond to physical changes in the system, and hence are especially important in system management. Such species were to be investigated in depth with regard to their life cycle events, habitat relations, and other ecological interactions. A primary concern was to produce information which could be used by people who manage the estuary. In this context, the benthic infauna was considered important because of its contribution to estuarine food chains, and because the comparatively sedentary mode of life of many infaunal species makes them useful indicators of local conditions.

Specific objectives outlined for the infauna work unit were to summarize existing information on the infauna of the estuary, determine habitat relations, determine and map density distributions, and provide information on food chain relations. Implicit in the last objective and in the CREDDP study plan was the need for energy flow and predator-prey studies of key species, such that dominant food chain events might be quantified and understood.

Three size classes of the infauna are commonly recognized. These are the microfauna (<0.063 mm), meiofauna (0.063 to 0.5 mm) and macrofauna (>0.5 mm). The divisions are based on the mesh sizes of collecting sieves. The macrofauna may be subdivided using a 4 mm mesh screen into the small macrofauna and large macrofauna, so that smaller worms and crustaceans are separated from large shrimp and bivalves. The small macrofauna (0.5 to 4 mm) commonly receives the most attention in benthic studies because it is easier to quantify and identify than the meiofauna, provides useful insights into community-habitat relationships and is important in estuarine food chains. Previous infaunal surveys in the Columbia River Estuary by the National Marine Fisheries Service (NMFS) (e.g., Sanborn 1975) and Oregon State University (OSU) (e.g., Higley and Holton 1975) have emphasized the small macrofauna since these surveys used grab samplers and approximately 0.5 to 1.0 mm mesh screens. In the present study, effort also concentrated on the small macrofauna.

The Columbia River flows 1,210 miles from its origin in Columbia Lake, B.C., Canada and has a combined drainage area of 259,000 mi<sup>2</sup> (Neal 1972). It has played a major role in the development of the Pacific Northwest, serving as a route for commercial traffic, supplying water for irrigation, municipalities and hydroelectric generation, providing a

recreational resource and acting as a waste disposal medium for municipalities.

Maximum flow in the river occurs in May, June and July from the melting of the winter snowpack in the headwater regions. Minimum flows are from September to March, although high water can occur in the winter due to heavy winter rains in the coastal regions (Neal 1972).

The lower Columbia River may be divided into two distinct parts. The upper portion from Aldrich Point at River Mile (RM) 31 to Longview (RM-65) consists of a single channel bordered by steep valley walls, while the region below Aldrich Point is a coastal plain estuary (Hubbell and Glenn 1973; Lutz et al. 1975). Sand deposition in the central region of the estuary forms vast shallow flats and shoals. Lands surrounding the estuary drain primarily through four large shallow embayments (Cathlamet Bay, Grays Bay, Youngs Bay and Baker Bay).

Maximum seawater intrusion extends to about RM-23 (just above Harrington Point) during high tide in late summer when river flow is lowest. During high river flow the seawater intrusion may extend less than 5 miles upriver (Neal 1972). The Columbia River Estuary is characterized mainly as a partially mixed estuary and can be divided into three sections along the salinity gradient. From the mouth to about RM-7 it is basically marine, from RM-7 to RM-23 it is transitional (mixing), and above RM-23 it is fluvial (fresh water) (Hubbell and Glenn 1973).

Information on the benthic infauna of the Columbia River Estuary was first provided by Haertel and Osterberg (1967), who identified some of the common forms at four locations in the main river between Harrington Point and the river mouth. Their taxonomic lists were cursory and without quantification. Subsequent infaunal surveys (e.g., Durkin et al. 1977; Higley and Holton 1975) generally have been site-specific inventories providing baseline distribution and abundance data.

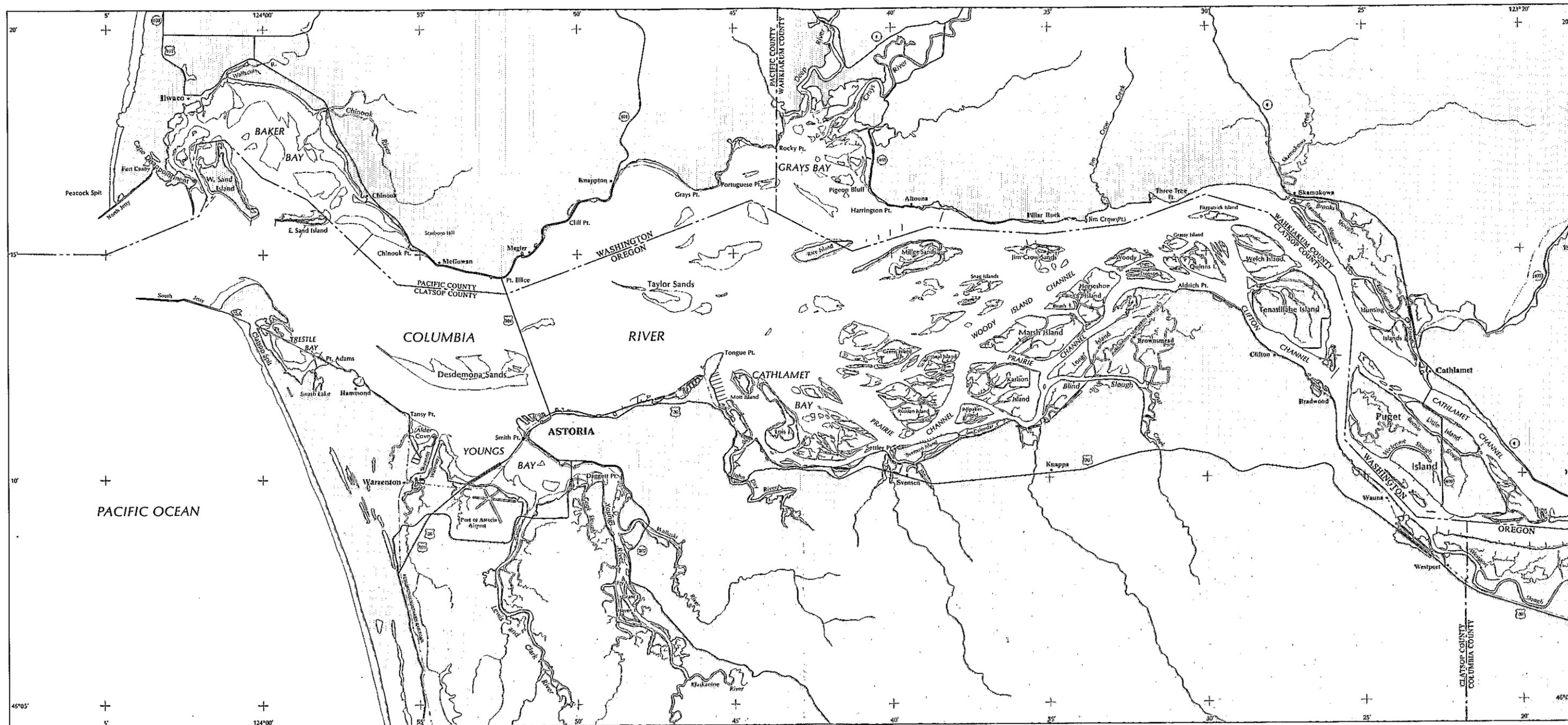
A brief NMFS survey of the lower Columbia and Willamette Rivers included one sandy-substrate station near Tongue Point (Sanborn 1973; McConnell et al. 1973), where the amphipod Eohaustorius spp. and the isopod Licerus spp. were common. Perhaps the most interesting observation, however, was that the amphipod Corophium salmonis existed as far up as RM-95 in the Columbia River, clearly establishing the freshwater tolerance of this highly important estuarine species. This was confirmed by a later NMFS study at Prescott (RM-72), where the amphipods Corophium spp. and Eogammarus spp., as well as unidentified polychaete species were found by Blahm and McConnell (1979).

In 1974, a NMFS survey of dredged-material effects at four sites (the mouth of the Youngs Bay, near Desdemona Sands, just inside the north jetty, and outside the river mouth) provided basic species lists and densities for sandy habitats in brackish and marine-dominated regions (Sanborn 1975). Data from this and similar studies may have been affected by the dredging activities under study.

During 1973 to 1975, OSU conducted a biological baseline study of Youngs Bay (Higley and Holton 1975; Higley et al. 1979). The study de-

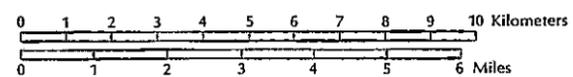
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Figure 1. Columbia River Estuary



# Columbia River Estuary

Scale 1:160,000



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

veloped infaunal abundance data (some seasonal) for 142 stations in Youngs Bay and the Youngs, Lewis and Clark, and Skipanon Rivers. This study established the pervasive abundance of Corophium spp. in fine-sediment, brackish and freshwater habitats, while indicating heavy predation by fish on this amphipod and on epibenthic shrimp (Crangon spp. and Neomysis spp.). Also provided were data on infaunal density and substrate characteristics, and on the size structure and sex ratios of Corophium salmonis and C. spinicorne populations along a 400 m transect. This information was complemented by studies of the diel appearance of infaunal and epifaunal forms in the water column. This latter work, later expanded into a thesis project by Davis (1978), provided the only life history work conducted on Columbia River Estuary infauna before the CREDDP study. Davis' thesis provided information on diel and seasonal changes in density, sex, length, maturity, and body color patterns for Corophium populations found in the water column and in bottom sediments, and related these to dispersal and predation. Some data were provided for other crustaceans as well. In 1976, the infauna of the intertidal zone in Youngs Bay adjacent to the east spit of the Skipanon waterways was first surveyed by Montagne and Associates (1976), and then by NMFS (Durkin et al. 1977). The results of both studies were similar to those of OSU, except for some possible differences in species identifications provided by Montagne and Associates.

A survey of infauna over the lower 28 miles of the estuary was performed by OSU (Higley et al. 1976; Higley and Holton 1978) as part of an assessment of infaunal and fish populations at a potential fill site located on the northeast side of Youngs Bay, adjacent to the Port of Astoria. These data and previously collected Youngs Bay data were interpreted as estuary-wide distribution charts for Amphipoda and Polychaeta. The survey showed that the brackish-water fauna of Youngs Bay gave way to a more complex marine-related fauna downriver, where a richer variety of amphipods and polychaetes occurred.

As part of a comprehensive study of habitat development, NMFS conducted seasonal infaunal studies in fine sediment areas of Miller Sands, located in the freshwater portion of the estuary (McConnell et al. 1978). The study revealed a fauna similar to that of the Youngs Bay region, but with higher densities of chironomid larvae and the Asiatic clam (Corbicula). Seasonal changes in population density were documented. This study together with zooplankton studies provided a basis for interpreting fish food habits studies. A similar but less intensive study at dredging sites near Pillar Rock, off Jim Crow Point (Durkin et al. 1979) identified a faunal group similar to that at the Miller Sands site.

Downriver, a dredging-related survey was made at the Chinook channel in Baker Bay by NMFS (Blahm et al. 1979). The fauna described was similar to that found in Youngs Bay, with the addition of Callianassa spp. (Decapoda) and possibly more polychaete species (not identified).

One infaunal group which has received little attention is the freshwater bivalves. Aside from the introduced Asiatic clam, Corbicula manilensis (= C. fluminea) mentioned above, the freshwater mussels

Anodonta oregonensis and A. wahlamentensis occur in intertidal habitats east of Tongue Point (Cory et al. 1970).

Overall, it appears that elements of the fine-sediment, brackish-water community characterized by the amphipod Corophium spp. occur from Baker Bay to well upriver of the study zone. In more coarse substrates, a simpler and less dense community characterized by the amphipod Eohaustorius spp. occurs. Both communities accumulate additional fauna up and down river: various insects upriver and additional amphipods and polychaetes downriver. Even near the river mouth, however, the fauna is much less diverse than that of the offshore region studied by Richardson et al. (1977).

Good, in the Columbia River Estuary Study Taskforce (CREST) inventory (Seaman 1978), synthesized survey data for the major infaunal groups to provide an overall picture of animal distribution. However, an adequate estuary-wide survey had not been conducted before CREDDP, and the early studies lacked an ecosystem perspective.

One of the first tasks undertaken in the CREDDP infauna research program was to identify those species which should receive concentrated research attention, both in the form of literature review and field studies. These key species were chosen based on their abundance in the estuary and their occurrence in fish stomachs, according to earlier studies of the estuary biota. The species selected were:

Polychaeta

Capitella capitata  
Hobson florida  
Neanthes limnicola  
Pseudopolydora kemp

Bivalvia

Corbicula manilensis  
Macoma balthica

Amphipoda

Corophium salmonis  
Eohaustorius estuarius.

These species, except for Corbicula manilensis, are of marine origin, have wide salinity tolerances and are common in other Pacific Northwest estuaries. Their abundance in the Columbia River Estuary reflects the brackish nature of this estuary. The available literature for each of these species was reviewed and has been submitted as a series of outline summaries to CREDDP. Also, distributional properties of several of the species are depicted in the Atlas (CREDDP 1984), and four of the species were the subjects of intensive year-round life history and production ecology studies. The latter work is presented in this report, while the literature reviews and the Atlas are separate reports.

The benthic infauna work unit consisted of essentially five separate studies. As a result, each major section of the final report (e.g., Introduction, Methods and Materials) contains a section which specifically addresses one of the five individual studies.

The first study examined the vertical distribution of macrofauna and meiofauna within sediments of Baker Bay, Desdemona Sands and Grays Bay, and also investigated the relative frequency with which different taxa were collected on screens of different mesh sizes. The data were based on deep cores collected at each site and were used in choosing sampling depth and screen sizes in the life history studies.

The production ecology of the small infauna in an intertidal mudflat of Baker Bay was examined in the second study. This year-round study determined seasonal density changes and reproductive events for three dominant members of the community (two polychaetes and a bivalve), and calculated annual secondary production rates for these species and for other less abundant members of the community.

The life history patterns of the amphipod Corophium salmonis in two habitats of the estuary were compared in the third study. Both study sites were intertidal sandflats, but differed in their exposure to saline water. The two populations responded to the different environmental conditions by developing different seasonal patterns of migration, reproduction and density change.

In the fourth study, the life history information on Corophium salmonis provided in the previous study was used to develop seasonal and annual secondary production rates for this species at both sites. Additionally, seasonal density changes and annual production rates for other taxa (which were much less abundant than C. salmonis) were calculated, and the structure and probable trophic relations of this community were assessed.

The fifth study determined the distribution and structure of infaunal communities over the whole estuary. This description was based on a late summer survey that distributed samples among several habitats and salinity zones within the estuary. Representative density values for individual taxa and for the sum of all small macrofauna were computed for each of the sampling strata, and the distributions of four community types were determined. This biological information was correlated with measurements of sediment properties and with amount of exposure to saline water.

Subsequent subsections of this chapter introduce these studies more completely.

Information supplementary to these five studies is provided in Appendices A and B. Appendix A summarizes literature information on the life history properties of most of the species identified in the CREDDP infaunal studies. The summary takes the form of a chart that indicates individual species' salinity range, substrate preference, life style, feeding type, and reproduction and dispersal properties. The chart is intended to provide background information on individual infaunal species of the Columbia River Estuary that complements the distributional and energy flow information provided by the field studies. Because literature information is incomplete for many species, the chart cannot be considered definitive. This chart, and the more extensive summaries

prepared for the key species, help define areas of needed research on the infauna of the estuary.

Appendix B describes the quality control procedures followed by the infauna research group in conducting the field studies described above. The subjects discussed include the criteria used in accepting or rejecting field samples, methods of cross-checking laboratory analyses of samples, and validation of computer coded data.

#### 1.1 VERTICAL DISTRIBUTION STUDY

As part of preliminary studies designed to establish long range sampling plans, large diameter deep sediment cores were sectioned and screened on successively smaller meshes to provide detailed information on the vertical distribution of various size organisms within the sediment. This information provided a basis for establishing sampling depth in other more extensive studies where the desire was to adequately represent all targeted species or groups without processing excessive amounts of sediment. This preliminary study resulted in increased sampling and analytic efficiency for these later studies, while providing useful benthic infauna information for the core sites. Specifically, screen mesh size retention data were used in choosing mesh sizes suitable for distributional, life history, and production studies. In addition, resource managers can use the screen retention information to help compare infaunal densities obtained in studies using different size screens, and can use the depth distribution information in understanding potential environmental impacts on the benthic infauna from such activities as dredging.

A body of literature exists on the distribution of microfauna and meiofauna (animals less than 0.063 mm and from 0.063 to 0.5 mm, respectively) in marine and estuarine sediments. For example, meiofauna were found to be abundant to at least 35 cm depth in the medium to fine sands of Algoa Bay, South Africa (McLachlan et al. 1977). At upper tide levels in Algoa Bay, meiofauna were common at the 90 cm depth (McIntyre 1979 and McLachlan 1975, both cited in McLachlan et al. 1977).

Stream invertebrates have also been shown to live deep in sand/gravel substrates of well-oxygenated streams. Coleman and Hynes (1970) vertically divided the sand/gravel substrate of a stream into four layers: 0 to 7.6 cm, 7.6 to 15.2 cm, 15.2 to 22.9 cm, 22.9 to 30.5 cm. Colonization occurred uniformly over a 28 day period in all layers. Chironomids (midge larvae) and other aquatic organisms were found at all depths and some animals were found as deep as 70 cm. Other research indicates that the peak organism abundance occurs at 10 cm in streams (Morris and Brooker 1979; Williams and Hynes 1974), but that the abundance does not drop sharply until depths greater than 30 cm (Williams and Hynes 1974).

Detailed information concerning the vertical distribution of estuarine benthic macrofauna (those animals retained on a 0.5 mm screen) at sediment depths greater than 10 cm is more scarce. However, Jefferts (1977) includes both an excellent literature review on existing informa-

tion and a study of the vertical distribution of infauna in dredged and undredged areas of Coos Bay, OR.

In the present study, three representative cores were collected. Since the infaunal studies concentrated on macrofauna, all macrofaunal portions of these three cores were processed. In addition, selected depth intervals of the cores were processed for meiofauna. Sediment grain size distribution information was developed for all depths in each core to aid interpretation of the infaunal data.

The three cores were collected on 15 to 17 May 1980 at intertidal sites selected to represent different salinity zones and substrates in the Columbia River Estuary. The first core was collected at a fine-sand site in Grays Bay (Station G), a fresh-water dominated location (Figure 2). The second core was collected on Desdemona Sands (Station D), a high-energy sandy shoal in the central estuary. The third core was collected at a muddy-sand site in Baker Bay (Station B), which has a comparatively strong marine influence.

## 1.2 BAKER BAY MUDFLAT COMMUNITY INTENSIVE STUDY

The first objective of this study was to determine the seasonal changes in community structure and species density of the small macrofauna on a Baker Bay mudflat. Community structure was studied in terms of taxonomic composition, organism abundance, community diversity, richness, evenness, and the relative importance of different feeding strategies. The second objective was to estimate annual secondary production by this community.

Research was conducted at a single site (Figure 3) chosen as typical of large expanses of intertidal mudflats in Baker Bay. The sediments at the site are mostly well mixed fine sands and silt. The dominant infauna are sedentary, and the young either have a short planktonic larval stage or remain in the mud. The site has the advantage that benthic primary production (McIntire and Amspoker 1984) and epibenthic organism studies (Simenstad 1984) were conducted as part of the CREDDP research program at a similar site within two hundred meters.

The study site supported a community dominated by the bivalve Macoma balthica and two polychaetes, Pseudopolydora kemp and Hobsonia florida. Research on similar communities has been conducted in Europe. Warwick and Price (1975) estimated annual production of an intertidal Macoma community in Lynher estuary, England, and Wolff (1977) studied the benthic food budget in the Grevelingen Estuary, the Netherlands. Glemarec and Menesguen (1980) have discussed some of the problems in estimating production of benthic infauna in a mud-sand habitat: large seasonal and year-to-year density fluctuations at all trophic levels, high mortality between the release of eggs and development of juveniles large enough to be retained on the commonly used sieve size (0.500 mm mesh), and difficulties in estimating the production of the less numerous and very small organisms that together may represent an important portion of the biomass.

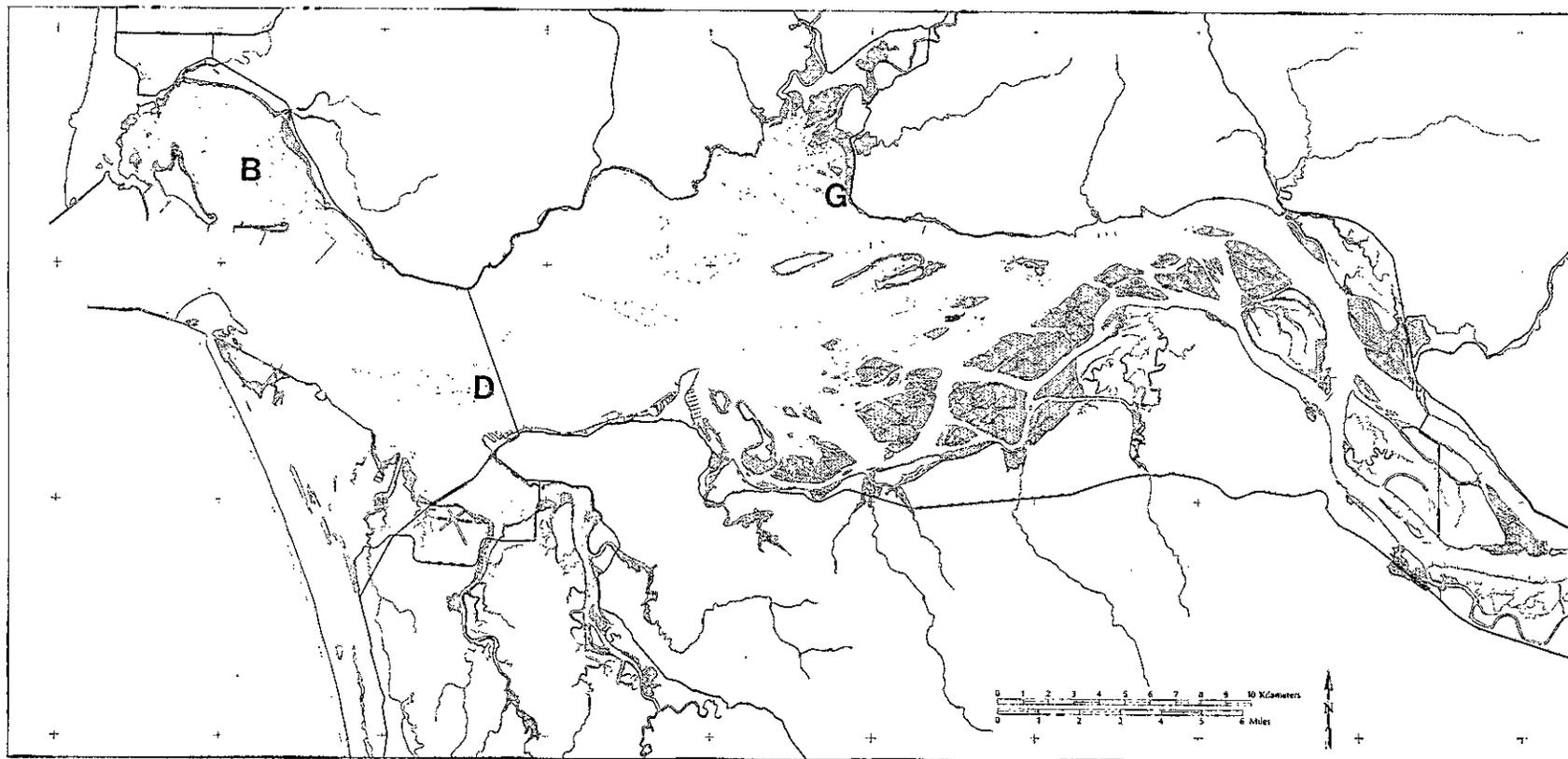


Figure 2. Location of Sites Where Vertical Distribution Cores were Collected. G = Grays Bay Site, D = Desdemona Sands Site, B = Baker Bay Site.

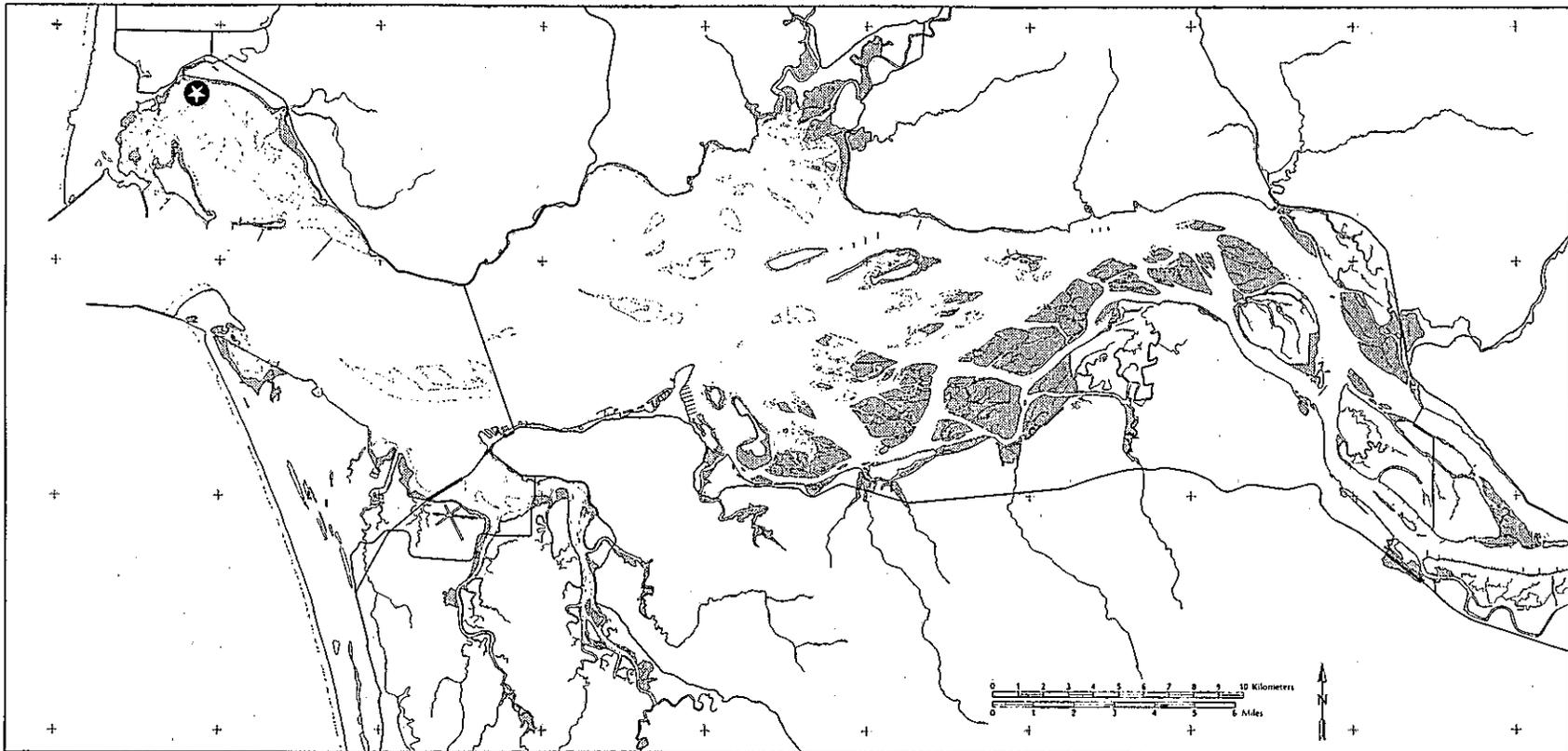


Figure 3. Location of the Baker Bay Intensive Study Site

In the present study, no allowance for year-to-year fluctuations could be made, since sampling covered only a 54-week period. However, biomass estimates and size frequency histograms could be compared from two sampling dates twelve months apart. The juvenile capture problem was handled by determining beforehand which mesh size was required to capture the smallest juveniles of the three principal species. The size chosen was 0.250 mm, which retained the juveniles as they developed in the mud or settled out of the water column. Finally, four methods (described in detail later) were used to compute production of the lesser taxa which composed 5.3% of the biomass measured as ash-free dry weight (AFDW).

A detailed study of the life histories of organisms and the calculation of secondary production is an important process in understanding the ecology of a benthic system. Taxonomic and density data for different species provide insights into community structure, but production estimates supply information on food resource utilization and amount of biomass available to the next trophic level. For example, community structure may be similar in two benthic communities, but production levels may differ. This suggests a different level of food availability in the benthos and, additionally, suggests a limitation on the ability of the benthic community to support the next higher trophic level.

Wolff (1977) discussed the levels of productivity associated with different types of estuaries and the mechanisms supporting high benthic secondary production. Two types of estuarine systems were described: 1) a salt-marsh, mangrove, or eelgrass detritus based system with a net export of nutrients and organic matter to the ocean, and 2) an estuarine system dependant on ocean derived detritus. The Columbia River Estuary, however, fits into a third category, a detrital system dependent on river input (McIntire and Amspoker 1983; Lara-Lara 1983). Residence time of Columbia River Estuary water is only 2 to 5 days and in this respect is comparable to the Congo River system (Lara-Lara 1983). Therefore, the Columbia River Estuary provided a different type of estuarine system in which to study the dynamics of secondary production.

The Columbia River Estuary is a fresh water-dominated system that receives flow discharges ranging from an average minimum of 4,248 cubic meters per second (cms) in the fall up to 16,900 cms during the spring freshet (Neal 1972), and experiences tides involving maximal changes of as much as 4 m. Baker Bay, located close to the river mouth (Figure 3), undergoes large seasonal variations in salinity, depending on tidal exchange and river flow.

The study site in Baker Bay was a relatively homogeneous habitat of coarse silt to fine sand covered by a highly productive benthic diatom flora. During the period from May 1980 to April 1981, benthic gross primary production reached a high of 81 mg C/m<sup>2</sup>/hr in June 1980, with an annual benthic gross primary production of 42 g C/m<sup>2</sup>/yr, or 80 g AFDW/m<sup>2</sup>/yr (McIntire and Amspoker 1984). Sparse patches of eelgrass (*Zostera marina*) were scattered over the surface of the mudflat and a three-square sedge (*Scirpus americanus*) marsh bordered the tidal flat 600 m from the study site. The mudflat was rich in organics. Organic matter in the top centimeter of the sediment ranged from a high of 330 mg AFDW/m<sup>2</sup> in May 1980 to a low of 165 mg AFDW/m<sup>2</sup> in September 1980 during

the May 1980 to April 1981 time period (McIntire and Amspoker 1983). Anaerobic black mud smelling of sulfides lay below a 4 to 6 cm surface layer of brown mud.

Sediment analysis showed that this mudflat site was relatively stable in terms of sediment composition during the study period. Median particle size measured in phi ( $\phi$ ) units ( $\phi = -\log_2[\text{diam. in mm}]$ ) and percent silt and clay fractions remained unchanged during the year (Figure 4).

Water temperatures ranged from 6 to 17°C and salinities from 3.5 to 20.2 ppt in the vicinity of the study site (Figure 5). In general, temperature and salinity were high during the late summer to early fall period, and low during the winter and spring. As indicated by Figure 5, greater variability in these measurements occurred at the present study site than at the Ilwaco boat basin site where McIntire and Amspoker made their collections. The differences may be attributed to the fact that water samples at the study site were collected at low tide and often from depressions where the residual water was subjected to evaporation and rainfall effects having little influence on the Ilwaco water.

### 1.3 COROPHIUM SALMONIS LIFE HISTORY STUDY

The amphipod genus Corophium was described in 1806 by Latreille with a single specimen of Corophium longicorne (Crawford 1937). It has since been expanded to contain approximately 45 species located throughout the world in a wide range of salinities (Green 1968). Most species in the genus inhabit marine and brackish waters but a few are freshwater forms (Green 1968).

Corophium species are characteristic of harbors and estuaries and frequently inhabit intertidal muddy shores (Crawford 1937; Meadows and Reid 1966). Crawford observed that all known species of the genus formed tubes of mud or muddy sand, either in the substratum or attached to solid objects. Corophium are capable of swimming and C. volutator has been observed walking over the surface of the mud, both when the tide was in and when it has just ebbed (Green 1968).

Hart (1930) described C. volutator as a true deposit feeder which was also capable of filter feeding. Particles of food, organic detritus and its associated micro-organisms are sorted out from the substratum by the gnathopods, the food handling appendages, and passed to the mouth-parts. Substrate is raked into the burrow by the second antennae while the animal is partly or wholly out of its burrow (Green 1968). Filter feeding occurs when the animal is in the burrow. The animal creates a respiratory current through the U-shaped burrow from which food particles are filtered (Green 1969). However, Meadows and Reid (1966) observed that borrow openings raised above the substrate surface allowed only fine, unfilterable particles to enter the burrow. It also appeared that the C. volutator did not feed while on the sediment surface but only when they were in their burrow.

In most species of the genus both sexes exist (Crawford 1937). The exception is the British species C. bonnellii which is parthenogenic with

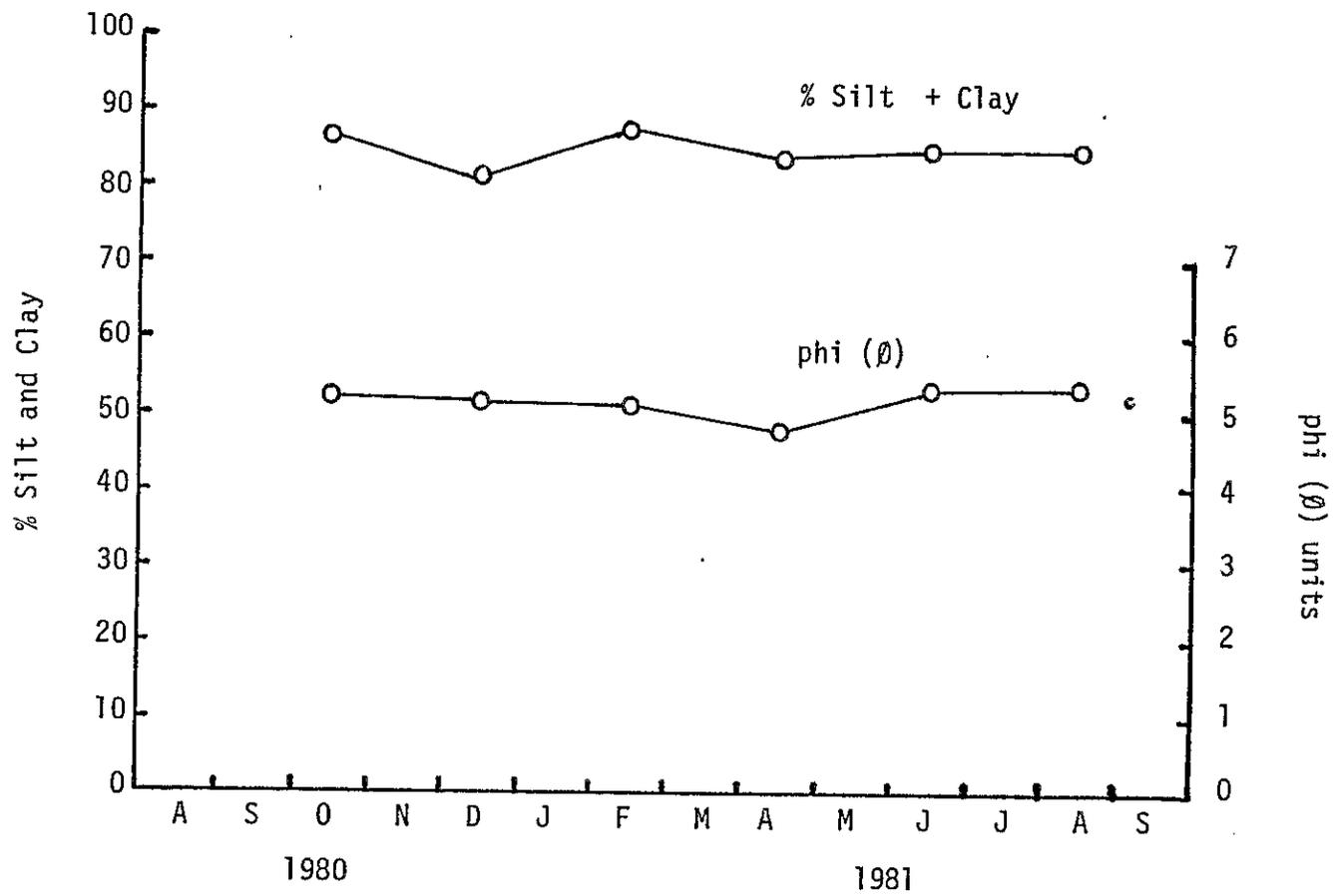


Figure 4. Sediment Composition at the Baker Bay Study Site

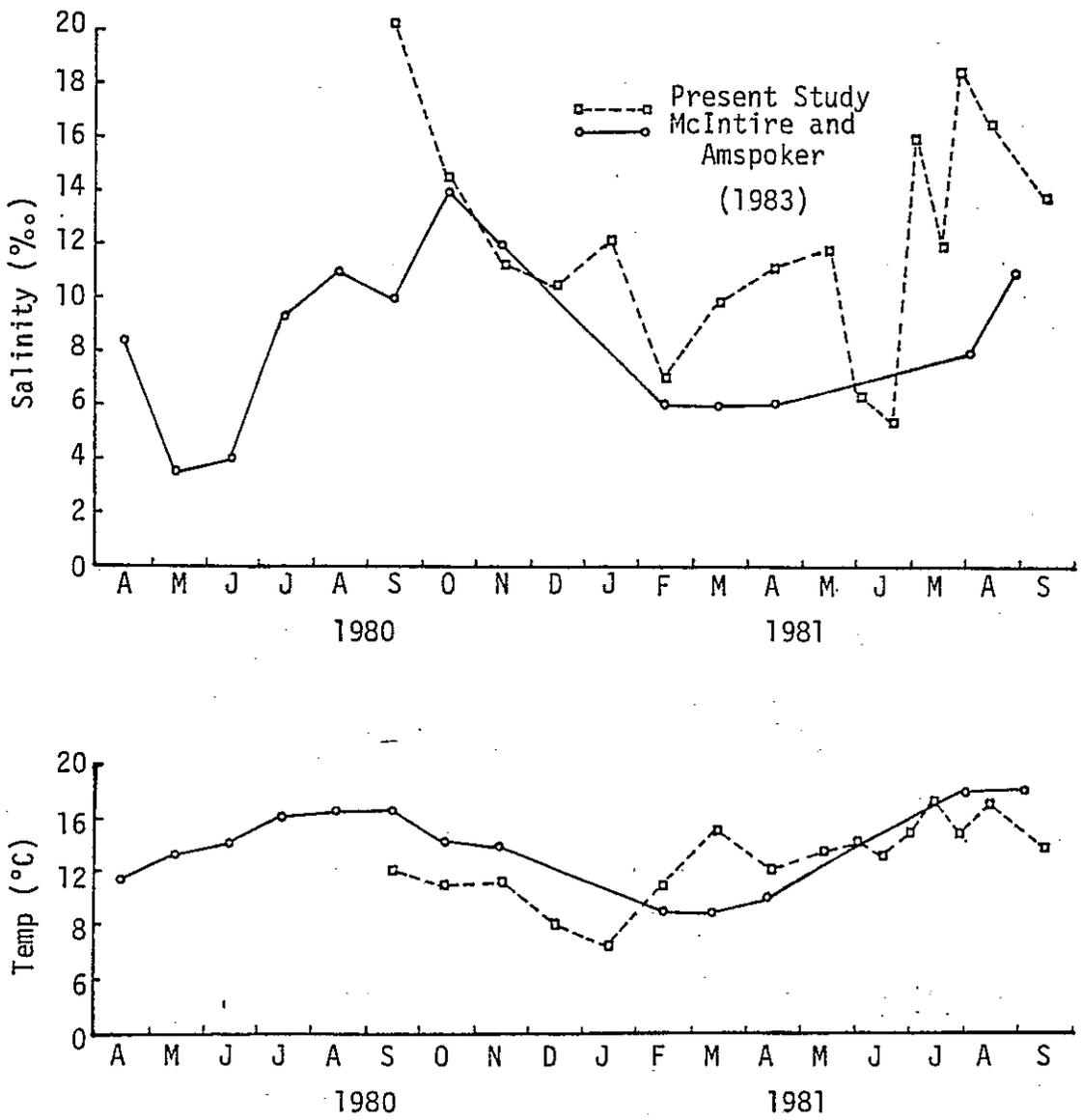


Figure 5. Salinity and Temperature in Baker Bay at Low Tide. McIntire and Amspoker Measured Surface Salinity at the Ilwaco Boat Basin. In the Present Study Surface Samples were Collected at the Study Site.

only females observed (Moore 1980). In British species where both sexes are present, Crawford (1937) observed that females were usually more abundant than males. Young Corophium remain in a maternal brood pouch until they are juveniles. They are released from the brood pouch into the maternal burrow (Green 1968).

Fourteen species of Corophium have been described from the west coast of America. Barnard (1954) described four species from Oregon which were collected from Coos Bay: C. acherusicum, C. brevis, C. salmonis and C. spinicorne. Of these species, three have been observed regularly in the Columbia River Estuary. C. brevis, primarily a marine species, has been captured sporadically in the lower estuary (Davis 1978). This species is apparently distributed in the more saline water downstream of Youngs Bay (Higley and Holton 1978) but was captured by Davis (1978) in Youngs Bay and was probably swept into the bay with the salinity intrusion. C. spinicorne, a more abundant species in the estuary, attaches its mucous tubes to algae, rocks and pilings along the shoreline of Youngs Bay and sporadically downstream and possibly upstream (Davis 1978). It is considered a broadly euryhaline species and may occur in waters ranging from fresh to marine (Hazel and Kelly 1966; Aldrich 1961). The most abundant species of Corophium in the Columbia River Estuary is C. salmonis, a major member of the freshwater and brackish water infauna of the estuary. One specimen of C. insidiosum was captured by Davis (1978) but its regular occurrence in the estuary has not been established. C. insidiosum builds tubes of mud on algae and hydroids (Sheader 1978) and is found in shallow brackish inshore areas and estuaries with a high degree of turbidity (Nair and Anger 1979).

Corophium salmonis is an important species in the Columbia River Estuary because of its frequent high abundance and heavy utilization as prey by other organisms in the estuary. It inhabits sandy mud deposits in the estuary, extending from Youngs Bay upstream at least to Portland (Higley and Holton 1978; Davis 1978). It is also found in isolated portions of Baker Bay. Densities commonly exceed 10,000/m<sup>2</sup> and may reach as high as 40,000/m<sup>2</sup> (Higley and Holton 1975). The higher densities were encountered where sandy mud sediments accumulated in quiet portions of Youngs Bay.

C. salmonis typically builds mucus and mud U-shaped tubes in fine sand, either intertidally or subtidally. It feeds mainly as a selective deposit feeder, using its second antennae to scrape surface deposits and detritus near its burrow (Eckman 1979). It may also filter feed utilizing the respiratory current generated through its tube. C. salmonis may be observed at low tide either crawling on the substratum surface or swimming in pools of water remaining after the ebb tide.

Estuarine fish known to prey on C. salmonis include juvenile chinook salmon (Oncorhynchus tshawytscha), chum and coho salmon (O. keta and O. kisutch), starry flounder (Platichthys stellatus), pacific staghorn and prickly sculpins (Leptocottus armatus and Cottus asper), shiner perch (Cymatogaster aggregata), longfin smelt (Spirinchus thaleichthys), pacific tomcod (Microgadus proximus) and American shad (Alosa sapidissima) (McConnell et al. 1978; Haertel and Osterberg 1967; Higley and Holton 1975; Hammann 1982). It is also eaten by larger benthic invertebrates

including polychaetes and nemerteans, as well as by shorebirds, wading birds, gulls and waterfowl (Hart 1930). The heavy utilization of C. salmonis as prey in the estuary makes knowledge of its life history patterns and production characteristics important. At present, there is no published information on C. salmonis life history except that of Davis (1978) and Albright and Armstrong (1982). Davis studied C. salmonis in Youngs Bay with regard to diel migration, coloration and life history. He reported that the life cycle of C. salmonis was similar to that of C. volutator in having two generations per year. Because of the widespread distribution of C. salmonis throughout the estuary, the present study was undertaken to examine variations in the life history of populations of C. salmonis from habitats with different salinity and energy regimes.

Populations of C. salmonis from two different habitats in the Columbia River Estuary were selected for examination of life history characteristics including reproductive season, seasonal density, sex ratio, size at sexual maturity and brood size.

Two sites previously established during preliminary surveys as supporting C. salmonis populations were selected for study. One site was in Grays Bay, a large protected embayment on the north side of the estuary on the edge between the mixing and the freshwater zones (Figure 6). The second site was located on Desdemona Sands, a midriver sand shoal that is situated in the mixing salinity zone and which differs from Grays Bay in both tidal energy and salinity.

#### 1.4 COROPHIUM SALMONIS COMMUNITY DYNAMICS STUDY

This study investigated the production ecology of the small macrofauna at the two intertidal sandflats sampled during the Corophium salmonis life history study. Data from that study were used here in estimating annual secondary production for C. salmonis. Production by other taxa was based on density data not included in the previous report.

Production rates for Corophium populations have been estimated in few cases. Birklund (1977) estimated production rates for C. insidiosum and C. volutator in Holbaek Fjord, Zealand, Denmark; and Albright and Armstrong calculated production by C. salmonis in Grays Harbor, Washington. As discussed by Birklund (1977), estimation of Corophium production is complicated by the difficulty of identifying discrete age groups. In these prior studies and in the present one, estimation therefore has relied at least in part on measurement of size-specific growth rate or mortality rate. For the Columbia River Estuary study sites, C. salmonis production was estimated by a combination of two methods: cohort analysis, and extraction of size-specific growth rates from length frequency histograms. Although Crisp (1971) recommends using individual growth rates as opposed to those derived from population studies, use of the population approach provided the only practical means of making the production estimates in this case. As will be seen, the growth rates developed for C. salmonis in the Columbia River Estuary were quite similar to those found for C. salmonis in Grays Harbor (Albright and Armstrong 1982), and for C. insidiosum and C. volutator in Holbaek Fjord (Birklund 1977).

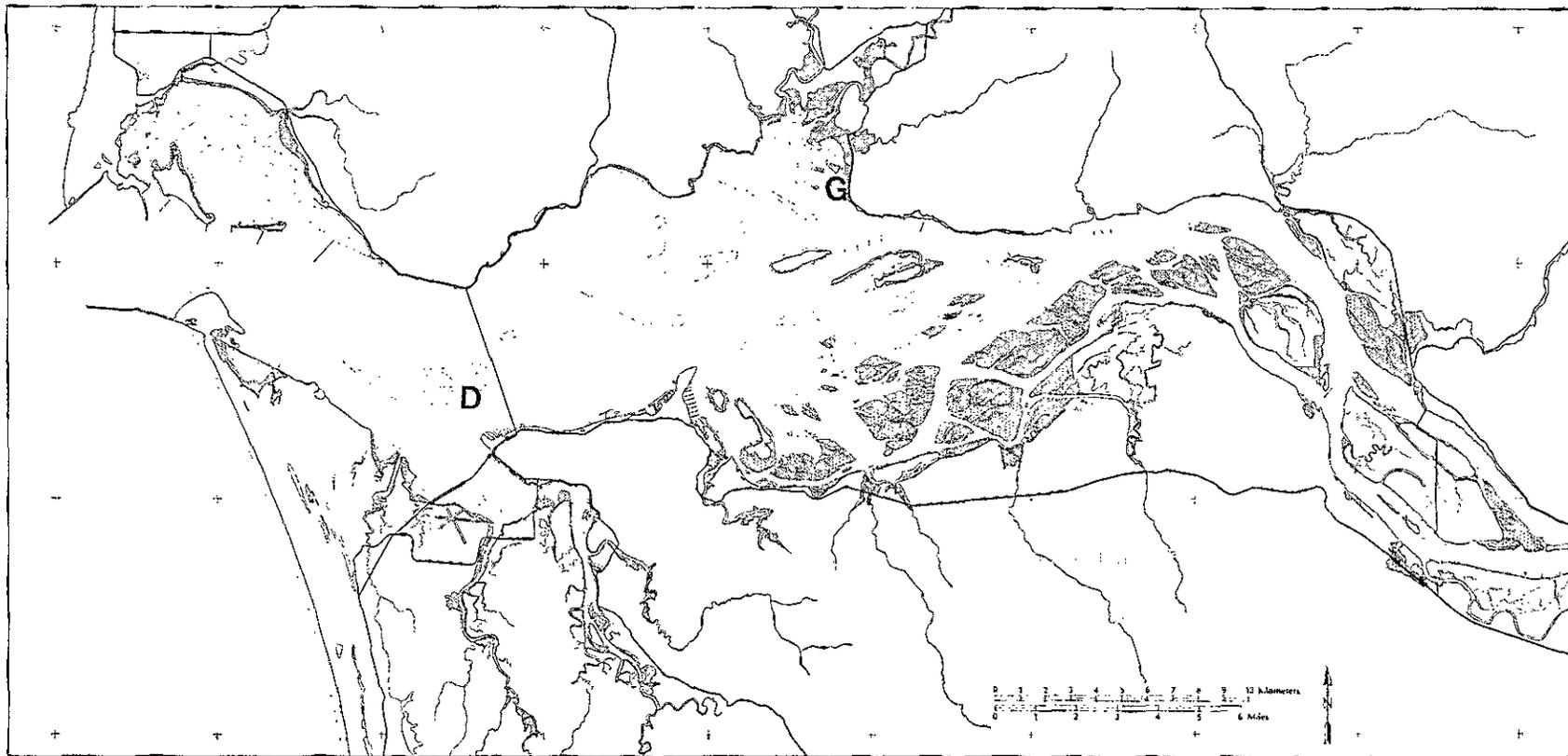


Figure 6. Location of Grays Bay (G) and Desdemona Sands (D) Intensive Study Sites

Other members of the small macrofauna (termed "lesser taxa") at the two sites were generally much less abundant than *C. salmonis* and production was estimated using mean annual biomass levels and turnover rates provided in the literature.

As described in Section 1.3, the study sites were located along the north-east shoreline of Grays Bay and on Desdemona Sands near the mouth of Youngs Bay (Figure 6). Tidal elevation of both sites was about .3 m above MLLW. Sediments at both sites were predominantly fine sands, median grain size averaging about 2.5 to 3.0 phi units, and the <0.063 mm fraction usually less than 15% of the sediment composition. The Desdemona Sands site had slightly coarser sediments due to its greater exposure to the strong tidal currents of the nearby shipping channel. The sandy character of the two sites is representative of the estuary's large expanses of sandy shallow habitats.

Salinity is highly variable in the Columbia River Estuary due to the large and variable tidal exchanges and to seasonally variable freshwater flows. Measurements made at low tide during the study showed the Desdemona Sands site to experience only slightly higher salinities (2 to 10 ppt) than the Grays Bay site (2 to 7 ppt). However, high tide salinities in the early fall were certainly much higher at the Desdemona Sands site than at the Grays Bay site due to its proximity to the ocean. Results of a modeling effort by Jay (1984) indicate that spring tide surface salinity maxima for October 1980 to have been around 25 ppt near the Desdemona Sands site and about 5 ppt near the Grays Bay site. Therefore, the two sites may be presumed to have experienced seasonally different salinity regimes.

#### 1.5 ESTUARY-WIDE DISTRIBUTION STUDY

Patterns of distribution and abundance of the benthic infauna of the Columbia River Estuary were investigated using a single stratified random survey conducted 8 to 11 September 1981. The survey comprised 194 grab samples collected in 16 strata (Figure 7) and 31 substrata, which were defined in terms of salinity influence, water depth and current regime. The data were analyzed so as to reveal the characteristic biotic content and physical features of each stratum, and to illustrate patterns of animal distribution in relation to the physical variables measured. The analytic methods employed in this task included simple tabular and graphical summaries as well as more complex statistical interpretations.

Work on CREDDP investigations was suspended soon after the survey samples were collected due to a temporary suspension of the program caused by budgeting problems. However, the U.S. Army Corps of Engineers (COE) provided interim funding that allowed continuance of certain parts of the project, including analysis of some of the survey samples. Subsequent refunding of CREDDP allowed completion of the several infauna projects.

Benthic infaunal habitat is not especially diverse in the Columbia River Estuary although the estuary is very large. The area below marshlands covers about 437 square kilometers within the boundaries estab-

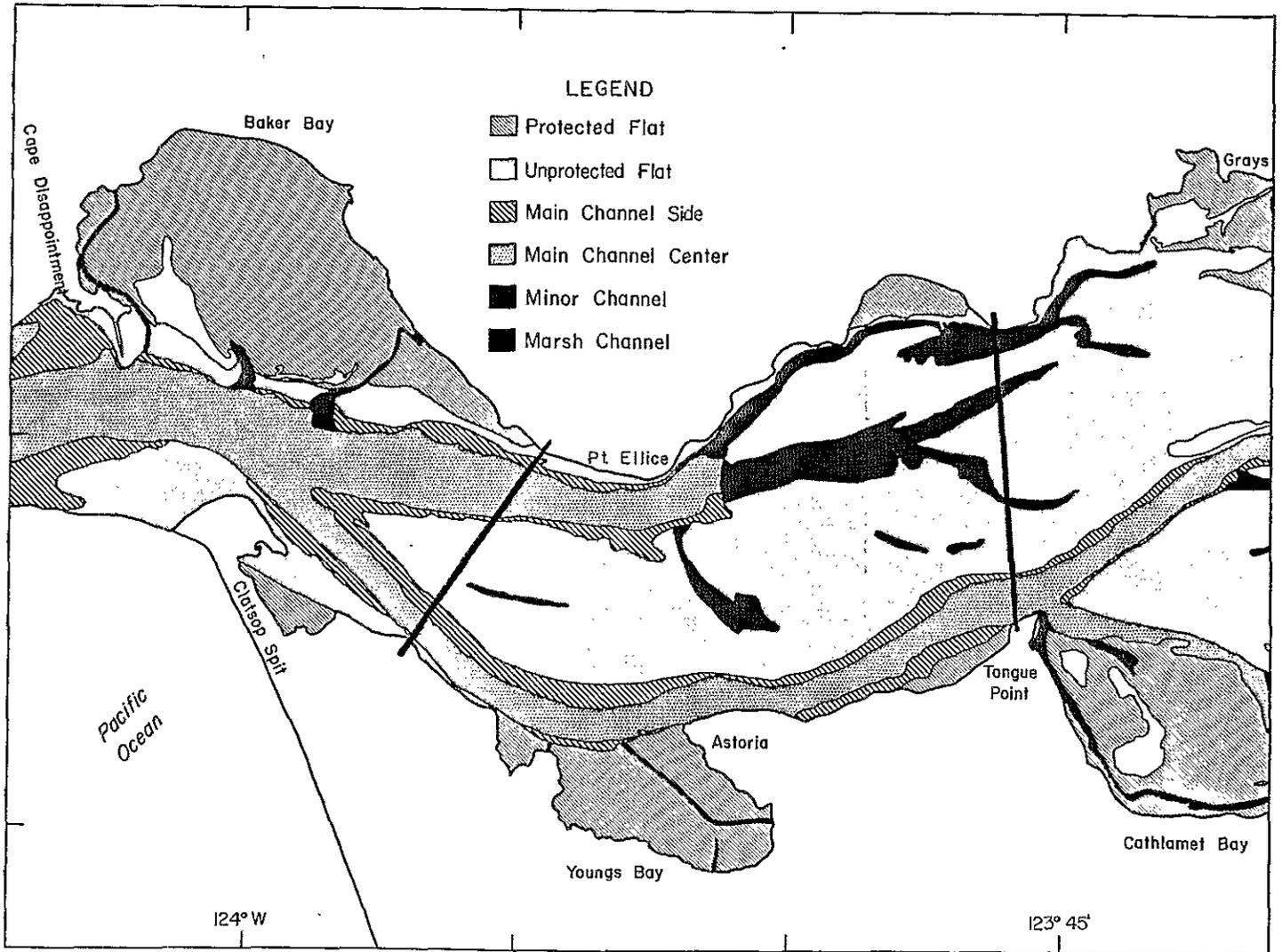
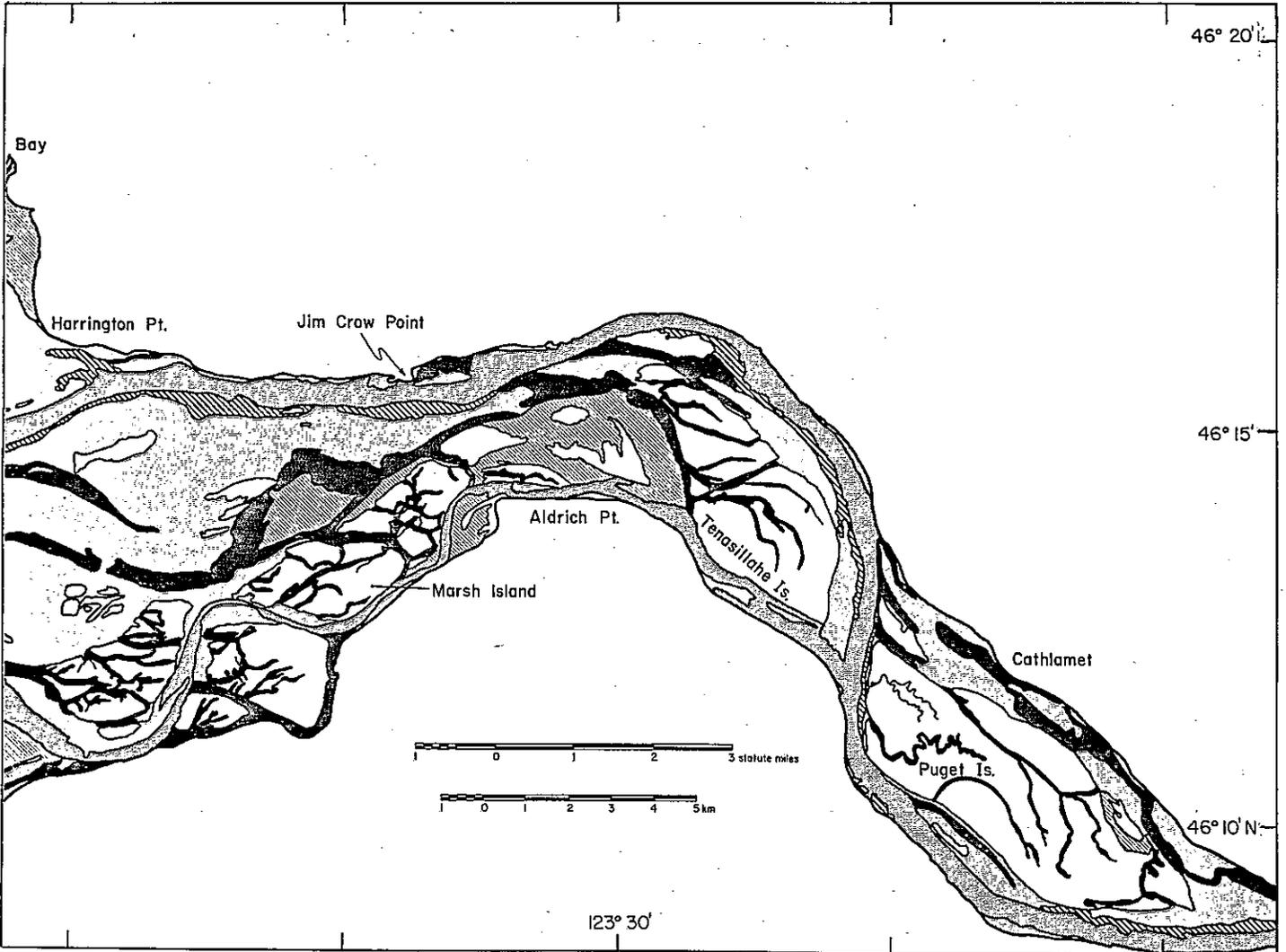


Figure 7. Distribution of Sampling Strata for the Distributional Survey. Bold Vertical Lines at RM-8 and RM-18 Indicate Division of Estuary into Marine, Transition and Fresh Water Salinity Zones.



lished by CREDDP as the study zone, which extends from the river mouth to RM-46. This zone encompasses large areas of mid-river shoals, embayments having a variety of habitat types, deep dredged shipping channels, and meandering smaller channels protected within the upper estuary island system. With this apparent complexity, however, the Columbia River Estuary, like most Pacific Coast estuaries, is not as physically complex as most North American Atlantic coast estuaries where relatively flat coastal features have produced convoluted shorelines and rich dendritic marsh systems. In contrast to this type of estuary, the Columbia River drops quickly to the ocean through a relatively undeveloped shoreline. The simplicity of the benthic habitats of the Columbia River Estuary is especially apparent in the dominance of the mid-estuary zone by the shoal habitat. This shallow sandy habitat is created by a high rate of sediment deposition stimulated by oscillating tidal currents and by chemical events associated with the mixing of marine water and fresh water. The shoals typify the benthic environment in that sand is the overwhelmingly dominant substrate within the estuary with medium to coarse sands forming the bottom of most deep channels, and fine sands forming both the shoals and much of the bottom material within embayments. Rubble, shell-strewn, and rocky substrates are essentially absent, the latter type of substrate being provided primarily by jetties and rip-rap. Muddy bottoms are restricted to portions of embayments, along developed shorelines, and in various upper estuary sites protected by islands. Faunal diversity, then, is not encouraged by the physical makeup of the estuary.

Another, and related, factor affecting faunal diversity is the high and variable freshwater flow rates which prevent the intrusion of most marine forms beyond the limits of the lower estuary. Thus, while partially saline water often extends as far upriver as RM-23, most of the included habitats experience immersion in nearly fresh water sometime during the year.

The present survey was designed to characterize the distribution of the infauna within the broad habitat types described above. Within the limits of 194 samples spread over so large a study area, little could be done to investigate the responses of individual species to local variations in habitat properties. The stratified random survey design employed provided a statistically valid method of determining representative density values for various habitats. This design, however, required that these habitats be identified before the survey was conducted, which forced some decisions to be based on meager knowledge. It is quite possible then that the pre-survey definition of habitat types failed to some degree in defining acceptably homogeneous animal assemblages. One of the objectives of the data analysis was therefore to determine how accurate the a priori habitat designations were in defining different animal communities. A poor correspondence of habitat designation to community distribution would strongly suggest stratum revisions in future studies.

Another objective of the analysis, which was especially suited to the survey design, was to compare the physical and biological characteristics of different salinity zones to determine if the mid-estuary zone appeared more productive than either fresher or more marine zones. This question was suggested by the enhanced sedimentation activity of the mid-estuary described above. Such processes are thought to encourage the

accumulation of detrital materials which support infaunal production, and may thus provide higher densities of prey animals for fish and other predators than might occur in zones which are more marine or more fresh water in character.

## 2. METHODS AND MATERIALS

### 2.1 VERTICAL DISTRIBUTION STUDIES

Sample collection at the three sites of the vertical distribution study employed a hand corer and extruder system. A large corer 20.3 cm (8 inches) in diameter was built for this purpose, so that sufficient animals would be included in each section. The rest of the system included 17.8 cm (7 inch) diameter section subsamplers which were 1, 2, and 5 cm in height, sediment slicing tools, and a light-weight screw-type core extruder.

The cores were collected by pushing the 20.3 cm corer 30 cm deep into the exposed substrate. The coring tube and its contents were placed on a stand having a piston that mechanically extruded the core. The center 17.8 cm of the emerging core was sectioned at 1 cm (from 0 to 10 cm deep), 2 cm (from 10 to 20 cm deep), and 5 cm (from 20 to 30 cm deep) intervals and subsampled using the 17.8 cm rings. Sediment outside of the rings was discarded to avoid side-distortion of animal and sediment distribution caused by drag along the interior of the coring tube as the sediment was extruded. The core sections were preserved in the field using a 5% buffered formalin solution and sieved in the laboratory using stacked sieves having mesh openings of 4.0, 1.0, 0.5, 0.25, 0.125, and 0.063 mm. The separate fractions were stored in a 70% isopropanol solution, and stained with rose bengal prior to picking and sorting.

The macrofaunal size fractions (those animals retained on 0.5 mm and larger screens) of all core sections were processed, sorted, and counted. In addition, certain size fractions of selected sections of the Grays Bay core were processed for meiofauna (0.063 to 0.500 mm). All sections could not be processed due to the large amount of time required to count each meiofaunal sample. Animal identification was generally to the genus or species level for bivalves, polychaetes and amphipods, and to higher taxonomic levels for other groups. Sediment grain size for each core section was analyzed by measuring the settled volume of each size fraction after it had been wet sieved.

### 2.2 BAKER BAY MUDFLAT COMMUNITY INTENSIVE STUDY

#### 2.2.1 Field and Laboratory Procedures

Sampling for the Baker Bay mudflat study was conducted within a 30 x 100 m grid located at a tidal level estimated at 0.15 m above MLLW. A metal stake was placed at the grid origin to allow measurement of changes in sediment level. Grid divisions were one meter in both dimensions, so that 3000 intersections or potential sampling points were available. Sampling points within the grid were selected using a random number table, and each point was sampled only once during the study period. The total number of samples collected was less than 10% of the potential sampling points. Five 10.16 cm diameter cores were collected monthly. Preliminary sampling demonstrated that small macrofauna were not present below 6 cm. Therefore, sample cores were taken only to a depth of 8 cm. The sampling period extended from 28 August 1980 through 11 September 1981.

The entire core was placed in a bag immediately upon collection. A 0.15% solution of 2-phenoxyethanol was added to relax the organisms (McKay and Harzband 1970), and after 15 minutes buffered formalin seawater solution was introduced to preserve the sample. The organisms remained in this solution for 3 to 4 days before processing. In the laboratory, the cores were sieved on a 0.125 mm mesh screen, and the residue remaining on the screen was stored in 70% isopropyl alcohol. To facilitate sorting, the residue was then subdivided into a 0.125 to 0.250 mm fraction, a 0.250 to 0.500 mm fraction, and a greater than 0.500 mm fraction. As described in the Introduction, the small mesh screens insured retention of juveniles of the dominant species that passed through the 0.500 mm mesh screen.

Three days before the organisms were sorted, the samples were stained with Rose Bengal. The samples were then sorted and identified to the most refined taxon that was practical. The 0.125 to 0.250 mm size fraction was not sorted, since the 0.250 mm screen was found to retain a very high percentage of the juvenile polychaetes and bivalves. Only Macoma balthica, Pseudopolydora kempfi, and Hobsonia florida were removed and counted from the 0.250 mm fraction, while all taxa, except Nematoda and Harpacticoida, were enumerated from the 0.500 mm fraction.

The three dominant species were measured so that age and/or size frequency histogram could be drawn. Macoma balthica, a small bivalve, was aged by growth rings and sized by shell height. The two polychaetes Pseudopolydora kempfi and Hobsonia florida were sized by measuring the maximum body width within the first five setigers adjacent to the head. Body length measurements were deemed less suitable since many polychaetes contract when placed in formalin or break during the screening process.

Individuals from October, January, April and July samples were weighed to obtain seasonal shell height or body width vs. weight regression equations. Individuals of the same size class were combined and weighed together. Macoma balthica was decalcified in a 5 to 10% HCl solution before weighing. In addition to these weight measurements, live specimens collected in January 1982 were weighed to determine the weight lost in preservation. This was done by comparing the live and preserved weight versions of the size-weight regression equations.

Small and infrequently captured taxa were combined by season to provide sufficient material for weight measurement. The seasonally based mean weights were then used to compute biomass levels for each sample date.

Weight determinations were AFDW, obtained by drying the animals at 90°C for at least 48 hours, weighing them, then re-weighing them following a 4 hour ashing period in a 550°C muffle furnace. AFDW was the difference between the two weighings. All weights were obtained with a Cahn electrobalance, Model G.

Reproductive state of Pseudopolydora kempfi and Hobsonia florida was determined through visual inspection of the gonads. For Macoma balthica,

a visual gonad index, GI, was employed to rate the ripeness of gonad tissue (Bachelet 1980):

$$GI = \frac{\sum_{n=1}^N i_n}{3N}$$

where:  $i_n$  = gonad maturity rating of the  $n^{\text{th}}$  individual  
 $N$  = number of individuals observed on a given date.

The value of the index ranges from 0 to 1, with 1 indicating a fully mature animal. Each individual was rated on a scale of  $i = 0$  to 3 based on the appearance of the visceral mass (Caddy 1969; Bachelet 1980):

- 0) undifferentiated - no gonad tissue
- 1) immature - gonads proliferating but not reaching the point of gills and labial palps attachment
- 2) half-mature - gonads reaching that point
- 3) fully mature - visceral mass wholly covered by gonad tissue.

#### 2.2.2 Data Analysis

Three community composition parameters were used to describe the 0.5 mm benthic macrofauna community during the year: Shannon-Weaver's diversity, Pielou's evenness, and Margalef's richness. The Shannon-Weaver common information measure was chosen to represent overall diversity. This index ranges in value from 0 (one species = no diversity) up to about 4. It reflects both species richness and evenness, increasing as each of these factors increases. The index weights the evenness of common species heavily while giving less emphasis to the number of species occurring rarely. Computation is as follows (Pielou 1977):

$$H'' = - \sum_{j=1}^s \left( \frac{n_j}{N} \log \frac{n_j}{N} \right)$$

where:  $H''$  = diversity  
 $s$  = total number of species (taxa)  
 $n_j$  = number of individuals of species  $j$   
 $N$  = total number of individuals in sample.

Pielou's (1975) evenness measure is based on the Shannon-Weaver diversity index and is determined as follows:

$$JH = H''/H''_{\max(s)}$$

where:  $H''$  = Shannon-Weaver index  
 $s$  = total number of species (taxa)  
 $H''_{\max(s)} = \log_e s$ .

The richness index used is that of Margalef (1958):

$$DLOG = s - 1/\log_e N$$

where: s = total number of species (taxa)  
 N = total number of individuals in sample.

Margalef called this a diversity index, but it will be referred to here as a richness index since it does not reflect evenness as does the Shannon-Weaver measure.

These community composition parameters were computed for each of the five samples of each sampling date. Initial computations based on all taxa produced uninterpretable results, and the list of taxa included was therefore reduced to completely identified taxa which were considered members of the benthic infaunal assemblage. Those excluded were Oligochaeta, Rhynchocoela, Insecta, unidentified Spionidae, and Crangonidae.

Annual secondary production was estimated using a method described by Crisp (1971) for stocks with recruitment and separable age classes. The sampling period (28 August 1980 to 11 September 1981) was considered to be one year for the purposes of production estimation. The age classes were separated by cohort analysis of the populations. Macoma balthica cohorts were determined on the basis of shell height and age rings, and Pseudopolydora kempfi and Hobsonia florida cohorts were separated on the basis of body width. Each recruitment group or cohort was considered as a separate, isolated population. The size of each cohort in each month was taken to be its median size, which was converted to a weight value.

Growth increments for each month were calculated by the equation:

$$\int Ndw = \sum \frac{1}{2} (N_t + N_{t+\Delta t}) \Delta \bar{w}$$

where:  $N_t$  = population size at time t  
 $N_{t+\Delta t}$  = population size at time t plus  $\Delta t$  (one month in this case)  
 $\Delta w$  = weight change since the previous sampling.

Production rates for all recruitment classes were summed to estimate production by the whole population during the year:

$$P_{ann} = \sum_{t=0}^{t=1} N_0 \Delta \bar{w} + \sum_{t=1}^{t=2} N_1 \Delta \bar{w} + \sum_{t=2}^{t=3} N_2 \Delta \bar{w} + \dots$$

where:  $N_i$  = population size of recruitment class i  
 $\Delta \bar{w}$  = change in median weight during  $\Delta t$ , where  $\Delta t$  is approximately one month.

Two assumptions were made. First, all members of a recruitment class started at the same time. Second, negative production during a

month was considered zero production. This last assumption was based on the fact that large individuals were of low abundance so that a net loss could represent sampling variation. Also, the loss of large individuals (which causes negative production) was not considered a lack of production, but rather a loss of biomass due to mortality or predation.

Ages of individual cohorts were based on time of recruitment. During the first year on the mudflat, a cohort was considered a 0+ year class. One year after recruitment, a cohort became a 1+ age group. For example, the Macoma balthica cohort that settled in September 1980 was considered to be a 0+ year class until September 1981 when that cohort became a 1+ age group.

## 2.3 COROPHIUM SALMONIS LIFE HISTORY STUDY

### 2.3.1 Sampling

In August 1980 a grid 100 x 30 m was established at each of the two sites sampled for the Corophium salmonis life history study. Both grids were located at approximately the 0.3 m tidal elevation. Five randomly placed samples were collected monthly from each grid until June 1981. Sampling frequency was then increased to twice monthly until August 1981, since the summer period was expected to be the period of high reproductive activity. Sampling ended in September 1981.

Samples were collected in August and September 1980 with a 10.16 cm diameter hand corer to a depth of 10 cm. The vertical distribution study at the Grays Bay site indicated that while sampling to a 10 cm depth captured 93% of the Corophium present, an additional 5 cm depth brought the percent captured to 99% (Section 4.1). Accordingly, a 7.62 cm diameter corer and a 15 cm depth were used for the remainder of the study. The diameter of the corer was reduced in order to keep the sample size within acceptable processing levels. All infaunal samples were preserved with 5 to 10% buffered formalin.

Water temperature and salinity were measured on each sampling date at each site. Samples were taken at low tide and were obtained from the nearby river channel, which provided the nearest water to the exposed grid. Salinity was measured to the nearest 0.1 ppt by hydrometer (G. M. Manufacturing Company) in the laboratory.

One sediment sample was collected from each site on each sampling date with a 3.5 cm diameter x 15 cm deep coring tube. Samples were frozen for later textural analysis using standard methods of sieving and pipette analysis. A sediment stake was also established at each site on the first sampling date. Sediment level relative to the stake was observed during each sampling.

### 2.3.2 Sample Analysis

In the laboratory the biological samples were sieved on three stacked screens having mesh openings of 0.5 mm, 0.25 mm and 0.125 mm. The use of several screens aided in the sorting process. The fine mesh screens were used to insure retention of juveniles. Fractions retained

on the 0.25 mm and 0.125 mm screens contained large amounts of sand and were elutriated prior to sorting. The elutriation process involved agitation of small portions of the sample within a water-filled jar and decanting off the fluid and suspended animals after the sand had settled. The animals sorted from both the 0.5 mm fraction and the elutriate fractions were sorted under a three diopter magnifier.

C. salmonis from each sample fraction were counted and individual length measured as the distance from the front of the rostrum to the tip of the telson. Each animal was classified according to its sexual development in a scheme modified from Davis (1978):

1. unsexable juveniles: have female type antennae but lack other sexual characteristics (genital papille or oostegites)
2. immature males: incomplete development of the male type spines on the second antennae
3. mature males: fully developed hook and male type spines on second antennae and complete development of the gonads
4. immature females: nonbreeding females; oostegites present but not full sized and lacking marginal setae
5. mature females: breeding females; oostegites fully enlarged and bearing marginal setae.

Mature females were further classified as gravid (brood pouch containing eggs or embryos) or nongravid (either before deposition of eggs into the brood pouch or after release of the brood). When gravid females had intact broods (those that did not appear damaged or partially released) the number of eggs or embryos was counted.

#### 2.4 COROPHIUM SALMONIS COMMUNITY DYNAMICS STUDY

The data for Corophium salmonis were obtained from the further analysis of samples and data described in Section 2.3. As described in that section, core samples were fixed in a 5 to 10% buffered solution of formalin and later sieved and preserved in a 70% solution of isopropanol. Samples were sieved on 0.5, 0.25 and 0.125 mm screens. All animals on the 0.5 mm screen were retained and identified, while only C. salmonis were retained from the smaller screens. This approach censused virtually all sizes of C. salmonis.

Seasonal weight-length relationships of C. salmonis were developed by weighing animals grouped into successive 0.5 mm size classes for October 23, 1980, January 15, 1981, April 21, 1981 and July 14, 1981. Weight was AFDW, obtained as the difference between dry weight (90°C, 48 hours) and ashed weight (550°C, 4 hours). A Cahn electrobalance Model G measured weights.

Production estimation for C. salmonis employed two methods. Where practical, size-specific growth rates were determined as the movement of the median length of an identifiable cohort. The median length was converted to weight according to the appropriate seasonal weight-length relation, and production, P, calculated according to Crisp's (1971) Method 3A:

$$P = \sum_{i=1}^n f_i w_i G_i \Delta t$$

where:  $n$  = number of size classes  
 $f_i$  = mean number of individuals in size class  $i$  during the interval  $\Delta t$   
 $w_i$  = weight of the median length animal for size class  $i$   
 $G_i$  = growth rate for size class  $i$ .

Growth rates,  $G$ , were interpolated or extrapolated from eye-fitted curves relating weight growth to length. Growth data were based on growth of the spring broods at the two study sites, and applied on a size-specific basis throughout the warm growth period. The method therefore assumed that size-specific growth was constant throughout this period. For winter months when growth was slow and a single cohort definable, production for each interval ( $\Delta t$ ) was calculated as:

$$P = N \Delta w$$

where:  $N$  = the mean number of animals present in interval  $\Delta t$   
 $\Delta w$  = the change in weight of the median size animal during  $\Delta t$ .

Since *C. salmonis* was absent from the Desdemona Sands site during the winter, this method applied only to the Grays Bay site.

In addition to the preserved animal analyses studied for length-weight, live animals were collected in Baker Bay, refrigerated, and processed in the same manner as the preserved animals. The resulting live animal length-AFDW relation was used to estimate production in terms of fresh, unpreserved tissue.

The lesser taxa were counted and identified, although often only to higher taxonomic levels (e.g., Oligochaeta). Random subsamples of each taxon were separated from the October 23, 1980, January 15, 1981, April 21, 1981 and July 15, 1981 Gray Bay collections, and mean AFDW determined for converting counts at both sites to weights on a seasonal basis. Production by these taxa was then estimated by multiplying mean annual biomass by published production:biomass ratios.

## 2.5 ESTUARY-WIDE DISTRIBUTION STUDY

### 2.5.1 Survey Design

The estuary-wide sampling plan called for a single areal survey covering the entire estuary, which had been defined for CREDDP study purposes as extending from the river mouth (RM-0) to just upstream of Puget Island (RM-46), as shown in Figure 1. Since the influence of salinity rarely extends above RM-23 (Haertel and Osterberg 1967), a large portion of the study area encompassed freshwater habitats. In fact, since salinity tends to stratify within the estuary, some shallow habitats below RM-23 might also be considered fresh water. This perspective

was kept when assigning different portions of the estuary to specific habitats.

Strata were defined according to bathymetric features displayed in NOAA charts 18521 and 18523, supplemented by literature describing animal distribution and by papers by Neal (1972) and Hubbell and Glenn (1973) who provide some generalized distributional patterns for salinity and substrate properties. Based on these information sources, the estuary was divided into 16 strata, first according to salinity influence and second according to substrate, water depth and current strength considerations (Figure 7). Individual strata were then divided into from 0 to 3 substrata to account for finer variations in habitat features. While stratum properties (e.g., animal density) were statistically built up from their component substratum properties, the characteristics and data for these substrata are not reported here. Division into substrata was accomplished to improve the estimation of stratum means and variance.

Three salinity zones were established, Marine, Transition and Fresh Water, with zone boundaries set at RM-8 and RM-18 (bold vertical lines in Figure 7). The Transition zone is the region where inflowing saline water mixes upward with overlying fresh water. Within each salinity zone, areas were assigned to the following six habitat types: Main Channel Center, Main Channel Side, Minor Channel, Unprotected Flat, Protected Flat, and Marsh Channel. The divisions were made according to depth boundaries illustrated in the NOAA navigation charts, and according to the apparent degree of protection from strong currents afforded by land masses. Main Channel Center and Main Channel Side refer to the North and South river channels. Main Channel Side is the 5.5 to 9.1-m (18 to 30-foot) depth interval along the edges of the shipping channel and the downstream portion of the North Channel, while Main Channel Center is the deeper portions of these channels. Minor Channel refers to small channels presumed to receive less water flow. Shallow zones (flats) lying within bays and otherwise protected from scour ("Protected Flat") were distinguished from current-swept shallow zones of the central estuary ("Unprotected Flat"). The final stratum, Marsh Channel, was established to allow for possible differences in fauna created by proximity to marsh habitats. The combination of three salinity zones and six habitats indicate a total of 18 strata. In fact, only 16 strata were established, since the Marsh Channel habitat is not present in significant amounts in either the Transition or Marine salinity zones.

Total sample size was set at about 200, based on the amount of time available for sample processing. A single sample was allotted to each station, as opposed to collecting replicate station samples, since the goal was stratum definition and not station definition. With one exception, samples were initially evenly distributed among the 16 strata. Fifteen of the strata were thus allocated 12 samples. The remaining stratum, the Marine Zone Protected Flat stratum (equivalent to Baker Bay), received 18 samples due to the relative lack of attention given this area in previous studies. Sampling conditions imposed some changes in sample distribution with the result that actual stratum sample sizes vary from 6-18, although most have 12.

Within each stratum, individual substrata were allocated approximately equal numbers of samples, as opposed to using a weighting procedure according to estimated variance or substratum dimensions. Such a weighting system was impractical in view of the overall small number of samples collected, since some substrata would thereby have received too few samples to allow proper estimation of means and variances. Rather, the unequal dimensions of member substrata were accounted for by weighting substratum means and variances.

To determine sample placement, a chart of the estuary with its substratum subdivisions was overlain with a fine resolution coordinate grid, and coordinates sequentially selected from a random number table until the proper number of sample sites was established for each substratum. Several alternate sites were also selected for each substratum, since difficulties in reaching some sampling sites were expected.

### 2.5.2 Field Methods

The survey was conducted on 8 to 11 September 1981, employing the 10.6-m Cathlamet Bay and the 6.7-m Skipanon operated by CREDDP. Stations were located using depth readings from the ship's fathometer, and line of sight on shoreline features and marker buoys. On some occasions, it was impractical or unsafe to occupy certain stations due to travel problems or sea conditions. In those cases, substitute stations were selected from the list of alternates.

At each station, water depth was recorded and a bottom sample collected with a 0.05 m<sup>2</sup> Ponar grab sampler. This sampler, while not penetrating as deep as larger and heavier samplers such as the 0.1 m<sup>2</sup> Smith-McIntyre sampler, usually provided adequate samples and was the largest sampler which could be safely deployed by the smaller of the two boats. The Ponar grab collected good samples (several cm deep) in loose sediments, but penetrated only 2 to 3 cm in hard packed sediment. The data set therefore does not reflect the true abundance of deep-dwelling species such as some large clams.

Samples were stored in buckets and heavy plastic bags until they could be preserved in the same containers using a 5 to 10% solution of buffered formalin.

Before the samples were stored, a small amount of sediment (10 g) was removed for sediment analysis. These subsamples were chilled, and later frozen until analysis for organic content and sediment texture.

### 2.5.3 Laboratory Procedures

Normally, formalin-preserved infaunal samples are processed after several days of fixation. However, CREDDP funding stopped very soon after sample collection. Therefore, the samples were sorted in formalin until COE funding began in early July 1982. At that time, all samples were washed on a 0.5 mm screen, and the retained material stored in a 70% solution of isopropanol. The preserved material was then stained with rose bengal, and sorted and identified under 3-diopter magnifying lens and stereoscopic microscope. Identification was conducted on the follow-

ing basis: crustaceans, polychaetes and molluscs were identified to species where possible, while oligochaetes, nematodes, turbellarians, rhynchocoelans and some minor taxa were not identified further.

A biomass version of the data set was prepared by weighing random subsamples of each taxon from each stratum, and multiplying the mean weights obtained by sample counts for that stratum. Weights obtained were AFDW, measured as the difference between dry weight (90°C, 48 hours) and ashed weight (550°C, 4 hours). Gastropods and bivalves were decalcified in 5 to 10% HCl prior to weighing.

Sediment subsamples were processed by the COE and by Portland State University. The samples were dried and sieved to determine the fraction less than 0.063 mm, and percent organic matter was determined by combustion using a small subsample removed prior to textural analysis.

#### 2.5.4 Data Analysis

The data set contained variables in two categories. The first category included the environmental variables, which were station water depth, the <0.063 mm sediment fraction (termed "fines"), percent organic matter, and location in the estuary. Location in this use refers to upstream distance from river mouth, and was included as an environmental variable to assure representation of salinity, which is a dominant influence on animal distribution. Salinity was represented in this fashion since a more direct measure was not available. The other highly important environmental variable represented was substrate character, represented here by the fine sediment and organic matter fractions.

The second category of variables was taxon density. The term "taxon" refers to any level of taxonomic identification, and was used in preference to "species" since not all animals were identified to the species level.

The objectives of data analysis were to:

- (1) characterize each stratum according to the physical measurements made and according to animal density levels;
- (2) identify patterns of distribution for individual taxa;
- (3) characterize community structure for each stratum by dominant animals present;
- (4) determine the accuracy of stratum definition;
- (5) identify community types independent of stratum designation;
- (6) determine the degree of correspondence between animal distribution and measured habitat properties.

Objective 1 utilized the methods of Cochran (1963) for treating the results of a stratified-random survey. Since individual stratum (and not whole-estuary) estimates were desired, each stratum comprised a population whose properties were to be estimated based on its component substrata sampling means and variances.

For stratum 2:

$$\bar{y}_{st} = \sum_{h=1}^l W_h \bar{y}_h$$

$$\hat{V}(\bar{y}_{st}) = \sum_{h=1}^l W_h^2 \hat{V}(\bar{y}_h)$$

where:  $\bar{y}_{st}$  = unbiased estimate of stratum mean

$\hat{V}(\bar{y}_{st})$  = unbiased estimate of variance of stratum mean

$W_h$  = a weighting factor for each substratum,  $0 \leq W_h \leq 1$

$\bar{y}_h$  = substratum sample mean

$\hat{V}(\bar{y}_h)$  = variance of substratum sample mean.

The weight factor,  $W$ , was the fraction that a particular substratum comprised of the areal dimension of its stratum. Since the area sampled was so large, a correction for finite populations was not employed in estimating the variance of the substratum mean.

For several variables, confidence intervals were computed based on

$$\bar{y}_{st} \pm t \sqrt{\hat{V}(\bar{y}_{st})}.$$

Due to the generally robust nature of the sampling design and to the mostly even distribution of sampling effort among substrata, degrees of freedom ( $v$ ) for this statistic were based on the pooled degrees of freedom for the substrata, i.e.

$$v = \sum_{h=1}^l (n_h - 1).$$

Objectives 2 and 3 utilized simple graphical and tabular summary techniques.

Objectives 4 to 6 concerned patterns of variation co-occurring in many variables (i.e., multiple taxa and several environmental measures), and therefore required use of multivariate statistical techniques. The two techniques employed were canonical analysis of discriminance, and reciprocal averaging ordination. Both techniques may be used to simplify complex data sets by identifying principal patterns of variation existing in animal distribution. While a detailed understanding of the techniques is not required to understand their results, a brief description is provided to aid comprehension.

Discriminant analysis is a multivariate statistical technique for distinguishing among two or more groups for which several "discrimina-

ting" variables have been measured. In this analysis the groups were strata, and the discriminating variables were the taxon densities measured at each station. In other words, strata which differed in their taxon densities were distinguished from each other using discriminant analysis. This statistical technique forms from one to several functions which are linear combinations of the discriminating variables. Each station was then represented by a "score" or value on each new axis, as defined by the sum of the weighted values for each variable. The important features of discriminant analysis are that dimensionality is reduced to a few functions retaining the bulk of system variation, and the functions are formed so as to maximize the distinctiveness among groups. Thus, evaluated in terms of the raw taxon counts, samples from different strata may appear less distinct than when evaluated in terms of the scores assigned to them on the new discriminant axes. Using the axes scores and other features of the model, it was possible to measure the success with which the stations were separated both by the discriminant functions and by the original variables upon which the functions were based. In the present use, the model was used to measure the accuracy with which the a priori strata divided the estuary into areas having relatively different and internally homogeneous animal communities (Objective 4).

The discriminant analysis was conducted on the CYBER computer at Oregon State University utilizing the Statistical Package for Social Sciences (SPSS) direct analysis method, which introduces all variables (taxa) simultaneously, as opposed to a stepwise procedure. Because of the complexity and size of a data set involving 16 groups and 194 samples, a separate run was made for each of the three salinity zones to determine the discriminance level among its member habitats.

Objectives 5 and 6 used the methods of ordination, which is a family of multivariate techniques often used in the analysis of community gradients and their relation to environmental gradients. The various ordination models find major patterns of variation in community structure and arrange samples along computed axes which correspond to those patterns. This is done in such a way that samples having similar community content are placed close together, and dissimilar ones far apart. By a similar process, ordination of taxa may be used to arrange taxa having similar distributional patterns close together on computed axes. These two types of results together greatly aid the process of visualizing how animal communities vary in structure along environmental gradients. In reciprocal averaging ordination as used here, sample ordination and taxon ordination were accomplished simultaneously and in such a way that each sample axis corresponded to a particular taxon axis. This simplified the interpretation process. The specific version of reciprocal averaging employed was the DECORANA program (Hill 1979), which has modifications to avoid problems of earlier programs involving undesired systematic relations between successive axes. An additional advantage to the DECORANA program is its high degree of efficiency which allowed all 194 samples to be run at once and thus provided a view of community gradients over the whole estuary.

Certain data editing procedures were followed preparatory to the analyses described above. First, taxa and life stages not strictly be-

longing to the macrofauna were deleted. This included adult insects, oligochaete cocoons, zooplankton, harpacticoid copepods, Mytilus edulis (bay mussel), and Acarina. The remaining 70 taxa were used in computing total density. Second, some taxa with incomplete identification or which occurred in fewer than four samples were deleted (Gauche 1982). This reduced the list to 49 taxa (most having species level identification) which were used in canonical analysis of discriminance and in reciprocal averaging analysis. Taxon counts and weights for these analyses and for the computation of means and confidence limits were log-normalized ( $\log_{10}[X + 1]$ ), which reduced the otherwise excessive influence of very high counts. Multivariate analyses utilized the numeric density data as opposed to weight density, which would heavily weight the results toward large animals.

Sediment data (fraction fines and fraction organics) were transformed by the arc-sine and square-root functions for statistical calculations.

### 3. RESULTS

#### 3.1 VERTICAL DISTRIBUTION STUDY

The following sections describe community composition and vertical distribution patterns for each core, and screen retention for the Grays Bay core.

##### 3.1.1 Community Description

At the Grays Bay site, the most numerous macrofaunal taxa collected were nematodes, oligochaetes, bivalves (Corbicula manilensis), amphipods (Corophium spp.), and Diptera larvae (Chironomidae and Heleidae). Dominant meiofaunal taxa were nematodes, oligochaetes, ostracods, and harpacticoid copepods. A total of 796 macrofaunal organisms were counted in the core. This is equivalent to 33,100/m<sup>2</sup>, a not uncommon density level for this community.

At the Desdemona Sands site, taxa were few and densities quite low. The most abundant taxon was Nematoda. Other taxa present included Oligochaeta and Corophium spp. Total macrofauna counted was just 56 individuals, equivalent to a density of 2,258/m<sup>2</sup>.

The Baker Bay core contained a comparatively diverse macrofaunal community, including nematodes, polychaetes (Ampharetidae, Neanthes spp., Eteone spp., Polydora spp., Pseudopolydora spp., and Pygospio spp.), oligochaetes, bivalves (Mya arenaria and Macoma balthica), and amphipods (Ampelisca spp., Eogammarus spp., and Paraphoxus vigitegus). Macrofauna in the core totaled 1,403, equivalent to 56,600/m<sup>2</sup>.

##### 3.1.2 Vertical Distribution

The vertical distribution of the major macrofaunal taxa in each core is depicted in Figures 8 through 10. In Grays Bay (Figure 8), it may be seen that Corophium spp. and Nematoda were concentrated in the top 10 cm of sediment, although they were also present as deep as 25 to 30 cm. Ampharetidae, Gastropoda, Corbicula manilensis, and insect larvae occurred primarily in the top two centimeters. Oligochetes were most abundant at the 6 to 14 cm depth and the few Nereidae present also occurred in that depth interval. Macrofauna were scarce or absent below 15 cm.

As indicated earlier, distributional patterns at the Desdemona Sands site are based on very low counts. Figure 9 shows that, except for one bivalve found at 16 to 18 cm depth, all taxa were concentrated in the surface 8 cm, and that total density peaked at 2 to 4 cm due to the relatively high abundance of Nematoda.

In Baker Bay, there was a greater concentration of animal life near the surface than in Grays Bay (Figures 8 and 10). The Polychaete taxa, Ampharetidae, Eteone spp., Neanthes spp., and Spionidae were concentrated in the top 6 cm. In these data, "Spionidae" includes Polydora spp., Pseudopolydora spp., Pygospio spp., and unidentified spionid species. Bivalvia spp. (unidentified juvenile bivalves) and Macoma balthica were also abundant at the surface. Amphipoda spp., representing the genera

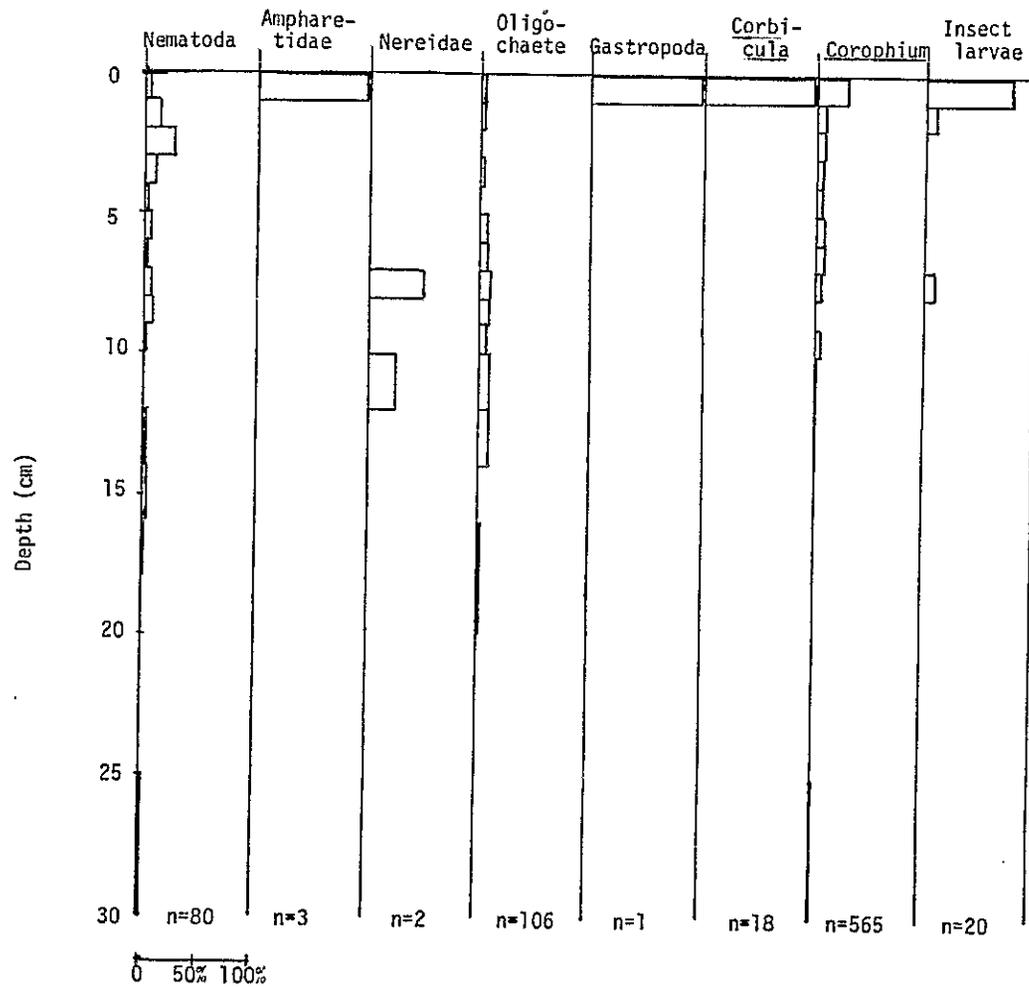


Figure 8. Vertical Distribution of Macrofauna (>0.5mm) in the Grays Bay Core

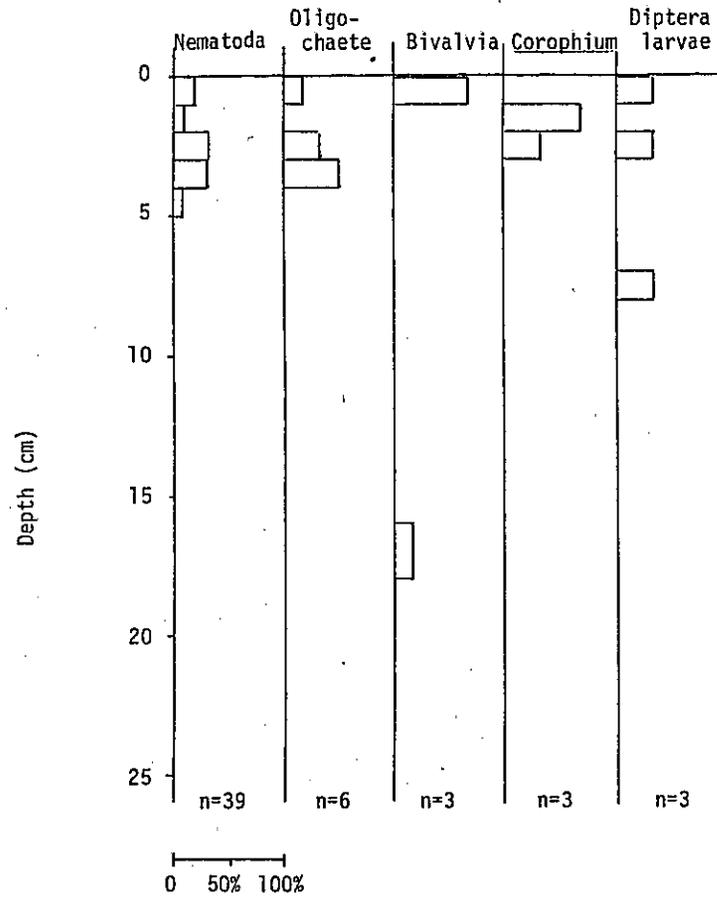


Figure 9. Vertical Distribution of Macrofauna (>0.5 mm) in the Desdemona Sands Core

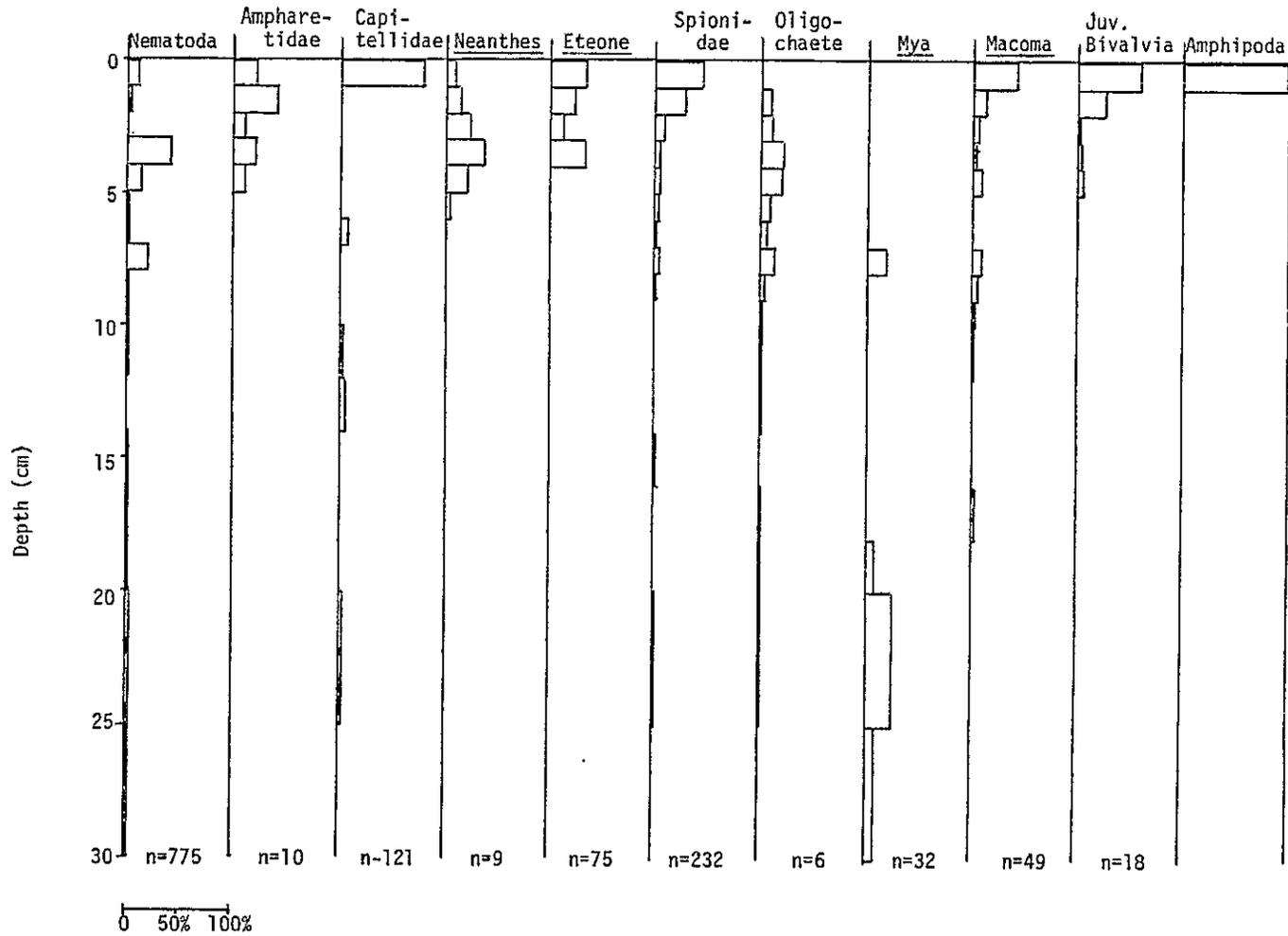


Figure 10. Vertical Distribution of Macrofauna (>0.5 mm) in the Baker Bay Core

Ampelisca and Eogammarus, as well as Paraphoxus vigitegus, were present only in the top centimeter. Nematoda and Capitellidae were erratic in their depth distribution. Oligochaetes were present primarily in the 1 to 9 cm interval and Mya arenaria captured were generally deeper than 18 cm.

Meiofaunal densities in selected depth intervals of the Grays Bay core are depicted in Figure 11. Three size divisions were summed: 0.063 to 0.125 mm, 0.125 to 0.25 mm, and 0.25 to 0.5 mm. Density values for uncounted meiofaunal samples have been estimated from the abundances in adjacent core sections and densities then summed across all size fractions to approximate a continuous pattern across depth. This figure therefore may be used to indicate trends, but is not accurate for defining peaks in abundance at particular depths. These trends show that ostracods, copepod nauplii, bivalve juveniles, Diptera larvae, and tardigrads were all concentrated near the surface. However, a few Diptera did occur as deep as 25 to 30 cm. Juvenile Corophium were present in the upper 15 cm as was found in the macrofaunal data. Rynchocoela were concentrated 3 to 16 cm, and Nematoda, Oligochaeta, and Harpacticoida were apparently present throughout the core.

Grain size distributions for each core are presented in Figures 12 through 14, expressed as percent fines (less than 0.063 mm) and median particle size, as measured in phi ( $\phi$ ) units. The phi scale corresponds to the following categories:

		fine gravel
4.0 mm	-2.0 $\phi$	
		very coarse sand and very fine gravel
1.0 mm	0.0 $\phi$	
		coarse sand
0.500 mm	1.0 $\phi$	
		medium sand
0.250 mm	2.0 $\phi$	
		fine sand
0.125 mm	3.0 $\phi$	
		very fine sand
0.063 mm	4.0 $\phi$	
		silt and clay.

Grays Bay median  $\phi$  size averaged 2.1 to 2.20 with percent fines ranging from approximately 10 to 20%. Surface sediments were very slightly coarser than deeper sediments.

Desdemona Sands was a relatively coarse sand environment. Median particle size ranged from 1.30 $\phi$  at the surface to 1.70 $\phi$  at 30 cm, while fine sediments were always less than 2% of total sediment volume. Again, sediment composition varied little throughout the core.

In contrast to the other two stations, the Baker Bay core exhibited strong increases in percent fines and decreases in median particle size beginning at the 12 to 14 cm depth. Above 12 cm, these properties were similar to those of Grays Bay. Below 12 cm, median particle size de-

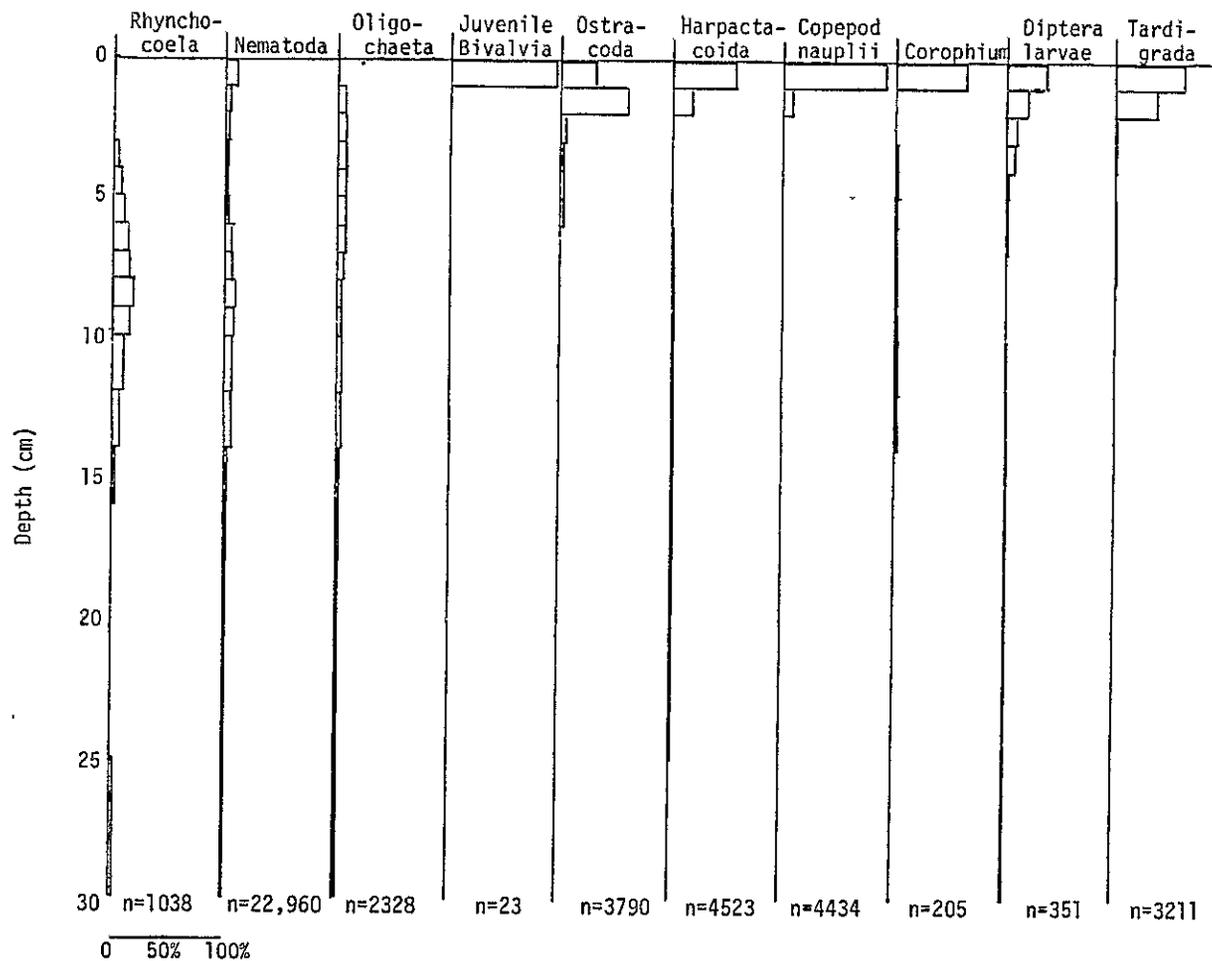


Figure 11. Vertical Distribution of Meiofauna (.063 to .5 mm) in the Grays Bay Core. Missing Values for Some Depth Intervals were Estimated by Linear Interpolation.

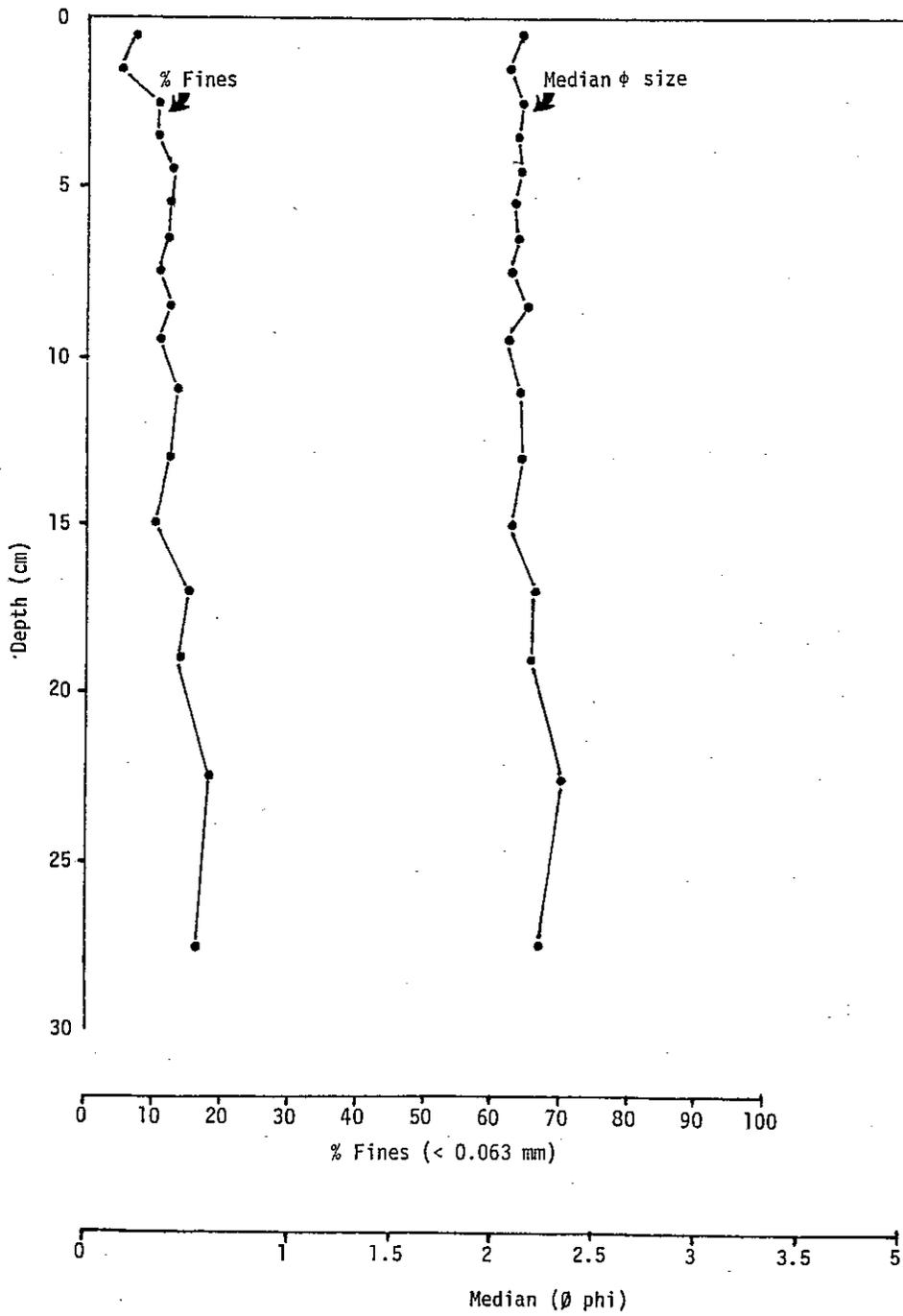


Figure 12. Sediment Composition of the Grays Bay Core

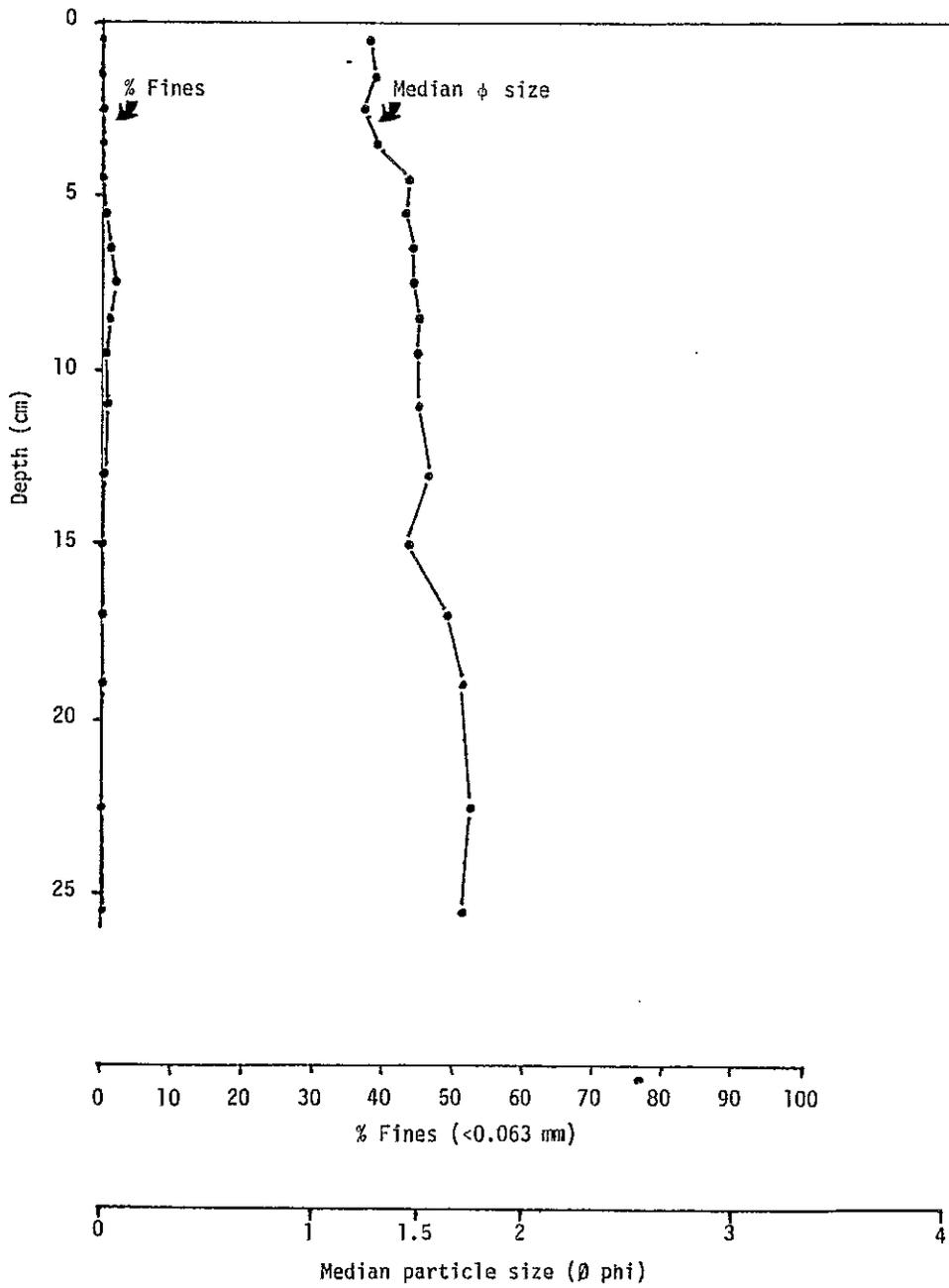


Figure 13. Sediment Composition of the Desdemona Sands Core

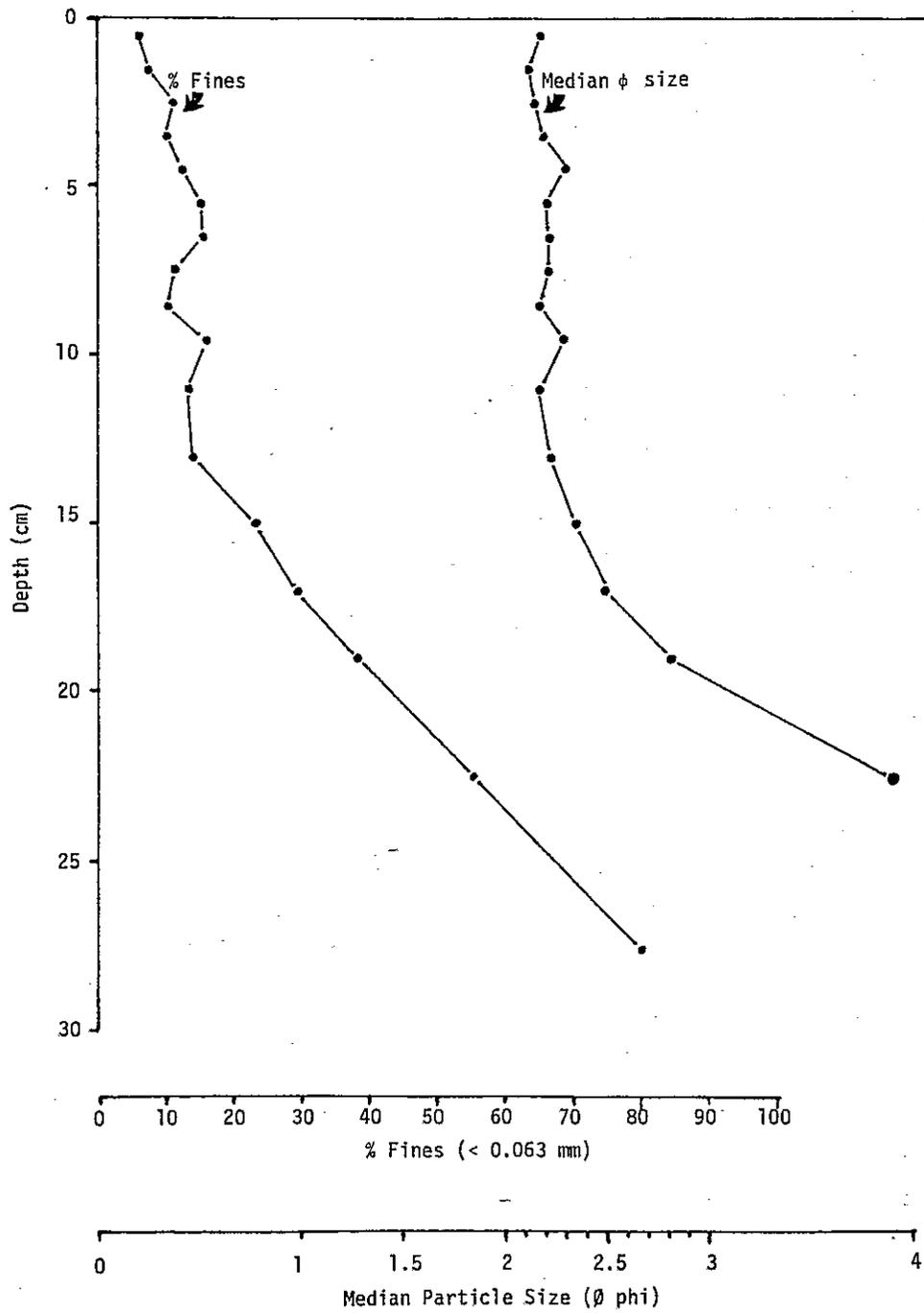


Figure 14. Sediment Composition of the Baker Bay Core

Table 1. Number of Animals Retained on Each of Six Mesh Sizes for the Grays Bay Core. Counts Were Summed Over the Following Depth Intervals: 0 to 1 cm, 4 to 5 cm, 8 to 9 cm, 14 to 16 cm, and 25 to 30 cm. Other Depth Intervals Were Not Processed in All Size Fractions, and Therefore Were Excluded.

Taxon	Screen Mesh Size (mm)					
	Macrofauna			Meiofauna		
	4.0	1.0	0.5	0.25	0.125	0.063
Ciliata spp.						*
Hydrozoa spp.				1		
Rhynchocoela spp.				*	235	18
Gastrotricha spp.					3	
Nematoda spp.		3	14	164	2289	4270
Ampharetidae spp.			3			
Nereidae spp.		*				
Oligochaeta spp.		1	15	105	212	158
Gastropoda spp.		1				
<u>Corbicula manilensis</u>		3	15			
Bivalvia spp. (unidentified juveniles)				23		
Acarina spp.			1	5	11	
Cladocera spp.				6		*
Ostracoda spp.				596	565	81 <sup>t</sup>
Harpactacoida spp.			1	129	1876	838
Copepoda spp. (nauplii)					46	3973
Isopoda spp.				*		
<u>Corophium</u> spp.		91	124	140	3	
Chironomidae spp. (larvae)				3		*
Heleidae spp. (larvae)			*	*		
Diptera spp. (larvae)			16	53	54	63
Pyralidae spp.				*		
Insecta spp. (larvae)			*		2	
Tardigrada spp.				*	80	1892

\* Present in depth interval(s) not represented here.

t 1949 additional ostracods occurred in a depth interval not represented here.

creased rapidly so that phi values exceeded 4.0, while percent fines increased correspondingly to 80%.

### 3.1.3 Mesh Size and Animal Retention

Selective retention of Grays Bay animals on the different screen mesh sizes was determined by summing counts over several depth intervals for each screen. Five depth intervals were chosen for which the data are complete for all mesh sizes (Table 1). The animals thus tallied numbered over 14,000, most of them belonging to the meiofauna.

Taxa commonly counted as macrofauna which are represented in this analysis include Rhynchocoela, Nematoda, Ampharetidae, Nereidae, Oligochaeta, Gastropoda, Corbicula manilensis, unidentified bivalve juveniles, Corophium spp., and larvae of several insect taxa, including Chironomidae and Heleidae. Meiofaunal taxa include (with some overlap) Rhynchocoela, Nematoda, Oligochaeta, Acarina, Ostrocooda, Harpacticoida, and the insect larvae.

Reviewing the taxa as they are listed in Table 1, Rhynchocoela and Nematoda appear as two taxa largely confined to the meiofauna. Data for the two polychaete families, Ampharetidae and Nereidae, are slight, but suggest these animals are macrofaunal. Oligochaeta were collected on all but the largest mesh size, but were obviously most abundant in the meiofaunal size fractions. Only one gastropod was collected; it appeared on the 1.0 mm screen. The bivalve Corbicula manilensis appeared on 1.0 and 0.5 mm screens, while bivalve juveniles (also presumably C. manilensis) were collected on the 0.25 mm screen. Acarina, Ostracoda and Harpacticoida all were predominantly meiofaunal in size. Copepod (presumably harpacticoid) nauplii were concentrated principally on the finest mesh (0.063 mm).

The amphipod genus, Corophium, was collected on the 1.0 mm through 0.25 mm screens, although very few organisms landed on the 0.25 mm screen. The several insect taxa all mostly appeared on meiofaunal screens. Finally, tardigrades were concentrated on the 0.125 mm and 0.063 mm screens.

## 3.2 BAKER BAY MUDFLAT COMMUNITY INTENSIVE STUDY

### 3.2.1 Community Structure and Dynamics

On a numerical basis, the Baker Bay mudflat community was composed predominantly of bivalves, polychaetes, and oligochaetes (Tables 2 and 3). Hobsonia florida and Pseudopolydora kemp were the numerically dominant polychaetes and Macoma balthica was the dominant bivalve. The cumacean Hemileucon sp., the polychaetes Polydora ligni, Neanthes limnicola, and Mediomastus spp., and unidentified turbellarians were also common inhabitants of the mudflat during the study period. Biomass rankings (Table 3) suggest that M. balthica, H. florida, and P. kemp were the most important members of the community, followed by Oligochaeta and N. limnicola.

Table 2. Benthic Infauna at the Baker Bay Study Site

Phylum Rhynchocoela  
Phylum Platyhelminthes  
  Class Turbellaria  
Phylum Annelida  
  Class Polychaeta  
    Family Ampharetidae  
      Hobsonia florida  
    Family Capitellidae  
      Heteromastus spp.  
      Mediomastus spp.  
    Family Nereidae  
      Neanthes limnicola  
    Family Phyllodocidae  
      Eteone spp.  
    Family Sabellidae  
      Manayunkia aestuarina  
    Family Spionidae  
      Polydora ligni  
      Pseudopolydora kempi  
      Pygospio elegans  
  Class Oligochaeta  
Phylum Mollusca  
  Class Bivalvia  
    Family Cardiidae  
      Clinocardium nuttallii  
    Family Myidae  
      Mya arenaria  
    Family Tellenidae  
      Macoma balthica  
Phylum Arthropoda  
  Class Crustacea  
    Order Mysidacea  
      Family Mysidae  
        Neomysis mercedis  
    Order Cumacea  
      Family Leuconidae  
        Hemileucon sp.  
    Order Isopoda  
      Family Spaeromatidae  
        Gnorimosphaeroma oregonensis  
    Order Amphipoda  
      Family Corophiidae  
        Corophium salmonis  
      Family Gammaridae  
        Eogammarus confervicolus  
      Family Phoxocephalidae  
        Paraphoxus milleri  
    Order Decapoda  
      Family Crangonidae

Table 3. Taxa from the Baker Bay Study Site Which Were Retained on a 0.5 mm Screen, Ordered According to Mean Annual Density. Numeric Density and Biomass are Expressed as Average Values for the Study Period. N/W = Weight Data Not Available.

<u>TAXA</u>	<u>NUMERICAL DENSITY/m<sup>2</sup></u>	<u>BIOMASS (mgAFDW/m<sup>2</sup>)</u>
<u>Oligochaete</u>	10745	192
<u>Hobsonia florida</u>	3162	265
<u>Pseudopolydora kemp</u>	2744	330
<u>Macoma balthica</u>	2182	8297
<u>Hemileucon sp.</u>	412	10
<u>Turbellaria</u>	366	32
<u>Polydora ligni</u>	314	57
<u>Neanthes limnicola</u>	227	93
<u>Mediomastus spp.</u>	155	3
<u>Pygospio elegans</u>	104	2
<u>Corophium salmonis</u>	79	15
<u>Rhynchocoela</u>	60	13
<u>Eteone spp.</u>	56	22
<u>Myidae sp.</u>	25	N/W
<u>Heteromastus spp.</u>	21	55
<u>Manayunkia aestuarina</u>	18	N/W
<u>Eogammarus confervicolus</u>	11	1
<u>Paraphoxus milleri</u>	4	1
<u>Neomysis mercedis</u>	4	N/W
<u>Gnorimosphaeroma oregonensis</u>	2	0.2
<u>Clinocardium nuttilli</u>	2	0.13
<u>Crangonidae (juvenile)</u>	7	N/W
<u>Decapoda (larvae)</u>	4	N/W
<b>TOTAL</b>	<b>20704/m<sup>2</sup></b>	<b>9388mgAFDW/m<sup>2</sup></b>

Total density of infauna retained on the 0.5 mm screen (macrofauna) was higher at the start of sampling in summer 1980 when densities exceeded 30,000 animals/m<sup>2</sup> (Figure 15), than at any subsequent time. This peak was followed by a general decline through spring of 1981 when densities as low as 12,000 organisms/m<sup>2</sup> were recorded. A rapid increase in density occurred in early summer 1981, but was followed by a rapid decline to 12,000 infauna/m<sup>2</sup>. These changes in total density closely followed oligochaete density (Figure 15), which comprised 52% of the total density.

Macoma balthica density (those retained by the 0.250 mm screen) remained fairly constant throughout the year except during the summer months (Figure 15). Numbers were low from May through August, but then jumped from the August minimum of near 2,300/m<sup>2</sup> to about 3,500/m<sup>2</sup> in September. The population peaked at about 5,000/m<sup>2</sup> during late fall in November and December. Analysis of variance showed that density change during the year was significant (Table 4).

The polychaetes exhibited marked seasonal changes in abundance. Hobsonia florida had a significant population peak during June and July (Figure 14, Table 4). In that period, the population increased ten-fold (3,000/m<sup>2</sup> to over 30,000/m<sup>2</sup>) and then declined to about 3,000/m<sup>2</sup> in September. There was also a small increase in September through October 1980, from 2,600/m<sup>2</sup> to 4,700/m<sup>2</sup>.

Pseudopolydora kemp peaked in August of 1980 and then declined gradually through the rest of the year until the next recruitment of juveniles in August 1981 (Figure 15). However the peak in August 1981 was followed by a very sharp decline in abundance. Again, changes in density during the year were significant (Table 4).

Among less numerous macrofaunal taxa, the spionid polychaete Polydora ligni peaked during October and November 1980, then completely disappeared by June 1981 (Figure 15). The nereid polychaete Neanthes limnicola had peak abundances in August 1980, and gain in July through September 1981. Eteone sp., a phyllodocid polychaete, was present at low densities all year. Mediomastus spp., a capitellid polychaete, was most abundant in September and December 1980. The cumacean Hemileucon sp. peaked in September 1980 and again in the the May through July 1981 period. Corophium salmonis, a gammaridean amphipod, also appeared to peak in both summer and fall, although density was always very low. Turbellaria peaked in September of both years, with the summer increase beginning in June. Oligochaetes decreased in abundance from 18,000/m<sup>2</sup> to 5,000/m<sup>2</sup> through the study period.

The community was also studied in terms of trophic groups, or feeding strategies (Table 5). Deposit feeding was the most prevalent feeding mode, and involved both subsurface and surface feeders. Rhynchocoela, Eteone spp., and possibly Neanthes limnicola were the only infaunal predators present. The only suspension feeders present were small myid clams (presumably Mya arenaria) which were all juveniles; siphon holes of adults were not seen in this portion of the mudflat. Trophic relationships did not change during the year; surface deposit feeders were dominant year round, followed (in order) by subsurface deposit feeders, predators, and suspension feeders.

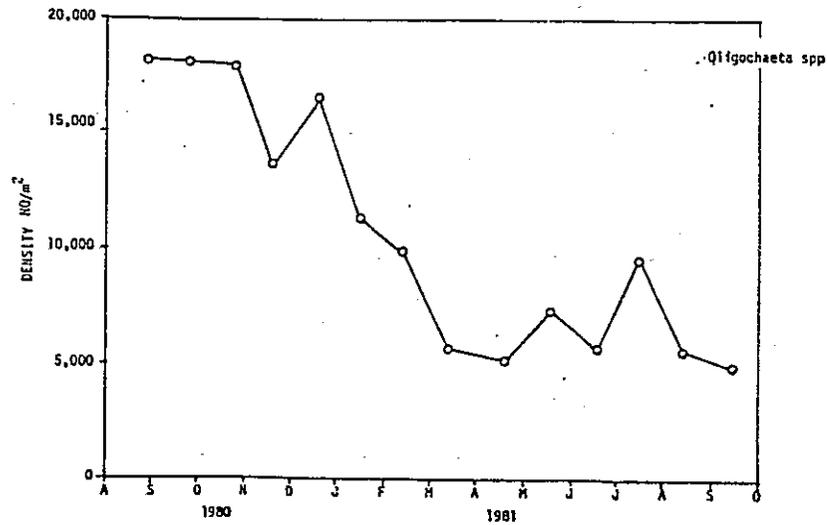
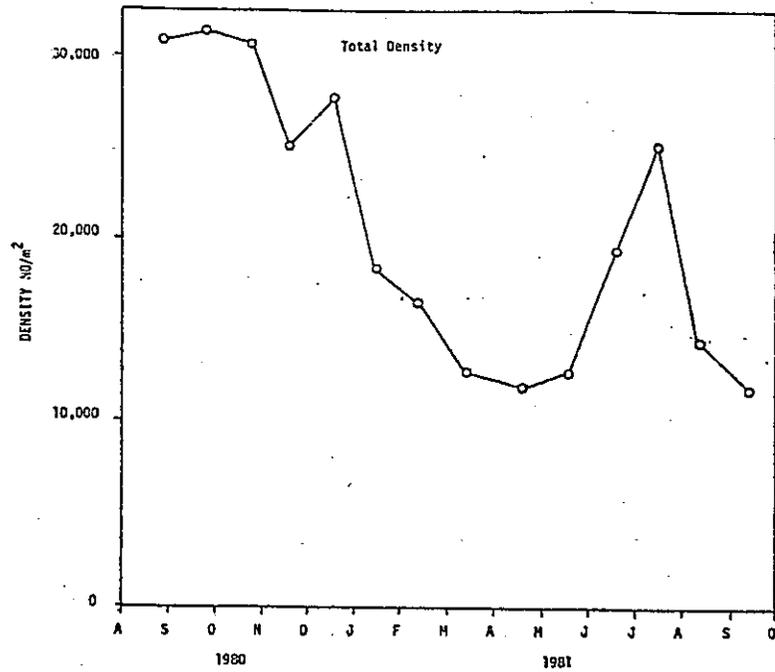


Figure 15. Monthly Changes in Total Density and Density of Common Taxa at the Baker Bay Study Site

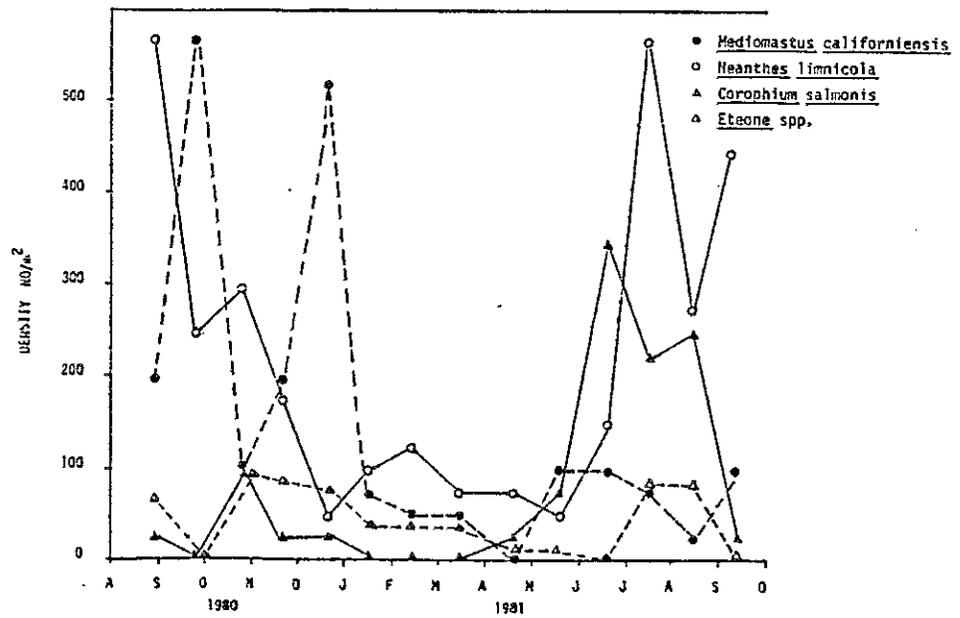
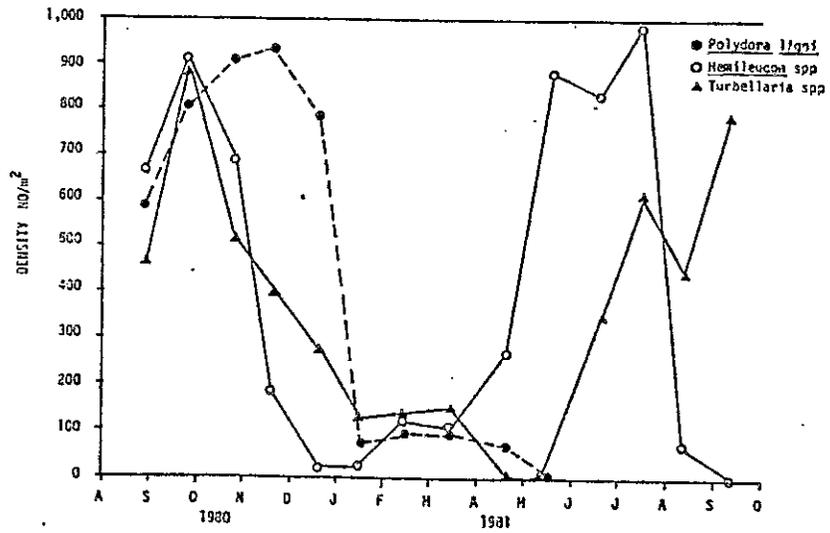


Figure 15. (cont.)

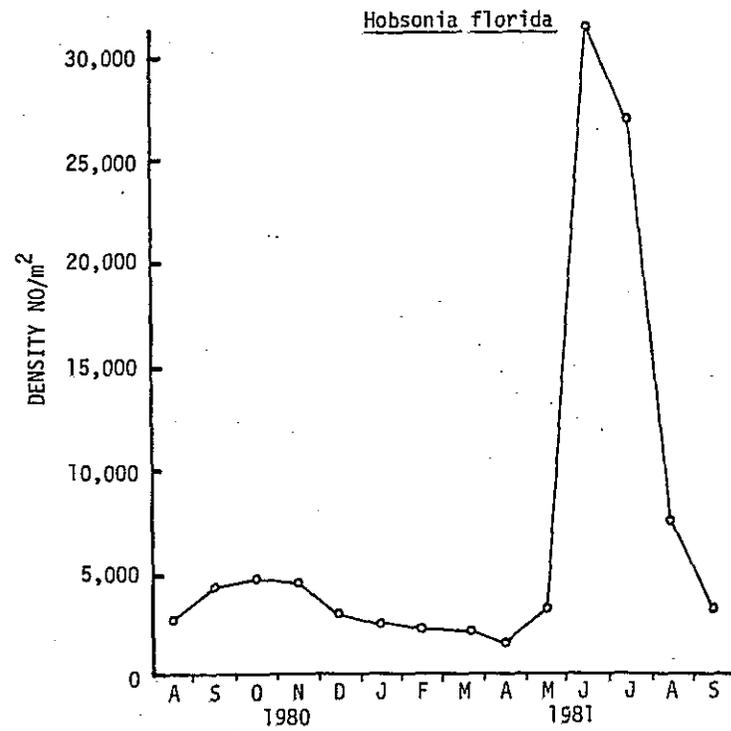
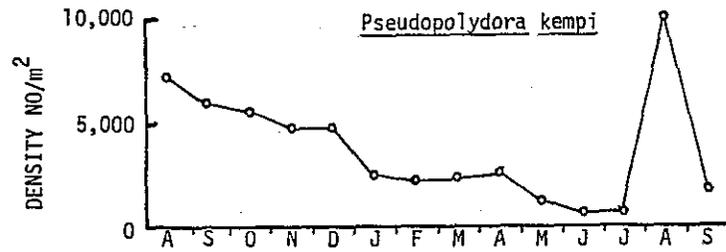
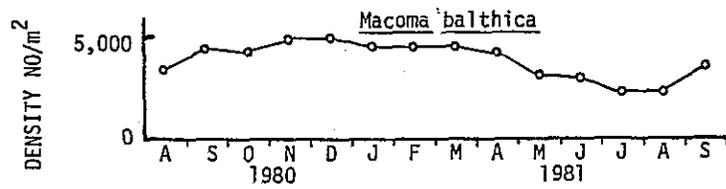


Figure 15. (cont.)

Table 4. Summary of Statistical Analysis of Changes in Total Density (Number/m<sup>2</sup>) and Density of Selected Taxa at the Baker Bay Study Site. Tukey's HSD (Honestly Significant Difference) Gives the Minimum Significant Difference ( $\alpha=.05$ ) Between All Possible Pairwise Combinations.

Month	A	S	O	N	D	J	F	M	A	M	J	J	A	S	Standard error	Sig/KS	Tukey's HSD
All taxa	30924	31490	30850	25203	27792	18273	16547	12798	12083	12823	19407	25227	14476	11985	2422	0.01	11965
<u>M. balthica</u>	3477	4488	4242	4907	4957	4538	4597	4562	4291	3206	3033	2367	2318	3527	410	0.01	2026
<u>P. Knap</u>	7102	5844	5499	4982	4735	2565	2096	2244	2540	1208	592	469	9865	1677	866	0.01	4277
<u>H. florida</u>	2664	3344	4636	4414	2861	2441	2071	2244	1480	4167	31418	26708	7324	4233	835	0.01	4125

Table 5. List of Common Taxa and Their Feeding Modes for the Baker Bay Study Site

Rhynchocoela	Mobile predators (capture prey with proboscis) <sup>1,2</sup>
Turbellaria	Predators (most species) <sup>1</sup>
Polychaeta	
<u>Mediomastus</u> spp.	Deposit feeder
<u>Eteone</u> spp.	Mobile predator <sup>3,4</sup>
<u>Neanthes limnicola</u>	Deposit feeders (may be predaceous) <sup>5</sup>
<u>Polydora ligni</u>	Suspension feeder (with palps) <sup>4,6,7</sup>
<u>Pseudopolydora kemp</u>	Surface deposit feeder (with tentacles) <sup>3</sup>
<u>Hobsonia florida</u>	Surface deposit feeder (with tentacles) <sup>3,8</sup>
<u>Pygospio elegans</u>	Surface deposit feeder (with tentacles) <sup>2,3,4</sup>
<u>Manayunkia aestuarina</u>	Suspension feeder (with tentacles) <sup>3,4</sup>
Oligochaeta	Mobile deposit feeder <sup>9</sup>
Cumacea	
<u>Hemileucon</u> sp.	Deposit feeder
Bivalvia	
<u>Macoma balthica</u>	Surface deposit feeder <sup>10,11</sup>
<u>Mya arenaria</u>	Suspension feeder <sup>12</sup>

- 
1. Nicol 1962
  2. Green 1968
  3. Eckman, 1979
  4. Fauchald and Jumars. 1979
  5. Smith 1950
  6. Muus 1967
  7. Dard and Polk 1973
  8. Banse 1979
  9. Pennak 1953
  10. Brafield and Newell 1961
  11. Caddy 1979
  12. McDonald 1969

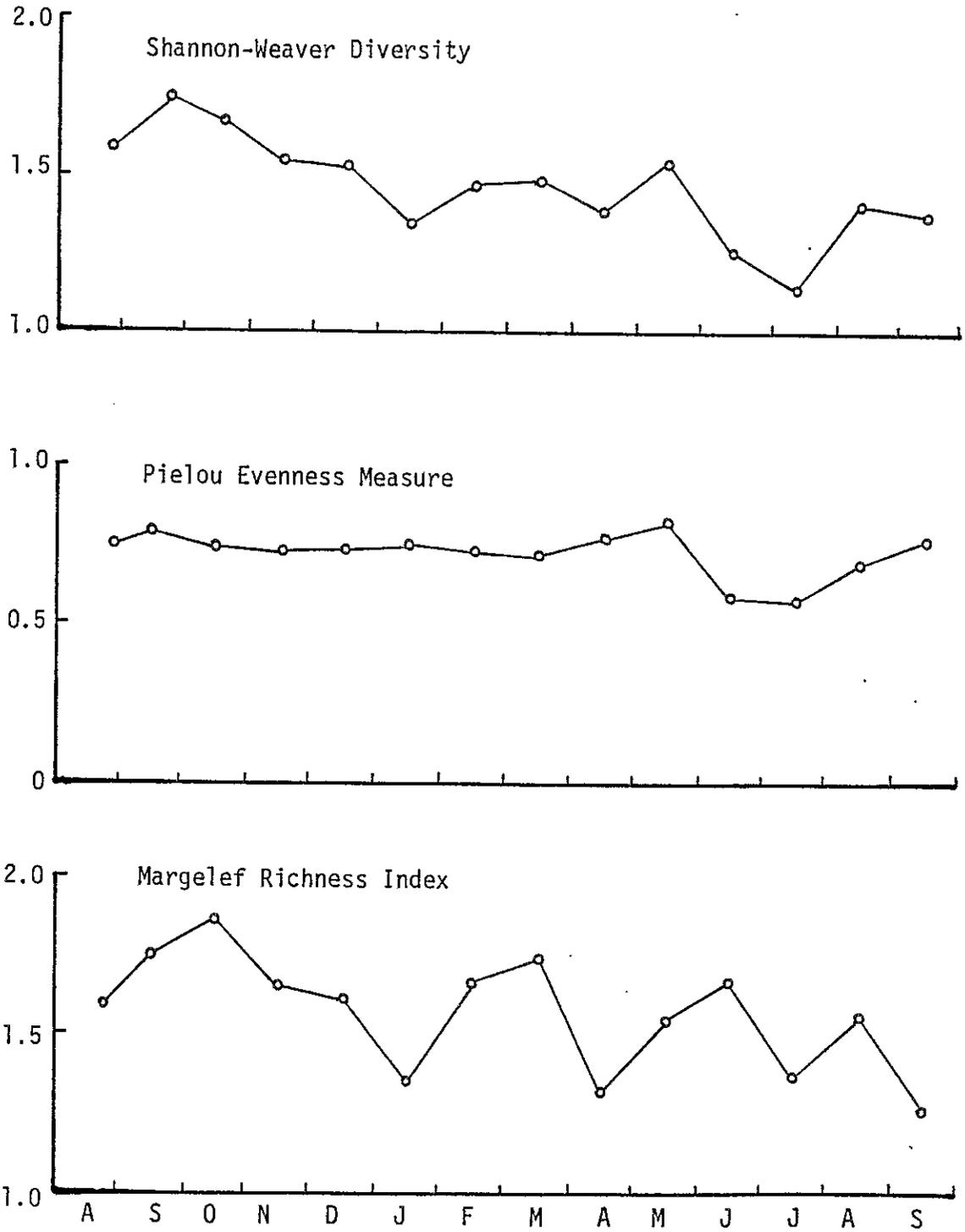


Figure 16. Community Composition Parameters Calculated for Benthic Infauna at the Baker Bay Study Site

### 3.2.2 Community Composition Parameters

Shannon-Weaver diversity generally decreased during the year of study, reaching a low in June and July (Figure 16). This change was statistically significant (Table 6), reflecting a decrease in number of species present during the year and a decrease in evenness in June and July. Evenness also changed significantly during the year. Evenness was low in June and July during the population peak of H. florida, but constant during the rest of the year. However, Margalef's richness index, responding to both density and number of taxa present, did not change significantly during the year.

### 3.2.3 Production Ecology

#### Macoma balthica

Five groups of M. balthica were recognized during the study period, ranging in age from 0+ to 3+ years (Figure 17). However, some individuals could have been older, since the specimens were extremely difficult to age accurately due to shell surface irregularities which often masked the age rings.

Shell heights ranged from 0.5 mm to 13 mm. The portion of the population having shell heights greater than 8 mm (1+ in age) developed a significant peak in gonad maturity during the year (Figure 18, Table 7). Most of the individuals had mature gonads in June and July, and a few became mature in September of 1980. This latter peak in gonad maturity was not reflected in the settling of spat, which occurred in August or September depending on the year.

Estimates of production of M. balthica were based on five cohorts identified on the basis of size and age (Figure 17). The first two cohorts (designated A and B) were the 3+, which disappeared in spring 1981, and the 2+ which became the 3+ in September 1981. However, during the period from January through April when the winter rings were laid down, the individuals were placed into cohorts on the basis of size. Two younger groups (designated C and D) were identified during 1980: a group larger than 2.0 mm that began as a 1+ in 1980 and became a 2+ group in September 1981, and a 0+ group that remained below 2.0 mm in size until April of 1981 when growth resumed. The D cohort then became a 1+ in September 1981. The fifth size group (designated E) appeared in August and September of 1981 as a new recruitment of young, and is referred to as a 0+ age group.

Seasonal shell height vs. body weight regression equations were developed to convert M. balthica size to weight for calculation of secondary production (Table 8, Figure 19). Live animals were also measured and weighed to determine weight loss due to preservation. Using these conversion factors, live AFDW was estimated on a seasonal basis. The correction of live to preserved weights was 71%. A test for equality of the regressions according to the procedure of Neter and Wasserman (1974) established that the shell height vs. preserved weight relation differed significantly by season (Table 9). Using the regression equations, the

Table 6. Statistical Analysis of Monthly Changes in Community Composition Parameters for the Baker Bay Study Site. Tukey's HSD Gives the Minimum Significant Difference ( $\alpha=0.5$ ) Between All Possible Pairwise Combinations.

Month	A	S	O	N	D	J	F	M	A	M	J	J	A	S	Standard error	Sig/NS	Tukey's HSD
Diversity	1.589	1.741	1.667	1.549	1.535	1.346	1.471	1.488	1.392	1.544	1.262	1.151	1.421	1.384	0.059	0.01	0.293
Evenness	0.750	0.792	0.739	0.731	0.736	0.753	0.730	0.719	0.781	0.827	0.587	0.576	0.706	0.776	0.023	0.01	0.112
Richness	0.597	1.756	1.868	1.645	1.602	1.376	1.662	1.741	1.314	1.543	1.671	1.367	1.546	1.246	0.149	NS	-

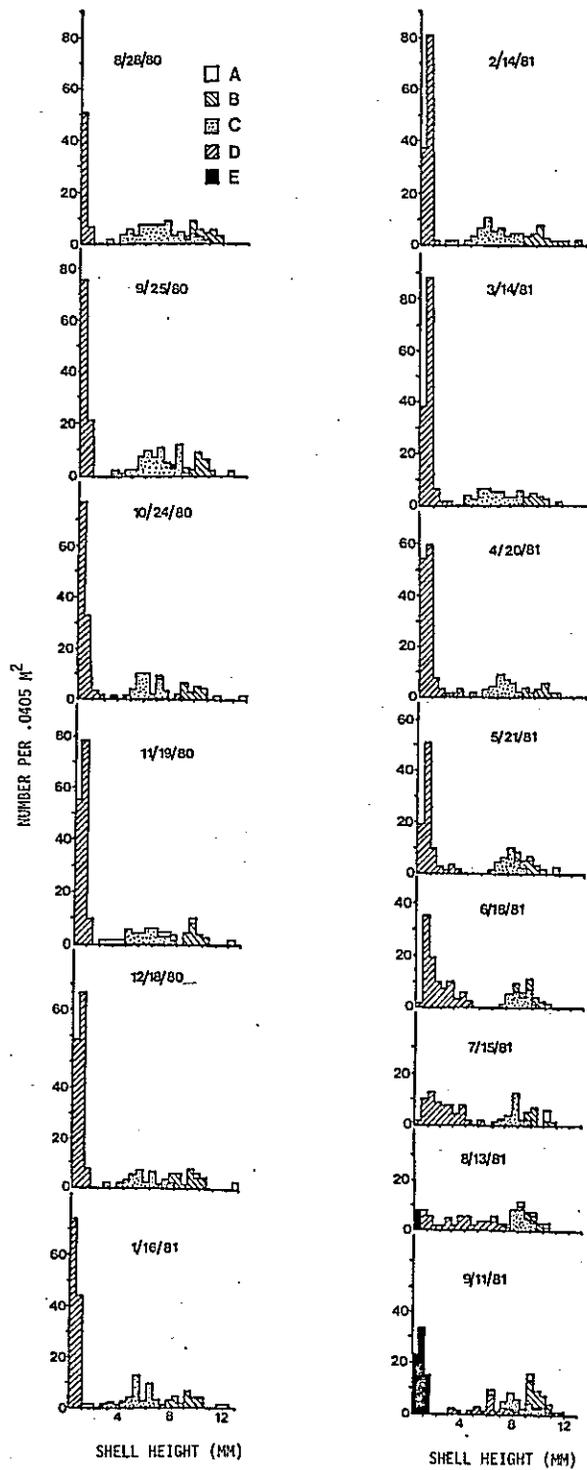


Figure 17. Shell Height Frequency Histograms for Macoma balthica. A to E Represent Successively Younger Cohorts, as Explained in Text.

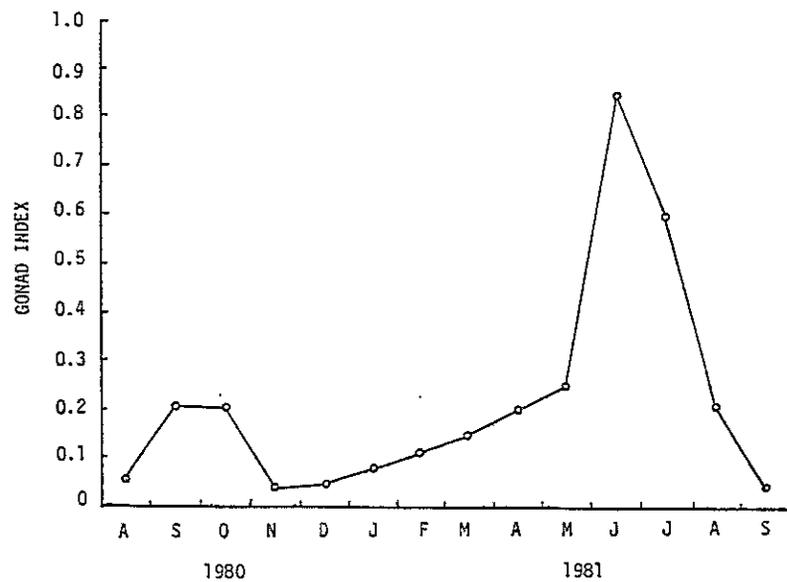


Figure 18. Gonad Index Expressing Maturity of Adult *Macoma balthica*

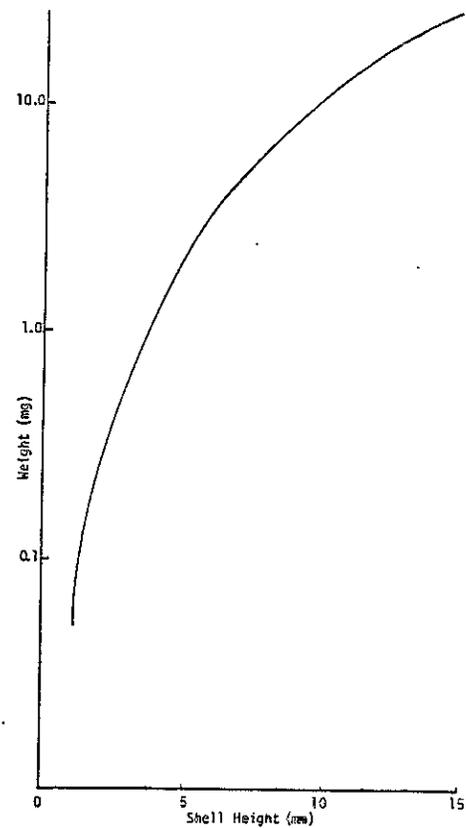


Figure 19. Weight as a Function of Shell Height for *Macoma balthica* (Yearly Average)

Table 7. Summary of Statistical Analysis of Changes in Gonad Maturity of *Macoma balthica*. Tukey's HSD Provides the Minimum Significant Difference ( $\alpha=0.5$ ) Between All Possible Pairwise Combinations.

Month	A	S	O	N	D	J	F	M	A	M	J	J	A	S	Standard error	Sig/NS	Tukey's HSD
Mean	0.056	0.203	0.200	0.036	0.043	0.078	0.008	0.147	0.193	0.255	0.844	0.596	0.203	0.040	0.090	0.01	0.446

Table 8. Regression Equations Relating Shell Height to Body Weight for Macoma balthica.  $X = \log_{10}$  Shell Height;  $Y = \log_{10}$  Weight.

<u>DATE</u>	<u>REGRESSION EQUATION</u>	<u>R<sup>2</sup></u>	<u>n</u>
1) January 1982 (live)	$Y = 2.82677X - 1.79541$	.9813	16
2) October 1980	$Y = 2.50285X - 1.56080$	.9878	6
3) January 1981	$Y = 2.55744X - 1.72167$	.9853	11
4) April 1981	$Y = 2.39896X - 1.50962$	.9849	9
5) July 1981	$Y = 2.16950X - 1.23169$	.9813	11
6) All preserved dates	$Y = 2.30797X - 1.43039$	.9667	37

Table 9. Statistical Analysis of Regression Equations Relating Shell Height to Preserved Body Weight of Macoma balthica

<u>SSE (reduced model)</u>	<u>SSE (full model)</u>	<u>d.f.</u>	<u>Sig./N.S. ( =.01)</u>
0.6976	0.3351	6,29	Sig.

weight changes of three individuals of different sizes were graphed during the year (Figure 20). Animals weighed most for a given shell height in the summer and fall, and least in the winter. This corresponded to gonad development in summer and fall, and low tissue increase in winter.

Total production by these five groups was estimated at 13.56 g/m<sup>2</sup>/yr (Table 10). The greatest portion of this production (5.56 g/m<sup>2</sup>/yr) came from the C group, individuals that began the sample period as 0+ and became the 1+ size class in 1981.

#### Pseudopolydora kempi

Young of P. kempi first appeared on the mudflat in August at a width of 0.1 mm to 0.3 mm (Figure 21). The large recruitment in 1980 was followed by a general decrease in density until the next recruitment of young in August of 1981. Even though the number of P. kempi settling in 1981 was high, subsequent survivorship was very low compared to 1980. Adults appeared to live for more than one year, since very large individuals were present past the time of recruitment.

Very few P. kempi had mature gonads at any time. The few mature individuals found occurred in April and July. However, large P. kempi tended to break in the region of the body where eggs are normally stored (just behind the 10th segment). The body was swollen in that region, delicate, and easily broken during screening. Thus, the frequency with which females were ovigerous probably was poorly represented in these data.

Seasonal width vs. weight regressions were calculated to estimate weight from the size data (Table 11, Figure 22). A test following the procedure of Neter and Wasserman (1974) showed no significant differences among either slopes or intercepts for equations 1 to 4, the four seasonal width vs. weight regression equations (Table 12). Therefore, the combined data (equation 5) were used to calculate weights for production estimates (Table 11, Figure 22). Since no P. kempi were collected live, preserved weights were assumed to be 60% of live weight based on information for Hobsonia florida.

Production was computed from the combined width/weight relation of equation 5 and an analysis of cohorts. The results of the computation are summarized in Table 13. Three cohorts were recognized: a 1+ that disappeared by May (group A), a 0+ that became a 1+ and continued through the sampling period (group B), and a new recruitment of 0+ in July 1981 (group C). Total production of these three cohorts was estimated at 1.12 g/m<sup>2</sup>/yr, with the largest contribution coming from the 0+ cohort that grew into a 1+ group in summer 1981 (group B). This group also contained the few gravid individuals found.

#### Hobsonia florida

The presence of gravid adults and recruitment peaks for H. florida suggested two reproductive periods, a large early summer peak and a smaller peak (Figures 23 and 24). Gravid H. florida were present in August and September 1980 and in February through September 1981. How-

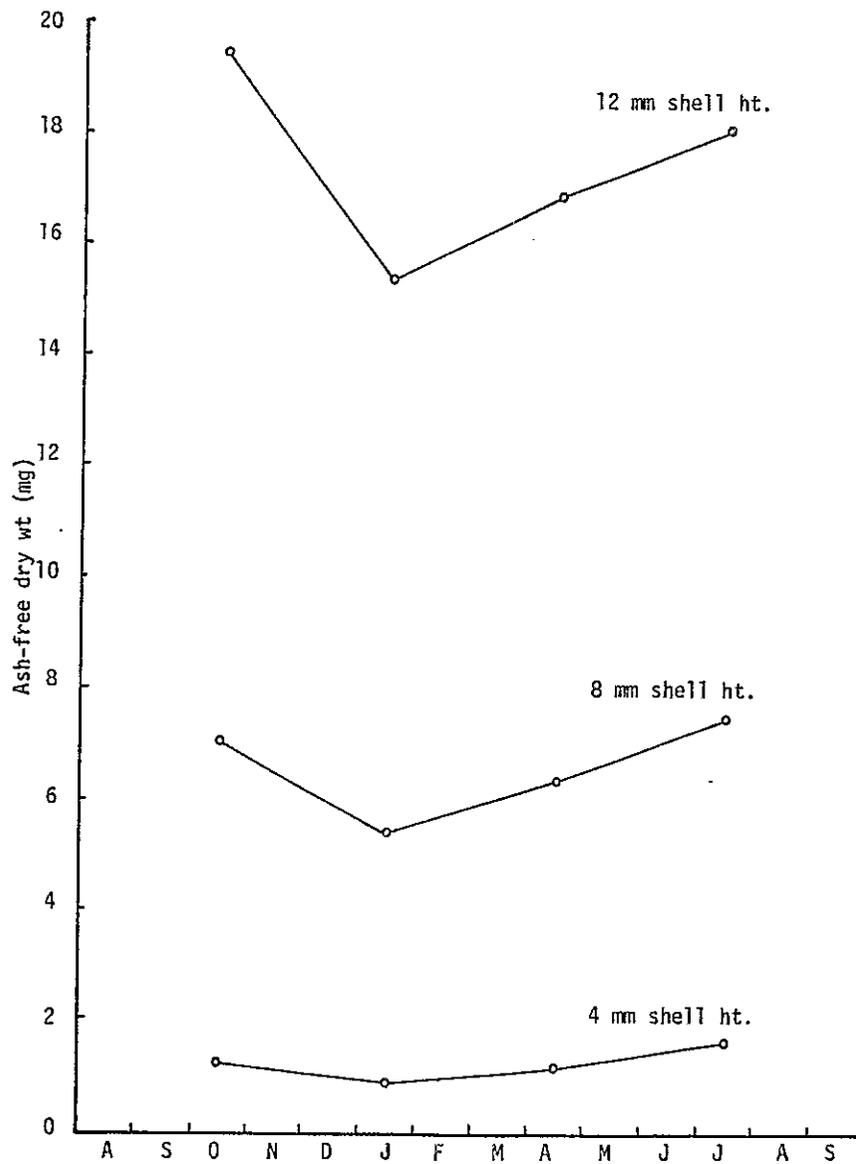


Figure 20. Seasonal Change in Weight of *Macoma balthica* at Three Different Shell Sizes

Table 10. Production (mg AFDW/0.0405 m<sup>2</sup>/yr) Calculations for Macoma balthica

Sampling month	Year class	No.	Mean wt./ indiv. $\bar{w}$ (mg)	Wt.increment since previous sampling $\Delta \bar{w}$ (mg)	Mean no. during $\Delta +$ $\bar{N}$	Production increment $\bar{N} \Delta \bar{w}$ (mg)
A	A	0	0	-	-	-
S	A	2	18.45	-	1	-
O	A	2	18.45	0	2	-
N	A	2	14.77	0	2	-
D	A	3	17.96	3.19	3	9.57
J	A	2	15.38	0	3	-
F	A	0	0	-	1	-
M	A	0	0	-	0	-
A	A	0	0	-	0	-
M	A	4	11.58	-	2	-
J	A	1	12.88	1.30	3	3.90
J	A	4	12.88	0	3	-
A	A	4	11.55	0	4	-
S	A	2	13.11	1.56	3	4.68
						<u>18.15</u>
A	B	21	10.31	-	-	-
S	B	22	10.14	0	22	-
O	B	19	8.82	0	21	-
N	B	21	10.14	1.32	20	26.40
D	B	24	7.91	0	23	-
J	B	24	7.91	0	24	-
F	B	20	9.91	2.00	22	44.00
M	B	14	7.92	0	17	-
A	B	15	9.05	1.13	15	16.95
M	B	15	7.92	0	15	-
J	B	11	9.14	1.22	13	15.86
J	B	11	10.31	1.17	11	12.87
A	B	12	10.31	0	12	-
S	B	25	11.57	1.26	19	23.94
						<u>140.02</u>

Table 10. (cont.)

Sampling month	Year class	No.	Mean wt./ indiv. w̄ (mg)	Wt. increment since previous sampling Δ w̄ (mg)	Mean no. during Δ+ N	Production increment N Δ w̄ (mg)
A	C	62	-	-	-	-
S	C	60	0	0	61	0
O	C	40	0	0	50	0
N	C	34	0.36	0.36	37	13.32
D	C	32	0	0	33	0
J	C	39	0	0	36	0
F	C	44	0.23	0.23	42	9.66
M	C	38	0.80	0.80	41	32.80
A	C	30	0.65	0.65	34	22.10
M	C	26	1.51	1.51	28	42.28
J	C	24	2.47	2.47	25	61.75
J	C	23	0	0	24	0
A	C	25	1.02	1.02	24	24.48
S	C	22	0.78	0.78	24	18.72
						<u>225.11</u>
A	D	56	-	-	-	-
S	D	96	0	0	76	0
O	D	111	0	0	104	0
N	D	142	0	0	127	0
D	D	141	0.0116	0.0116	142	1.65
J	D	120	0	0	131	0
F	D	120	0.012	0.012	120	1.44
M	D	134	0.009	0.009	127	1.14
A	D	123	0	0	129	0
M	D	84	0	0	104	0
J	D	88	0.1122	0.1122	86	9.65
J	D	58	0.144	0.144	73	10.51
A	D	46	0.175	0.175	52	61.10
S	D	22	2.347	2.347	34	79.80
						<u>165.29</u>
A	E	-	-	-	-	-
S	E	-	-	-	-	-
O	E	-	-	-	-	-
N	E	-	-	-	-	-
D	E	-	-	-	-	-
J	E	-	-	-	-	-
F	E	-	-	-	-	-
M	E	-	-	-	-	-
A	E	-	-	-	-	-
M	E	-	-	-	-	-
J	E	-	-	-	-	-
J	E	-	-	-	-	-
A	E	7	-	-	-	-
S	E	71	0.0147	0.0147	39	0.5733
						<u>0.5733</u>
						P=549.14mg/0.0405m <sup>2</sup>

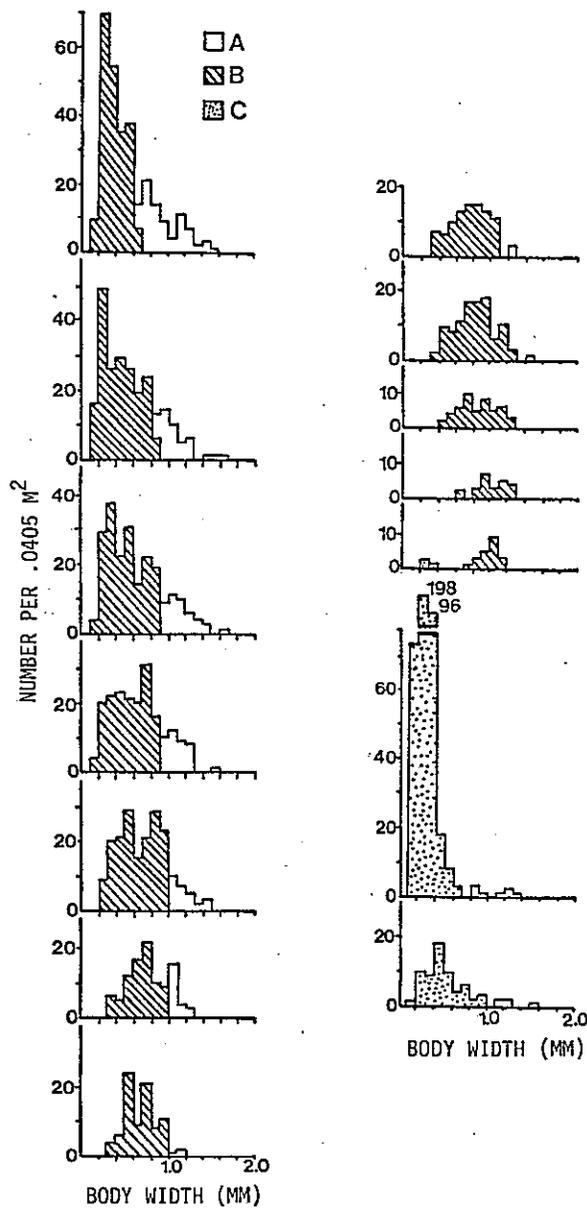


Figure 21. Body Width Frequency Histograms for *Pseudopolydora kempfi*. A to C Represent Successively Younger Cohorts, as Explained in Text.

Table 11. Regression Equations Relating Body Width to Weight for Pseudopolydora kempi.  $X = \log_{10}$  Body Width;  $Y = \log_{10}$  Weight.

<u>DATE</u>	<u>REGRESSION EQUATION</u>	<u>R<sup>2</sup></u>	<u>n</u>
1) October 1980	$Y = 3.16106X - .821695$	.9746	11
2) January 1981	$Y = 3.02889X - .803000$	.8841	9
3) April 1981	$Y = 2.54867X - 1.01292$	.9390	7
4) July 1981	$Y = 1.93583X - .855050$	1.0000	2
5) All data combined	$Y = 2.97008X - .962368$	.9200	29

Table 12. Statistical Analysis of Regression Equations Relating Body Width to Weight of P. kempi

<u>SSE</u> (reduced model)	<u>SSE</u> (full model)	<u>d.f.</u>	<u>Sig./N.S.</u> ( = .01)
0.6134	0.4429	6,21	N.S.

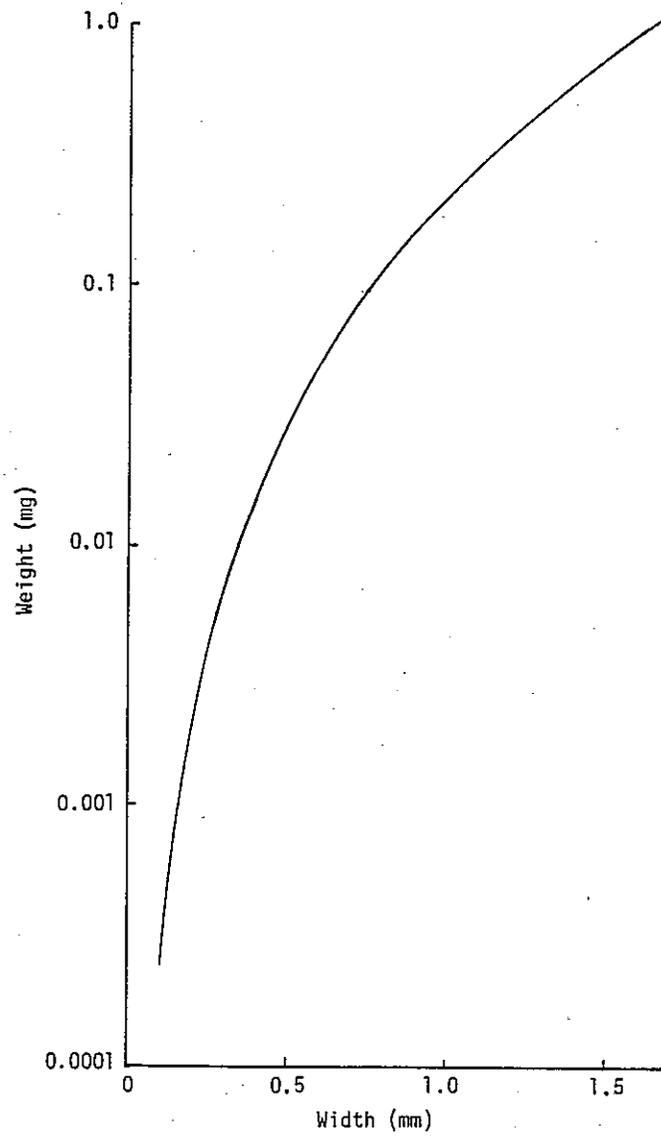


Figure 22. Weight as a Function of Body Width for Pseudopolydora kempii

Table 13. Production (mg AFDW/0.0405 m<sup>2</sup>/yr) Calculations for Pseudopolydora kempii

Sampling month	Year class	No.	Mean wt./ indiv. w (mg)	Wt. increment since previous sampling Δ w (mg)	Mean no. during Δ N	Production increment N Δ w (mg)
A	A	79	0.1412	-	-	-
S	A	45	0.2645	0.1233	62	7.6446
O	A	44	0.3465	0.082	45	3.69
N	A	40	0.2645	0	42	0
D	A	27	0.3465	0.082	34	2.788
J	A	23	0.2645	0	25	0
F	A	3	0.3465	0.082	13	1.066
M	A	3	0.4439	0.0974	3	0.2922
A	A	1	0.6899	0.246	2	0.492
M	A	0	-	-	-	-
J	A	0	-	-	-	-
J	A	0	-	-	-	-
A	A	0	-	-	-	-
S	A	0	-	-	-	-
						15.9728
A	B	211	0.0101	-	-	-
S	B	196	0.0214	0.0113	204	2.3052
O	B	177	0.0214	0	187	0
N	B	157	0.0388	0.0174	167	2.9058
D	B	167	0.0638	0.0249	162	4.0338
J	B	81	0.0974	0.0337	124	4.1788
F	B	83	0.0637	0	82	0
M	B	90	0.0974	0.0337	87	2.9319
A	B	101	0.1412	0.0438	96	4.2048
M	B	49	0.1412	0	75	0
J	B	24	0.1965	0.0553	37	2.0461
J	B	21	0.2645	0.068	23	1.564
A	B	8	0.2645	0	15	0
S	B	5	0.4439	0.1794	7	1.2558
						25.4262
A	-	-	-	-	-	-
S	-	-	-	-	-	-
O	-	-	-	-	-	-
N	-	-	-	-	-	-
D	-	-	-	-	-	-
J	-	-	-	-	-	-
F	-	-	-	-	-	-
M	-	-	-	-	-	-
A	-	-	-	-	-	-
M	-	-	-	-	-	-
J	-	-	-	-	-	-
J	C	3	0.0038	-	-	-
A	C	394	0.0038	0	199	0
S	C	63	0.0214	0.0176	229	4.0304
						4.0304

P=45.4294mgAFDW/0.0405m<sup>2</sup>

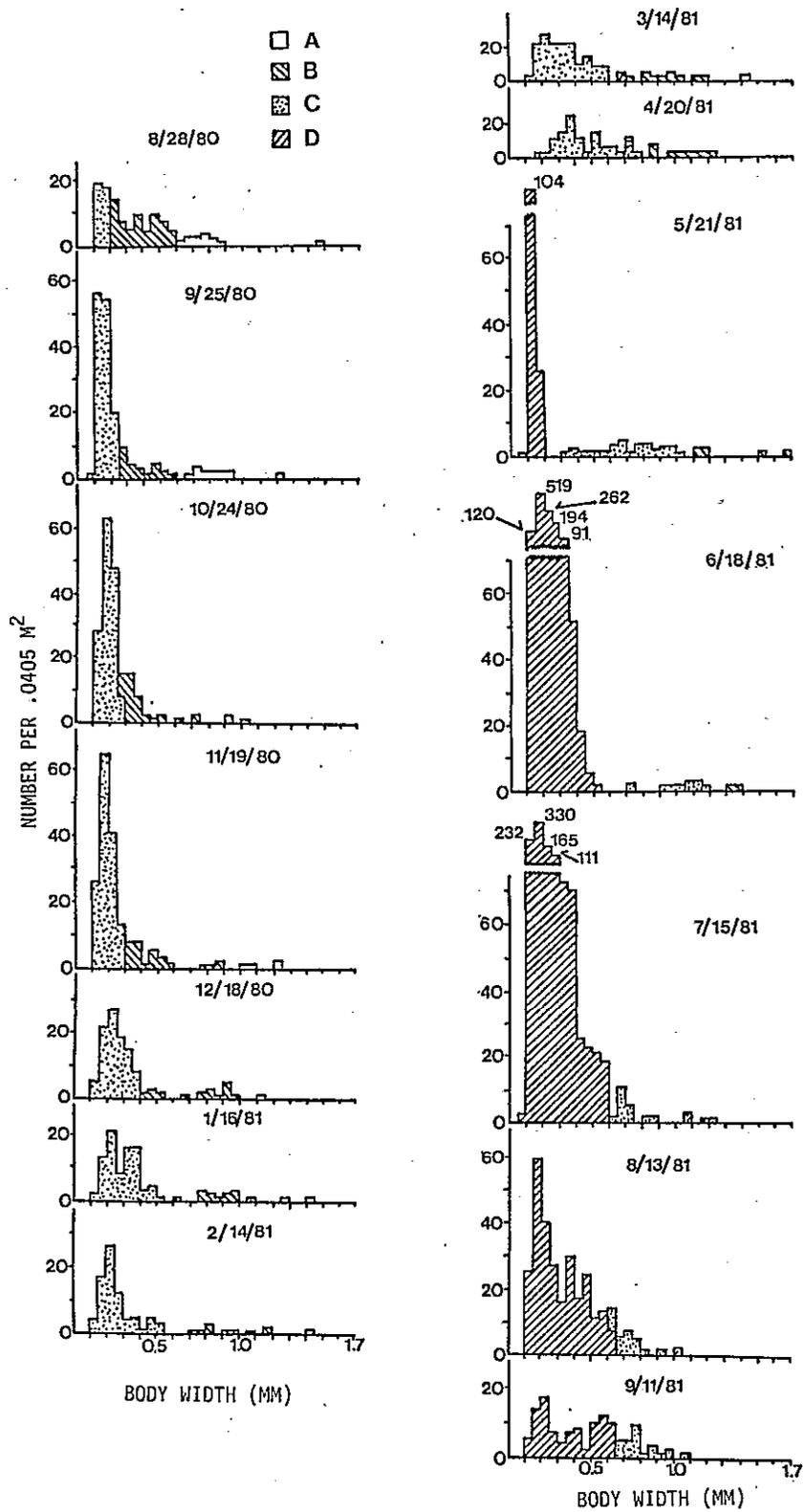


Figure 23. Body Width Frequency Histograms for Hobsonia florida. A to D Represent Successively Younger Cohorts, as Explained in Text.

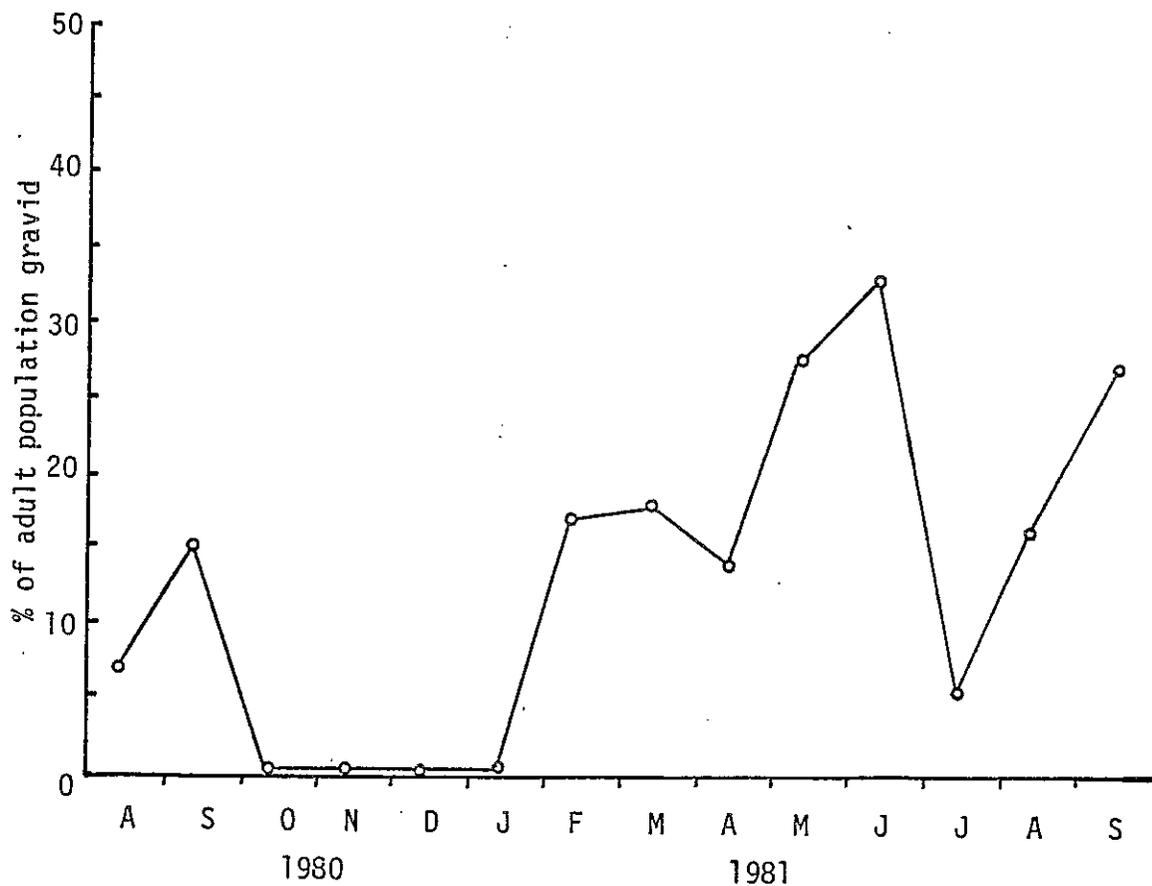


Figure 24. Change in Gonad Condition of Hobsonia florida. Adults were Considered to be Those Animals Greater Than 0.5 mm in Width, Which Was the Width of the Smallest Gravid Animal Found.

ever, the largest number of gravid individuals was present in fall and late spring. The small cohort of young individuals that appeared in September, October, and November 1980 decreased in numbers during the year, but increased steadily in individual length. The next pulse of small individuals began in May 1981. This increase in numbers was far greater than that of the previous fall.

Regression equations estimating the width/weight relationship of H. florida were calculated for both live and preserved individuals (Table 14). A test of regression lines (Neter and Wasserman 1974) demonstrated that the weight of H. florida for a given body width did not vary across seasons (Table 15). Therefore, equation 6 was used in all production calculations to estimate weight for a given size of individual (Table 14, Figure 25). Based on the average difference between the weights and preserved weights derived from the January regression equation (3), preserved values were adjusted to live values by dividing preserved weights by 0.60.

Four H. florida cohorts were identified during the year: 1) a fall 1979 group (1+) which disappeared in April 1981 (group A); 2) a spring 1980 cohort that disappeared in July 1981 (group B); 3) a fall 1980 recruitment that was present during the whole study (group C); and 4) a late spring/early summer 1981 recruitment (group D). Total production of these four groups was 1.37 g/m<sup>2</sup>/yr (Table 16). The largest contribution (0.53 g/m<sup>2</sup>/yr) came from the fall 1980 recruitment which was present all year. However, within three months the large summer 1981 recruitment produced 0.46 g/m<sup>2</sup>.

#### Lesser Taxa

Weight data were collected on the lesser taxa to assist in interpreting the density data and to estimate production (Table 17). These weight data were considered either as yearly or seasonal averages. In addition, enough Neanthes limnicola and oligochaetes were collected live to compare preserved to live weights for these taxa. Preserved N. limnicola were 67% of their live weight and preserved oligochaetes were 53% of live weight.

Secondary production of the lesser taxa (Table 18) was estimated using four methods: 1) Lesser taxa contributed 5.3% of the average biomass during the study period. The assumption was made that these taxa also contributed 5.3% of total production (Buchanan and Warwick 1974). On this basis, the lesser taxa added 0.90 g AFDW/m<sup>2</sup>/yr. 2) Production was estimated by comparing biomass of the lesser taxa with the biomass of H. florida and P. kempfi, considered to be more similar to the lesser taxa in turnover rates than M. balthica (Warwick et al. 1977). The lesser taxa contributed 45% of the biomass of all species excluding M. balthica. On this basis, production of lesser taxa was estimated to be 2.04 g AFDW/m<sup>2</sup>/yr. 3) Estimates were calculated based on the invertebrate production:biomass (P:B) ratios summarized by Banse and Mosher (1980). These authors derived an equation relating maximum species weight to P:B. Using the macrofaunal equation, production was estimated as 4.97 g AFDW/m<sup>2</sup>/yr. 4) In the final method, oligochaetes and Pygospio elegans were considered as meiofauna, and production was recalculated for

Table 14. Regression Equations Relating Body Width to Weight for Hobsonia florida.  $X = \log_{10}$  Body Width;  $Y = \log_{10}$  Weight.

<u>DATE</u>	<u>REGRESSION EQUATION</u>	<u>R<sup>2</sup></u>	<u>n</u>
1) January 1982 (live)	$Y = 2.91645X - .330543$	.9490	10
2) October 1980	$Y = 2.76001X - .536804$	.9827	4
3) January 1981	$Y = 2.22675X - .610148$	.8360	12
4) April 1981	$Y = 2.92300X - .357501$	.9718	10
5) July 1981	$Y = 2.15164X - .577173$	.9790	11
6) All preserved dates	$Y = 2.38632X - .536086$	.9040	37

Table 15. Statistical Analysis of Regression Equations Relating Body Width to Weight of Hobsonia florida

<u>SSE</u> (reduced model)	<u>SEE</u> (full model)	<u>d.f.</u>	<u>Sig./N.S.</u> ( = .01)
1.4121	1.0760	6,29	N.S.

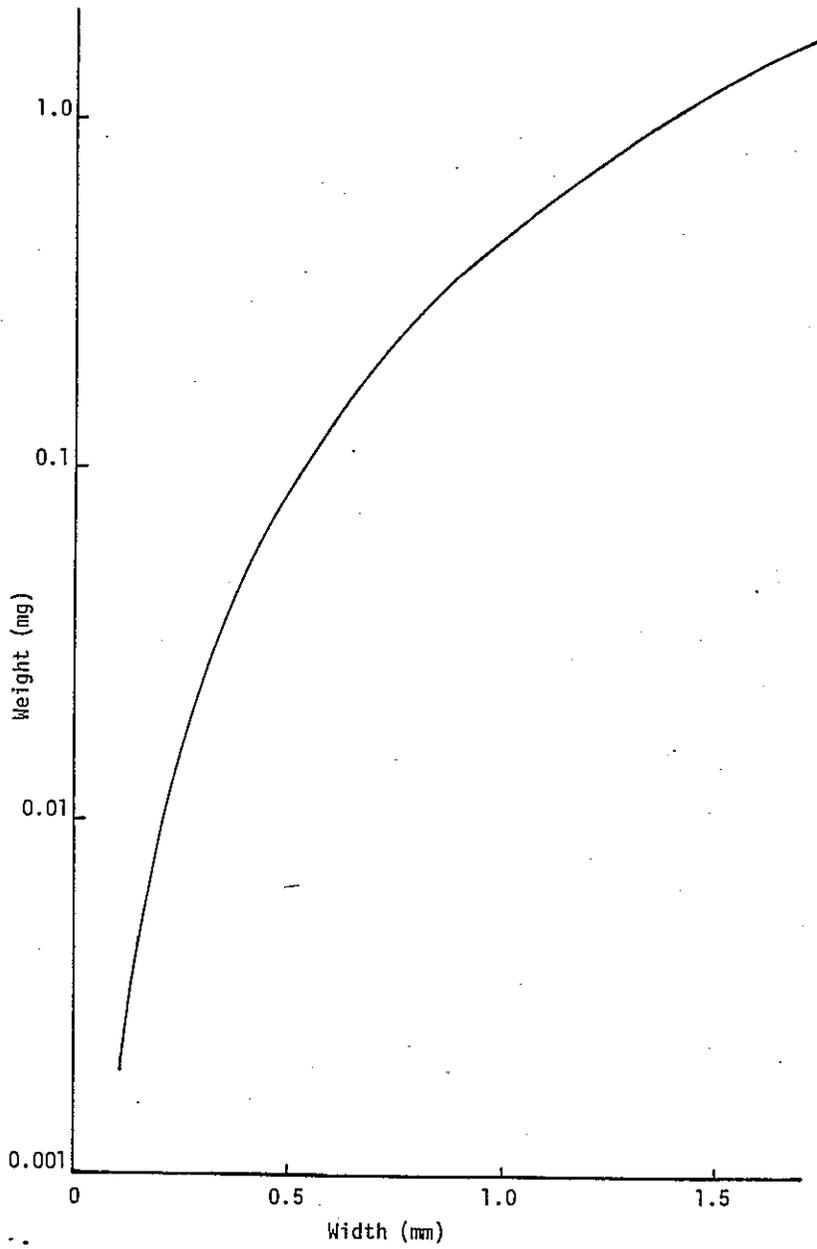


Figure 25. Weight as a Function of Body Width for Hobsonia florida

Table 16. Production (mg AFDW/0.0405 m<sup>2</sup>/yr) Calculations for Hobsonia florida

Sampling month	Year class	No.	Mean wt./ indiv. w̄ (mg)	Wt.increment since previous sampling Δ w̄ (mg)	Mean no. during Δ+ N̄	Production increment	
						N̄ Δ	w̄ (mg)
A	A	12	0.2640	-	-	-	-
S	A	13	0.3605	0.0425	13	0.5525	0.5525
O	A	3	0.4027	0.0962	8	0.7696	0.7696
N	A	4	0.6770	0.2743	4	1.0972	1.0972
D	A	1	0.6424	0	3	0	0
J	A	2	0.9926	0.3502	2	0.7004	0.7004
F	A	1	1.129	0.1364	2	0.2728	0.2728
M	A	1	1.129	0	1	0	0
A	A	0					
M	A	0					
J	A	0					
J	A	0					
A	A	0					
S	A	0					
						<u>3.3925</u>	
A	B	59	0.0467	-	-	-	-
S	B	24	0.0332	0	42	0	0
O	B	38	0.0332	0	31	0	0
N	B	30	0.0467	0.0135	34	0.459	0.459
D	B	20	0.2848	0.2381	25	5.9525	5.9525
J	B	13	0.3527	0.0679	17	1.1543	1.1543
F	B	10	0.3527	0	12	0	0
M	B	0	0.4566	0.1039	10	1.039	1.039
A	B	0	0.5145	0.0579	9	0.5211	0.5211
M	B	6	0.7127	0.1982	8	1.5856	1.5856
J	B	2	0.9926	0.2799	4	1.1196	1.1196
J	-	0					
A	-	0					
S	-	0					
						<u>11.8311</u>	

Table 16. (cont.)

Sampling month	Year class	No.	Mean wt./ indiv. $\bar{w}$ (mg)	Wt.increment since previous sampling $\Delta \bar{w}$ (mg)	Mean no. during $\Delta +$ $\bar{N}$	Production increment $\bar{N} \Delta \bar{w}$ (mg)
A	C	37	0.0034	-	-	-
S	C	131	0.0076	0.0042	84	0.3528
O	C	147	0.0076	0	139	0
N	C	145	0.0076	0	146	0
D	C	96	0.0138	0.0062	121	0.7502
J	C	84	0.0223	0.0085	90	0.765
F	C	77	0.0138	0	81	0
M	C	81	0.0332	0.0184	79	1.5326
A	C	52	0.0545	0.0213	67	1.4271
M	C	32	0.2640	0.2095	42	8.799
J	C	10	0.5449	0.2809	21	5.8989
J	C	23	0.1899	0	17	0
A	C	29	0.2252	0.0354	26	0.9204
S	C	27	0.2640	0.0388	28	1.0864
						<u>21.5324</u>
A	-	-				
S	-	-				
O	-	-				
N	-	-				
D	-	-				
J	-	-				
F	-	-				
M	-	-				
A	-	-				
M	D	131	0.0034	-	-	-
J	D	1261	0.0076	0.0042	696	2.9232
J	D	1069	0.0076	0	1165	0
A	D	269	0.0223	0.0147	765	11.2455
S	D	96	0.0467	0.0244	183	4.4652
						<u>18.6339</u>
						$P=55.3899\text{mgAFDW}/0.0405\text{m}^2$

Table 17. Weights (mg AFDW) of Lesser Taxa by Season or Yearly Average

<u>TAXON</u>	<u>OCT.</u>	<u>JAN.</u>	<u>APRIL</u>	<u>JULY</u>	<u>AVE.WT.</u>	<u>n</u>
<u>Neanthes limnicola</u>	0.647	1.105	0.621	0.085		44
<u>Eteone spp.</u>	1.258	0.225	0.033	0.458		11
<u>Polydora ligni</u>	0.161	0.245	0.189	-		35
<u>Oligochaete</u>	0.015	0.020	0.012	0.023		217
<u>Hemileucon sp.</u>	0.011	0.033	0.037	0.023		49
<u>Corophium salmonis</u>	0.167	-	0.617	0.143		16
<u>Turbellaria</u>	0.077	0.080	-	0.100		43
<u>Rhynchocoela</u>					0.017	5
<u>Heteromastus spp.</u>					2.630	2
<u>Mediomastus spp.</u>					0.222	8
<u>Pygospio elegans</u>					0.014	22
<u>Clinocardium nuttilli</u>					0.067	1
<u>Eogammarus confervicolus</u>					0.133	1
<u>Paraphoxus milleri</u>					0.350	2
<u>Gnorimosphaeroma oregonensis</u>					0.100	1

Table 18. Production Estimates of Lesser Taxa by Four Methods

1) Lesser taxa production proportional to biomass of dominant taxa (Buchanan and Warwick, 1974).

Species	% of biomass	Production (g/m <sup>2</sup> /yr)
<u>M. balthica</u>	88.4	13.559
<u>H. florida</u>	2.8	1.368
<u>P. kempi</u>	3.5	1.122
Sub-total	94.7	16.049
Lesser taxa	5.3	0.898
Total	100.0	16.947

2) Lesser taxa production proportional to biomass of common polychaetes (Warwick, Joint, and Radford, 1977).

Species	% of biomass	Production (g/m <sup>2</sup> /yr)
<u>H. florida</u>	24.3	1.368
<u>P. kempi</u>	30.2	1.122
Sub-total	54.5	2.490
Lesser taxa	45.5	2.079
	100.0	

3 & 4) (Banse and Mosher, 1980)

Taxon	Max. AFDW (mg)	Wet Wt. <sup>1</sup> (mg)	Kcal <sup>2</sup>	Macrof. <sup>3</sup> P:B	Meio. <sup>3</sup> P:B	Production (mg/m <sup>2</sup> /yr)
<u>Oligochaete</u>	0.023	0.144	0.00144	17	4.3	3264 826
<u>Hemiteucon sp.</u>	0.037	0.333	0.00033	12		120
<u>Turbellaria</u>	0.10	0.62	0.00062	10		320
<u>P. ligni</u>	0.245	1.53	0.00153	7		399
<u>H. limnicola</u>	1.105	6.91	0.00691	4		372
<u>Mediomastus spp.</u>	0.222	1.39	0.00139	7		21
<u>P. elegans</u>	0.0143	0.09	0.00009	20	5.1	40 10
<u>C. salmonis</u>	0.617	4.54	0.00454	5		75
<u>Rynchocoela</u>	0.250	1.55	0.00155	7		91
<u>Eteone spp.</u>	1.258	7.86	0.00786	4		88
<u>Heteromastus sp.</u>	2.63	16.40	0.0164	3		165
<u>E. confervicolus</u>	0.133	0.98	0.00098	8		8
<u>P. milleri</u>	0.35	2.57	0.00257	6		6
<u>G. oregonensis</u>	0.10	0.71	0.00071	9		2
<u>C. nuttilli</u>	0.067	0.86	0.00086	9		1

3) All considered macrofauna: 4.972 g/m<sup>2</sup>/yr

4) All considered macrofauna except oligochaetes and P. elegans (meiofauna): 2.504 g/m<sup>2</sup>/yr

<sup>1</sup>Conversion from AFDW to Wet wt. (Richardson, Carey, Colgate, 1977)

<sup>2</sup>Conversion from Wet wt. to Kcals (Banse and Mosher, 1980)

<sup>3</sup>Conversion from Kcal to P:B (Banse and Mosher, 1980)

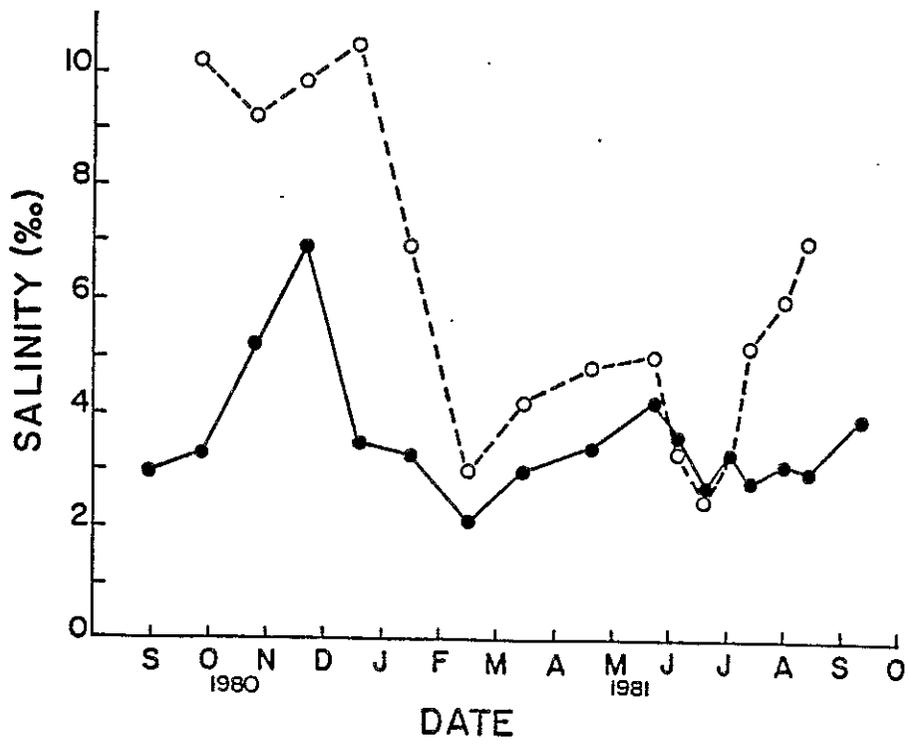
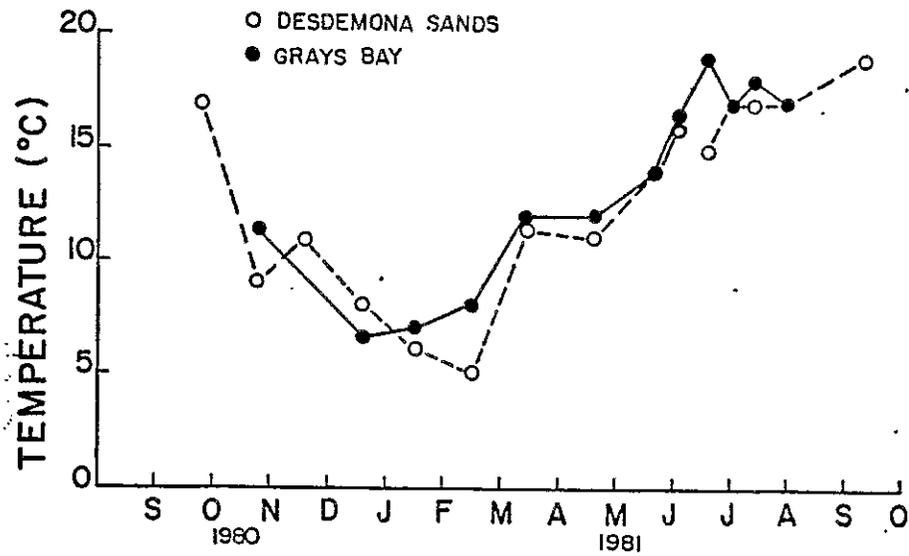


Figure 26. Temperature and Salinity at the Grays Bay and Desdemona Sands Study Sites

these taxa using the meiofauna equation of Banse and Mosher and added to the macrofaunal estimates for the other taxa. This approach lowered production of lesser taxa to 2.50 g AFDW/m<sup>2</sup>/yr. These four estimates suggested that production by the lesser taxa was on the order of 1 to 5 g AFDW/m<sup>2</sup>/yr.

### 3.3 COROPHIUM SALMONIS LIFE HISTORY STUDY

#### 3.3.1 Physical Variables

Water temperature at low tide at the two Corophium salmonis life history study sites was very similar throughout the year (Figure 26). Temperatures were lowest at 6.5°C for Grays Bay in December 1980 and 5.0°C for Desdemona Sands in February 1981. The highest temperature was 19.0°C at both sites, occurring in June 1981 at Grays Bay and in August 1981 at Desdemona Sands.

Low tide salinity varied more than temperature between the two sites (Figure 26). Salinity at Desdemona Sands was higher than at Grays Bay during the winter of 1980-1981. Peak salinities at Grays Bay were 5.2 ppt and 6.9 ppt occurring in October and November 1980. For the rest of the study the salinity at Grays Bay ranged from 2.1 ppt to 4.2 ppt. Desdemona Sands salinities peaked in the winter at 10.5 in December 1980. Salinities at Desdemona Sands dropped in February 1981 to 3 ppt and remained below 5 ppt until July 1981 when they again began to increase.

These salinity and temperature measurements were made at low tide in the nearby river channel. They do not reflect the total salinity and temperature regimes experienced by the animals at the sites but are an indication of seasonal changes experienced by the fauna.

Sediment texture was similar at the two study sites and was mostly stable during the study period. Median particle size ranged between 2.48φ and 2.89φ at Grays Bay and between 2.25φ and 2.50φ at Desdemona Sands (Figure 27). Percent silt and clay at Desdemona Sands was consistently low throughout the study with a range of 3.4% to 5.8% (Figure 28). However, at Grays Bay percent silt and clay rose sharply in April 1981 to a high of 21%. The lowest value in Grays Bay was 3.0% in October 1980.

Sediment level at the sediment stakes appeared constant at both sites indicating that no major erosional or depositional events occurred.

#### 3.3.2 Population Structure of Corophium salmonis

Length-frequency histograms were constructed for both sites on each sampling date to examine seasonal population size structure patterns. Histograms for Grays Bay (Figure 29) indicate that the population was producing young when sampling began in August 1980 and continued to produce juveniles through November 1980. By November, breeding females observed in the previous three months had disappeared leaving a population dominated by juveniles, immatures and mature males. From December 1980 until April 1981 juveniles produced the previous fall grew and matured until those released in early fall became adults and those in late

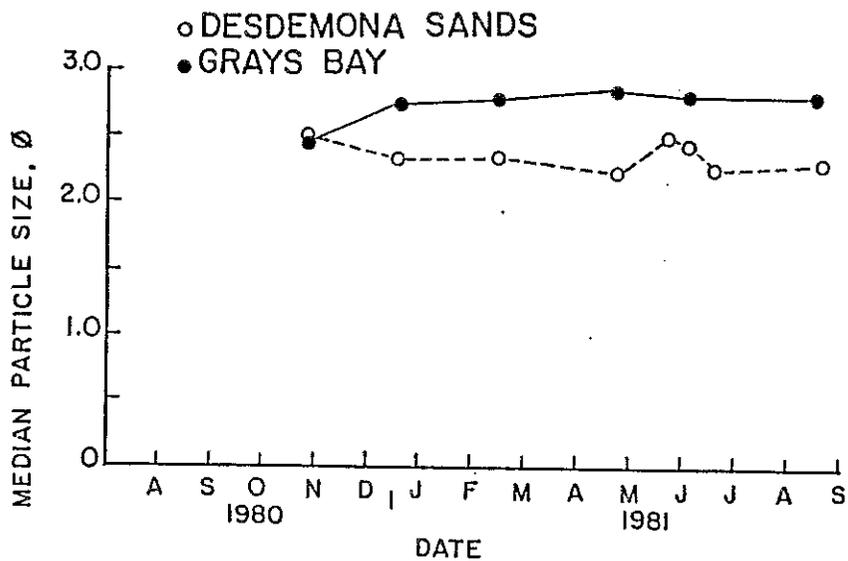


Figure 27. Median Particle Size at the Grays Bay and Desdemona Sands Study Sites

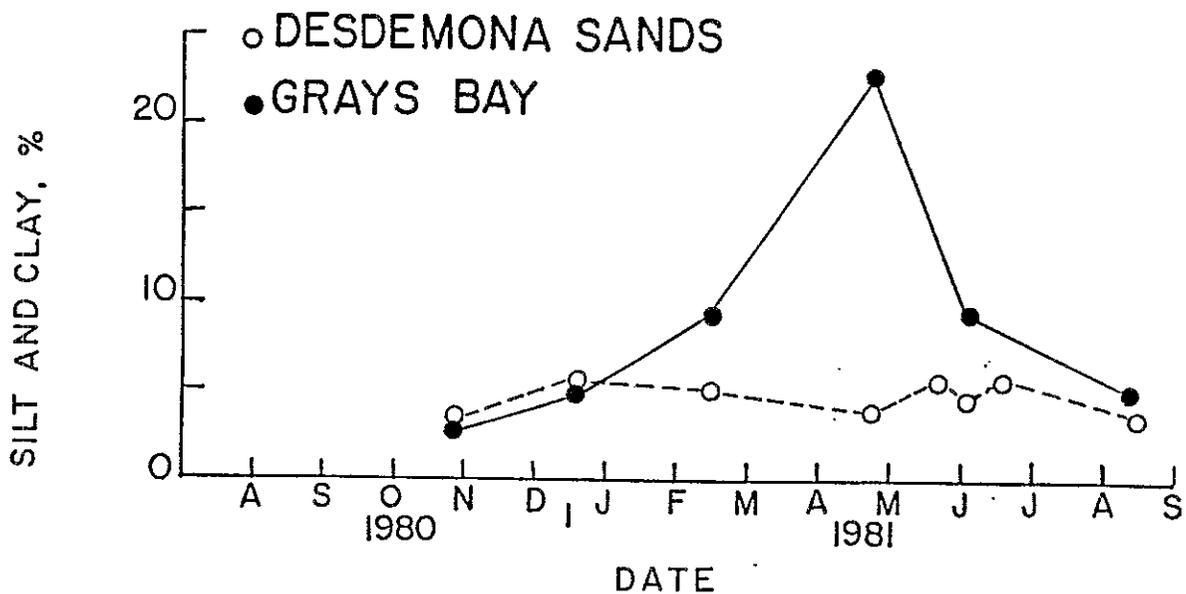


Figure 28. Percent Silt and Clay at the Grays Bay and Desdemona Sands Study Sites

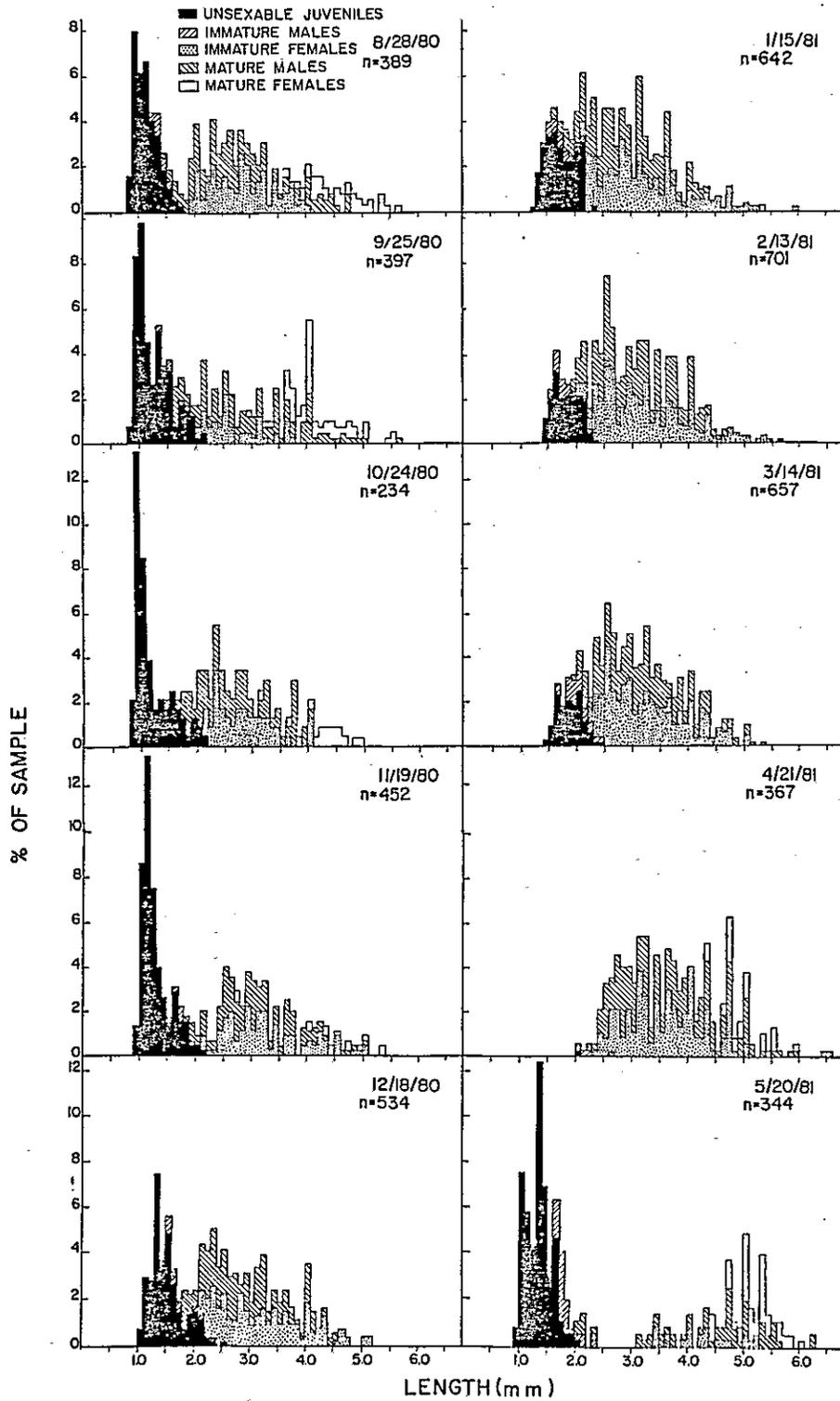


Figure 29. Percentage Length-Frequency Histograms for Corophium salmonis from the Grays Bay Study Site

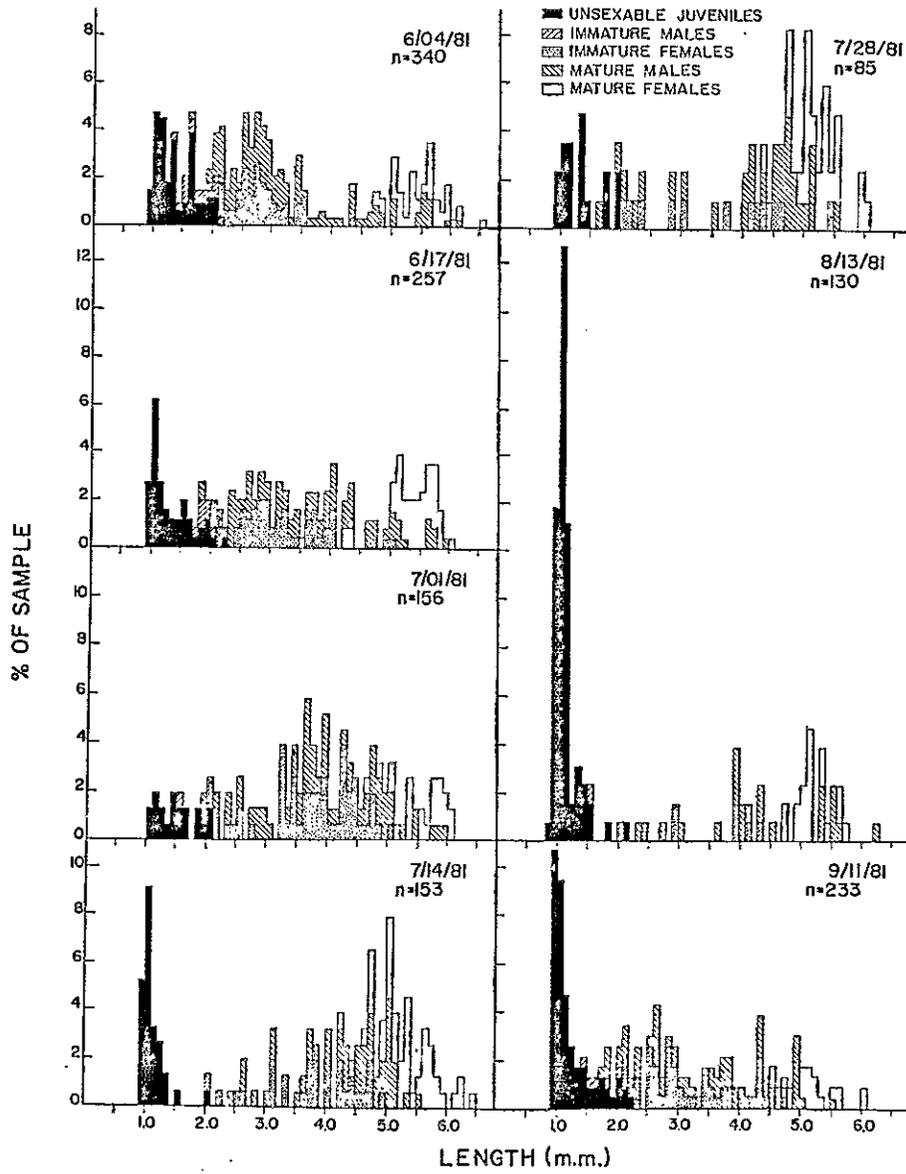


Figure 29. (cont.)

fall became immatures. At this time, the population was dominated by early adults and later stage immatures.

In May 1981, a second peak of juveniles, the spring generation, appeared resulting in a population having two distinguishable cohorts, juveniles and adults, with some late stage immatures also present. As indicated by Figure 29, the juveniles increased in length throughout the summer and matured to adults by August. The appearance of juveniles tapered off in June 1981 and was low until August when another peak of juveniles appeared to form the 1981 fall brood. The juveniles produced between the spring and fall were from the previous year's late fall brood. These data indicate that the C. salmonis at Grays Bay produced two main generations per year, one in the spring and the other in the fall.

The length-frequency histograms for Desdemona Sands (Figure 30) document the same two generation per year reproductive cycle found at Grays Bay. However, the pattern of animal residence was very different from that at Grays Bay. A fall brood began appearing in August 1980 as it had at Grays Bay. However, instead of continuing into the fall the population, which consisted mainly of juveniles, early immatures and a few small adult males, disappeared in September 1980. No animals were captured on any of the seven sampling trips from October 1980 to April 1981. The population which reappeared in April 1981 was composed entirely of adults and older immatures, a structure similar to that of Grays Bay. Similar to Grays Bay, reproduction began again in May 1981 with a large pulse of juveniles. Juveniles of the spring cohort increased in length throughout the summer becoming the breeding adults in July. The breeding females produced a fall brood in late July and continued reproduction until sampling ended in September 1981.

Figure 31, which illustrates the percent gravid females of total females, shows that the Grays Bay population contained increased percentages of breeding females in May and again in August 1981, corresponding to the spring and fall reproductive seasons. Fall and spring increases also occurred at Desdemona Sands.

Throughout the study the average size of males was smaller than that of females at both sites. The maximum size of males at Desdemona Sands was 5.4 mm and at Grays Bay was 6.2 mm. The maximum female size at Desdemona Sands was 6.6 mm and at Grays Bay was 6.5 mm. In addition to these apparent differences in maximum size, differences in average size may have been influenced by differences in the size at which the two sexes could be indentified. C. salmonis juveniles initially all have females type second antennae (Davis 1978). Females are identified when oostegites are formed while males are identified when the spines on the second antennae begin to form the characteristic male hook. As a result, males are identifiable at a smaller size than females, approximately 1.5 to 2.0 mm, as compared to 2.0 to 2.5 mm for females. Some juveniles were as small as 0.8 mm but most were 1.0 mm or greater in length.

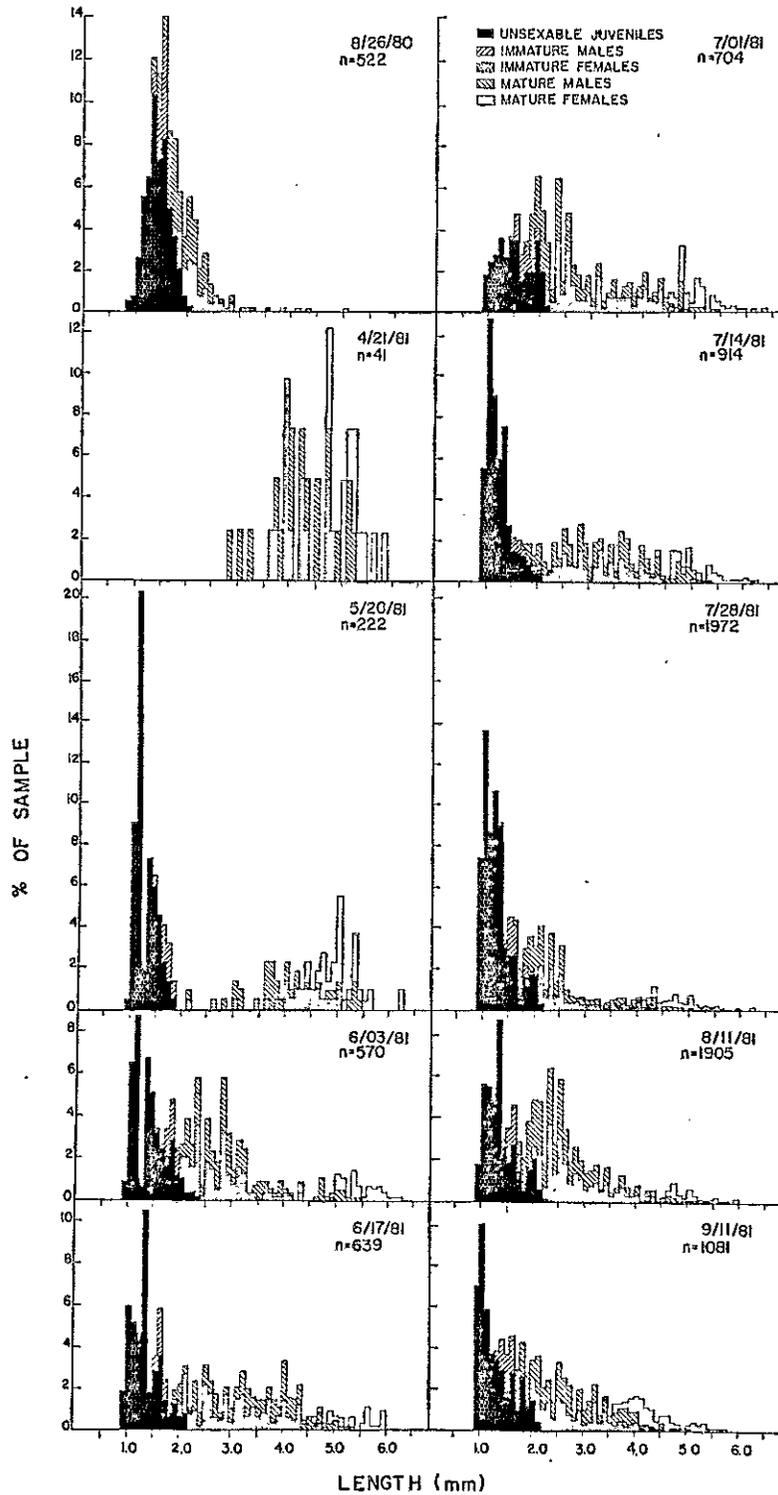


Figure 30. Percentage Length-Frequency Histograms for Corophium salmonis from the Desdemona Sands Study Site

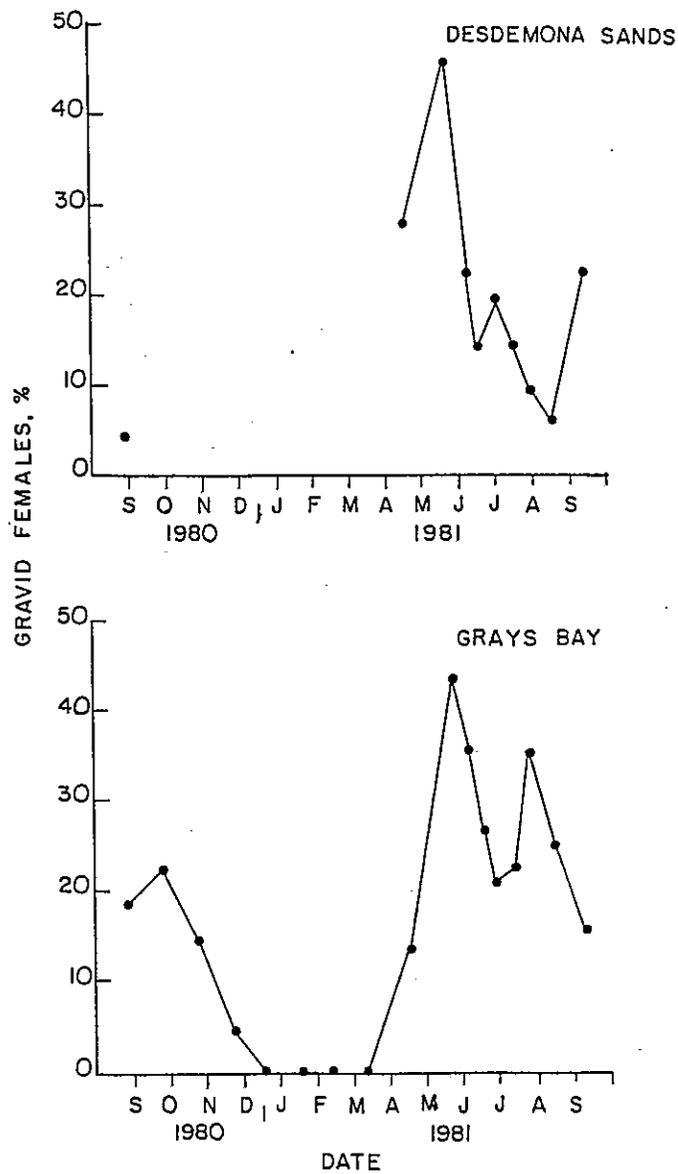


Figure 31. The Number of Gravid Corophium salmonis Females as a Percentage of the Total Female Population at the Grays Bay and Desdemona Sands Study Sites

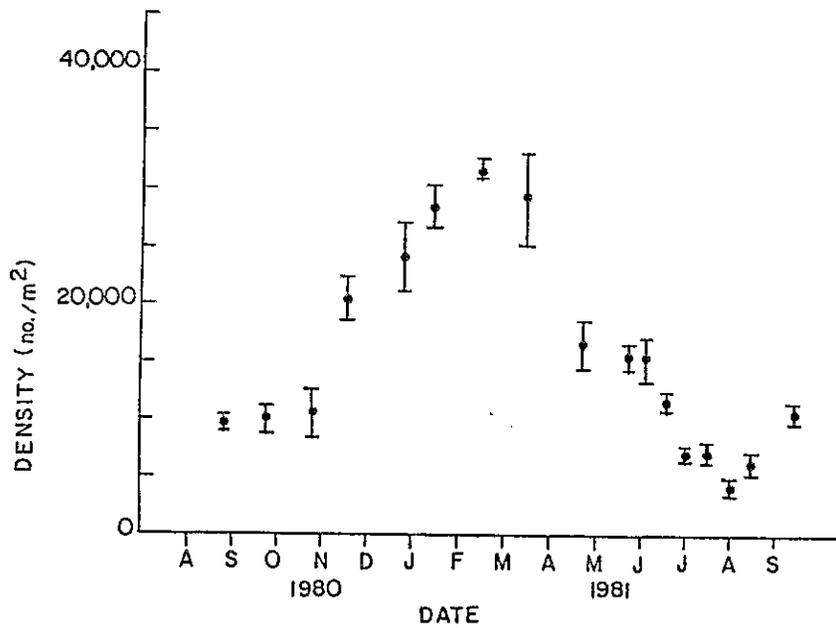


Figure 32. Density of Corophium salmonis at the Grays Bay Study Site. Brackets Indicate Standard Error.

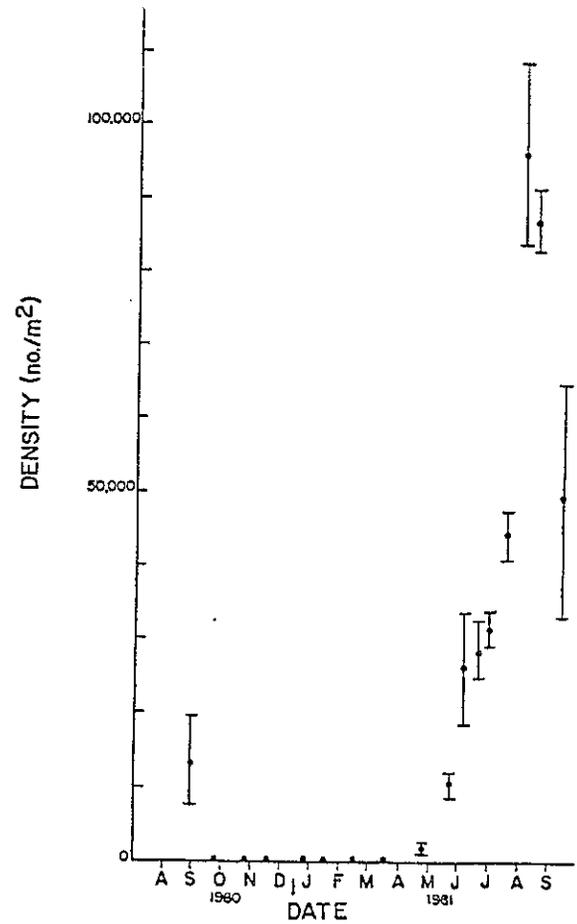


Figure 33. Density of Corophium salmonis at the Desdemona Sands Study Site. Brackets Indicate Standard Error.

### 3.3.3 Density of Corophium salmonis

Mean densities were calculated for each date at both sites (Figures 32 and 33). Density at Grays Bay increased steadily through the winter of 1980-1981 from 9,741/m<sup>2</sup> in August 1980 to a high of 31,754/m<sup>2</sup> in February 1981. Density then declined through the spring and summer to a low of 4,122/m<sup>2</sup> on July 28, 1981. The subsequent increase in the fall followed the pattern exhibited during the previous year. Length-frequency histograms based on absolute density (Figure 34) indicate that the density increase which began in December 1980 and continued through the winter was not due to recruitment of juveniles, but was due to the immigration of adults and immatures into the population.

Density decreased in March and April 1981 during a period of no reproduction. This strongly suggests the disappearance of adults and immatures. In contrast, during the spring reproductive period, density neither decreased nor increased significantly. Since juveniles appeared during this season without a corresponding increase in total density, it may be assumed that a loss of adults or immatures from the population occurred. The rise in density observed in August and September 1981 appear to have been due to the production of the fall generation of juveniles, which apparently exceeded the loss of older animals.

The seasonal density pattern at Desdemona Sands differed from that at Grays Bay (Figure 35). The Desdemona Sands population disappeared in September 1980 and reappeared in April 1981. Density increased throughout the summer to a peak density of 96,096/m<sup>2</sup> in August 1981, the highest level observed in this study. When Corophium salmonis reappeared in April, the population was composed of adults and late stage immatures. The increase in density through the summer appears to have been due mainly to recruitment of juveniles into the population from both the spring and the fall generations. The decline in density that occurred in September 1981 resulted from a loss of immatures or adults from the population. Non-quantitative field observations conducted in October 1981 indicated that the population had again disappeared as during the previous fall.

A one way analysis of variance was conducted to test density differences across sampling dates (Table 19). The seasonal effect was found to be highly significant, indicating that the mean densities changed significantly over the sampling periods at both sites.

### 3.3.4 Life History Characteristics of Corophium salmonis

The sex ratio (M/F) of the Grays Bay population remained near 1.0 throughout the year until early summer 1981 (Figure 36). In mid June 1981 the ratio dropped below 1.0 where it remained the rest of the study. A Chi Square test (Table 20) showed that only two of the sample sets (June 17, 1981 and July 14, 1981) had sex ratios that significantly differed from 1.0. In both cases females outnumbered males.

For Desdemona Sands, Chi Square tests indicated that the sex ratio was significantly different from 1.0 on August 26, 1980 and on three

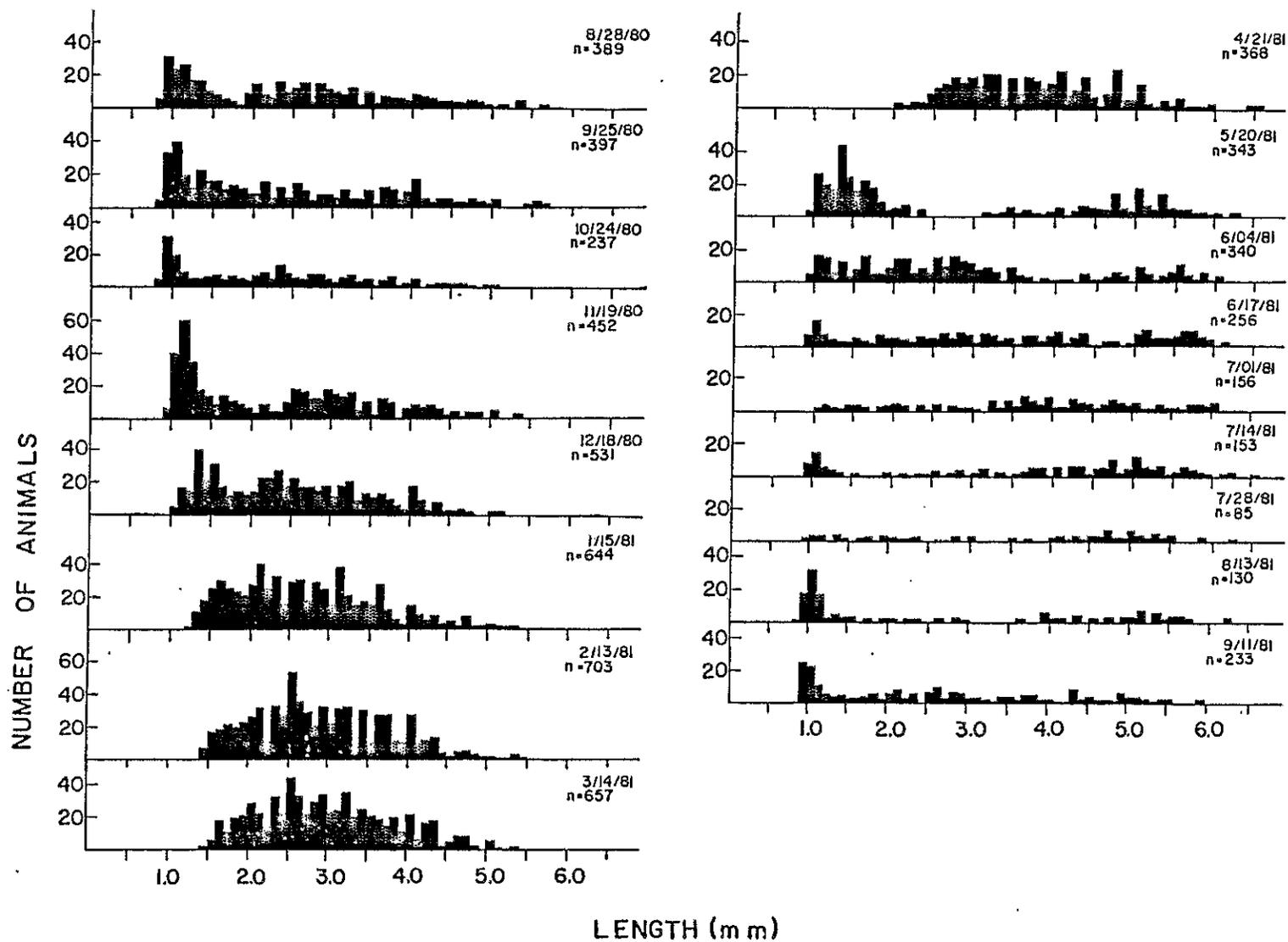


Figure 34. Absolute Length-Frequency Histograms for *Corophium salmonis* from the Grays Bay Study Site

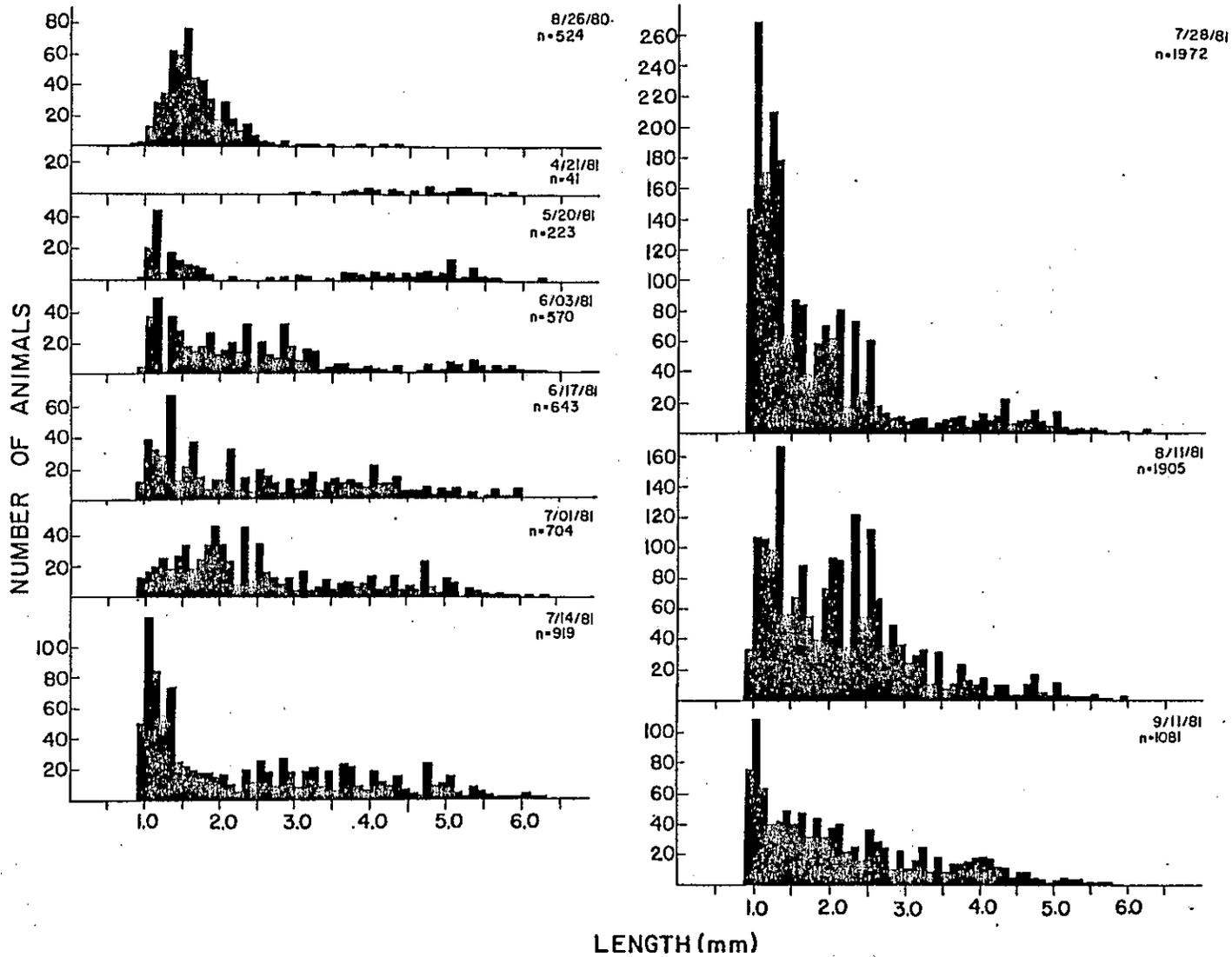


Figure 35. Absolute Length-Frequency Histograms for *Corophium salmonis* from the Desdemona Sands Study Site

Table 19. Analysis of Variance of Seasonal Changes in Corophium salmonis Density at the Grays Bay and Desdemona Sands Study Sites

GRAYS BAY

Source	MS	ANOVA d.f.	F	p
Date	$3.77 \times 10^8$	16	23.89	.005
Error	$1.57 \times 10^7$	68		

C.V. = 26.16%

DESEMONA SANDS

Source	MS	ANOVA d.f.	F	p
Date	$4.71 \times 10^9$	16	27.17	.005
Error	$1.73 \times 10^8$	68		

C.V. = 18.26%

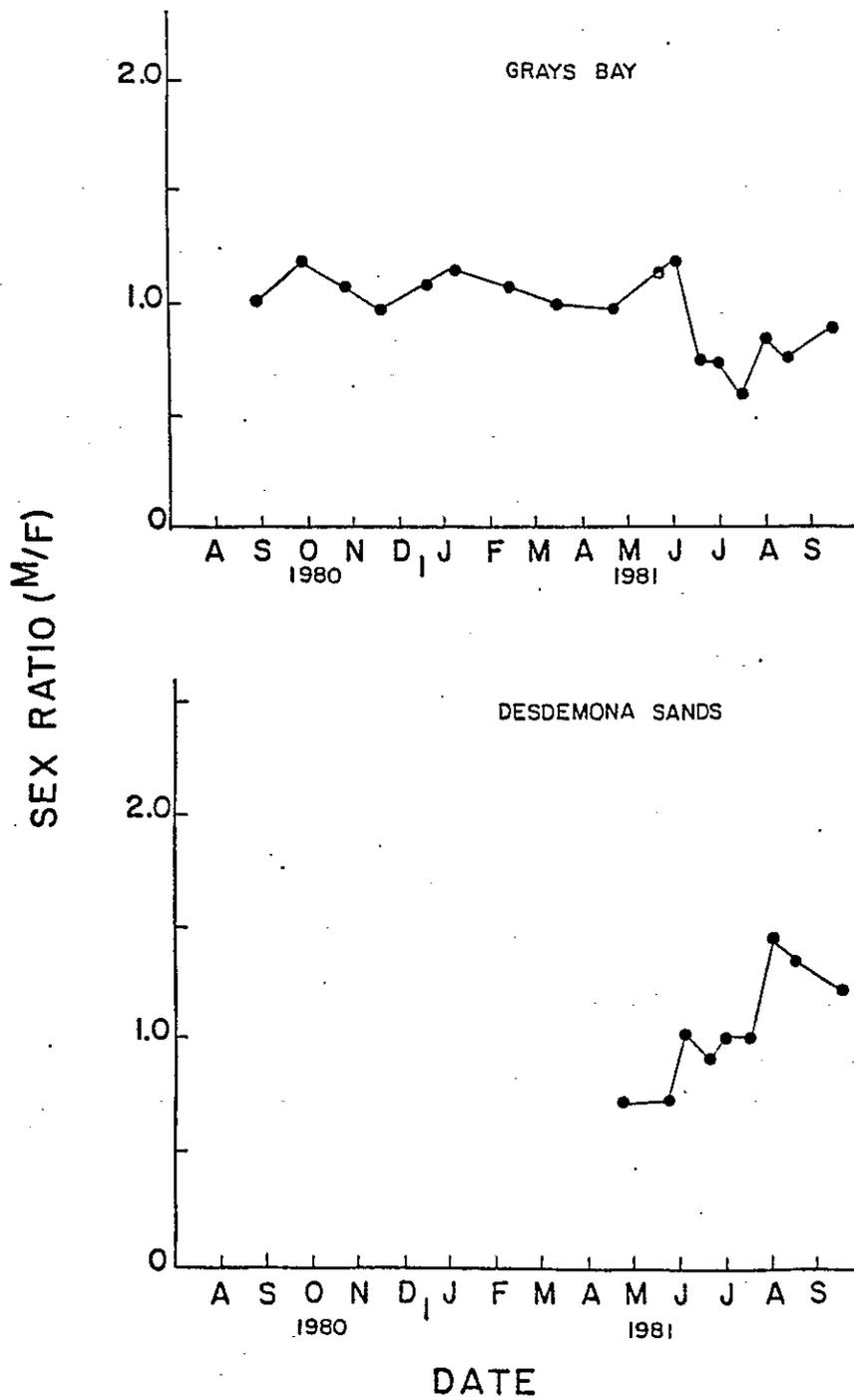


Figure 36. Seasonal Sex Ratios of Corophium salmonis at the Grays Bay and Desdemona Sands Study Sites

Table 20. Chi Square Analysis of Sex Ratios for Corophium salmonis From the Grays Bay Study Site

Date	Frequency		$\chi^2$	p	M/F
	males	females			
8-28	131	129	.015	NS	1.02
9-25	123	103	1.770	NS	1.19
10-24	72	67	.180	NS	1.07
11-19	121	123	.016	NS	.98
12-18	189	175	.539	NS	1.08
1-15	262	228	2.359	NS	1.15
2-13	310	290	.667	NS	1.07
3-14	289	291	.007	NS	.99
4-21	185	188	.024	NS	.98
5-20	94	83	.684	NS	1.13
6-04	140	118	1.876	NS	1.19
6-17	85	115	4.500	.05	.74
7-01	58	79	3.219	NS	.73
7-14	44	75	8.076	.005	.59
7-28	34	40	.486	NS	.85
8-13	21	28	1.000	NS	.75
9-11	69	77	.438	NS	.90

Table 21. Chi Square Analysis of Sex Ratios for Corophium salmonis From the Desdemona Sands Study Site

Date	Frequency		$\chi^2$	p	M/F
	males	females			
8-26	176	73	42.606	.005	2.41
4-21	18	25	1.140	NS	.72
5-20	45	61	2.415	NS	.74
6-03	168	163	.076	NS	1.03
6-17	182	198	.674	NS	.92
7-01	254	228	1.403	NS	1.11
7-14	240	231	.172	NS	1.04
7-28	421	290	24.136	.005	1.45
8-11	648	479	25.343	.005	1.35
9-11	331	270	6.191	.025	1.23

dates the following summer (July 28, August 11 and September 11, 1981 (Table 21). In these cases, however, males outnumbered females.

Mean brood sizes were calculated separately for females with eggs and females with embryos. At Grays Bay, 76 females with intact egg broods were collected over the 12 month sampling period. These animals had a mean brood size of 14.17 (Table 22). Only 7 intact embryo brood pouches were found and these averaged 4.00 embryos and ranged from 2 to 6 embryos. At Desdemona Sands, 85 intact egg broods averaged 16.10 eggs while 12 intact embryo brood pouches had a mean of 6.83 embryos and a range of 1 to 13 embryos. A Z test was used to test the difference between two population means with large sample sizes (McClave and Dietrich 1979). The Z test indicated that mean egg brood sizes at the two sites differed significantly, with Desdemona Sands having larger broods than Grays Bay (Table 22). A similar test was not done for mean embryo brood size due to the small sample sizes and the difficulty in judging whether or not these broods were intact.

The average length of all mature females (both gravid and nongravid) is presented for each site in Table 23. At Grays Bay a total of 435 mature females were collected. These had a mean length of 5.03 mm. At Desdemona Sands 514 mature females averaged 4.90 mm in length. A Z test found the mean length of the Grays Bay females to be significantly higher than that of the Desdemona Sands females (Table 23), although the difference (0.13 mm) was small.

Mean brood size and mean length of gravid females were calculated for each site (Figure 37). A one way analysis of variance with date was conducted for both brood size and length of gravid female for each site. Length and brood size both varied significantly over sampling date at both Desdemona Sands and Grays Bay (Tables 24 and 25).

To determine if the patterns of change in reproductive state could be related to seasonal effects, the data were subjected to decomposition of the sum of squares which allowed testing of differences within and between the major reproductive seasons (Table 26). For this analysis, the sampling dates were divided into spring and fall groups, corresponding to the two reproductive peaks observed. At Grays Bay there was an initial fall appearance of juveniles followed by a spring and a second fall pulse of juveniles. The decomposition of brood size sum of squares according to season at Grays Bay indicated that the brood size within each of the reproductive periods (fall 1980, spring 1981 and fall 1981) varied significantly by date at the 0.05 level. Additionally, brood size varied significantly at the 0.05 level between the fall 1980, spring 1981 and fall 1981 groups, with the spring 1981 broods being generally larger than either the fall 1980 or the fall 1981 groups. A similar pattern was observed for the lengths of mature females at Grays Bay except that the lengths within the fall 1981 group were not significantly different at the 0.05 level by date (Table 27). However, the lengths differed within both the fall 1980 and the spring 1981 groups. A significant difference at the 0.05 level also existed between the spring 1981 group and the fall 1980 and fall 1981 groups. The spring 1981 and fall 1981 females were generally larger than the fall 1980 females. Spring 1981 females were only slightly larger than the fall 1981 females.

Table 22. Summary of Statistical Analysis  
of Corophium salmonis Brood Size

MEAN BROOD SIZE FOR GRAYS BAY.			
Type	$\bar{x}$	S	n
egg	14.17	5.449	76
embryo	4.00	1.915	7

MEAN BROOD SIZE FOR DESDEMONA SANDS			
Type	$\bar{x}$	S	n
egg	16.10	5.613	85
embryo	6.83	3.589	12

RESULTS OF Z TEST FOR MEAN BROOD SIZE BETWEEN DESDEMONA SANDS AND GRAYS BAY (BROODS CONTAINING EGGS).	
Z	P
-2.216	>.05

Table 23. Summary of Statistical Analysis  
of Corophium salmonis Gravid  
Female Length

Site	$\bar{x}$	S	n
Grays Bay	5.03	.64	435
Desdemona Sands	4.90	.58	514

RESULTS OF Z TEST FOR MEAN LENGTH BETWEEN DESDEMONA SANDS AND GRAYS BAY.	
Z	P
3.338	<.05

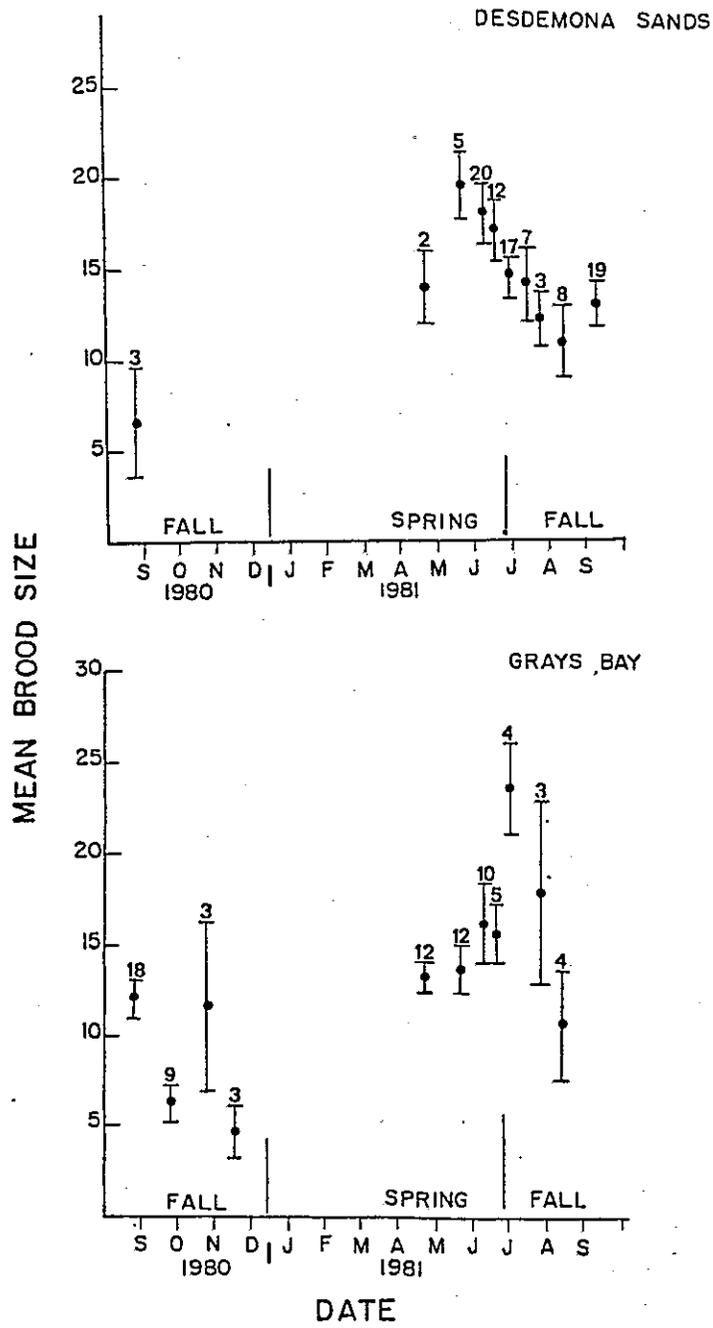


Figure 37. Mean Brood Size of *Corophium salmonis* at the Grays Bay and Desdemona Sands Study Sites. Brackets Indicate Standard Error. Numbers Indicate Number of Broods Examined.

Table 24. Results of Analysis of Variance on Brood Size and on Mature Female Length of Corophium salmonis Collected From the Grays Bay Study Site

BROOD SIZE

Source	MSE	ANOVA d.f.	F	P
Date	135.24	10	5.77	<.05
Error	23.43	71		

C.V. = 37.09%

MATURE FEMALE LENGTH

Source	MSE	ANOVA d.f.	F	P
Date	1.92	10	10.67	<.05
Error	.18	70		

C.V. = 8.54%

Table 25. Results of Analysis of Variance on Brood Size and on Mature Female Length of Corophium salmonis Collected From the Desdemona Sands Study Site

BROOD SIZE

Source	MSE	ANOVA d.f.	F	P
Date	87.61	8	2.45	<.05
Error	35.76	85		

C.V. = 38.97%

MATURE FEMALE LENGTH

Source	MSE	ANOVA d.f.	F	P
Date	2.30	8	9.82	<.05
Error	.23	84		

C.V. = 9.68%

Table 26. Analysis of Variance for Brood Size of Corophium salmonis From the Grays Bay Study Site

Source	MSE	ANOVA d.f.	F	p
Between spring and fall	296.48	2	12.65	<.05
W/in fall 1	94.14	3	4.02	<.05
W/in spring 1	91.09	4	3.89	<.05
W/in fall 2	112.67	1	4.81	>.05
Error	23.43	71		

Table 27. Analysis of Variance For Length of Gravid Corophium salmonis Females From the Grays Bay Study Site

Source	MSE	ANOVA d.f.	F	p
Between spring and fall	7.12	2	39.56	<.05
W/in fall 1	.97	3	5.41	<.05
W/in spring 1	.49	4	2.74	>.05
W/in fall 2	.04	1	.19	>.05
Error	.18	70		

Table 28. Analysis of Variance For Brood Size of Corophium salmonis From the Desdemona Sands Study Site

Source	MSE	ANOVA d.f.	F	p
Between spring and fall	369.66	1	10.34	<.05
W/in fall	11.88	2	.33	>.05
W/in spring	61.49	5	1.72	>.05
Error	35.76	85		

Table 29. Analysis of Variance For Length of Gravid Corophium salmonis Females From the Desdemona Sands Study Site

Source	MSE	ANOVA d.f.	F	p
Between spring and fall	13.21	1	56.45	<.05
W/in fall	.67	2	2.86	>.05
W/in spring	.75	5	3.21	>.05
Error	.23	84		

Decomposition of brood size and mature female length for the Desdemona Sands data was confined to the spring 1981 and fall 1981 seasons because the fall 1980 population disappeared in September 1980. The results indicated that brood sizes did not differ significantly at the 0.05 level within the spring season or within the fall season. However, as at Grays Bay, the spring brood sizes were found to be larger than the fall brood sizes (Table 28).

Length of gravid females at Desdemona Sands did not vary significantly at the 0.05 level by date within the fall group, but varied significantly within the spring group. The values for the length of mature females for the spring were significantly different at the 0.05 level from the values for the fall mature females (Table 29). The spring females were larger than the fall females.

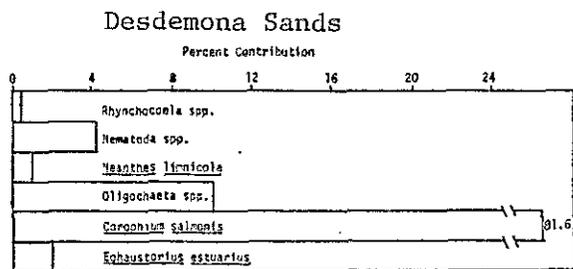
### 3.4 COROPHIUM SALMONIS COMMUNITY DYNAMICS STUDY

#### 3.4.1 Community Composition and Dynamics

On a numeric basis, Corophium salmonis dominated community composition at both Grays Bay and Desdemona Sands (Figure 38). Rhynchocoela, Nematoda, Oligochaeta and the polychaete Neanthes limnicola were also common at the two sites, which also shared such less common taxa as Turbellaria, the amphipods C. spinicorne, Monoculodes spinipes, and Eogammarus confervicolus, the mysid Neomysis mercedis, and larvae of the dipterous families Chironomidae and Heleidae. Some brackish water species were collected only at Desdemona Sands. These included the amphipod Eohaustorius estuarias, the polychaete Eteone spp., and the bivalve Macoma balthica. Oligohaline species more prevalent at or exclusive to the Grays Bay site were the bivalve Corbicula manilensis and the gastropods Fluminicola virens and Goniobasis plicifera.

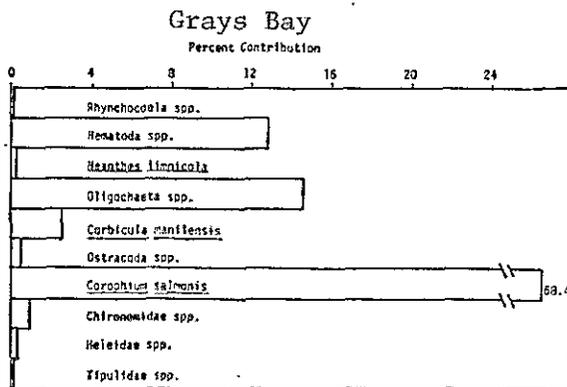
Although community composition was similar at the two sites, seasonal dynamics were quite different. Total density at Grays Bay peaked in the winter and maintained moderate levels in the summer (Figure 39). At Desdemona Sands, total density peaked in the summer and was very low through the winter. These distinctive density patterns were created primarily by Corophium salmonis (Figure 40). Analysis of the two C. salmonis populations (Section 3.3) provided evidence that these striking differences in seasonal abundance patterns were caused by spring and fall breeding peaks combined with differing migration patterns at the two sites. Emigration at the Desdemona Sands site appeared related to increased fall salinities there. This hypothesis is supported by evidence of high C. salmonis mobility (Davis 1978), and by distributional survey data (Section 3.5) which show that the density of this species generally diminishes downstream of Youngs Bay.

Two other taxa, Oligochaeta and Nematoda, followed a summer-high, winter-low pattern at both sites (Figure 40). Corbicula manilensis at Grays Bay exhibited fall and summer increases, and maintained high densities through the winter. The specimens were predominantly juveniles, and probably represented the downstream extension of this freshwater clam.



Taxa with <0.1%

- Turbellaria spp.
- Eteone spp.
- Corbicula manliensis
- Macoma balthica
- Neomysis mercedis
- Saduria entomon
- Eogammarus confervicolus
- Corophium spinicorne
- Monoculodes spinipes
- Crangon franciscorum
- Chironomidae spp.
- Heleidae spp.



Taxa with <0.1%

- Turbellaria spp.
- Fluminicola virens
- Gonfobasis pilicifera
- Acarina spp.
- Neomysis mercedis
- Gammaridae spp.
- Corophium spinicorne
- Monoculodes spinipes
- Eogammarus spp.
- Pantoporeia affinis

Figure 38. Structure of Infaunal Communities at the Grays Bay and Desdemona Sands Study Sites, Based on Average Contribution to Numeric Density

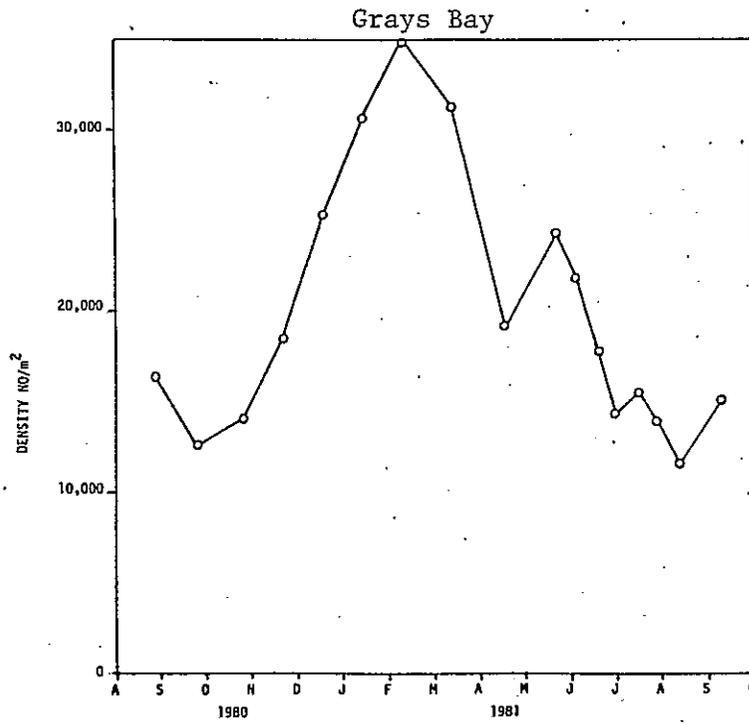
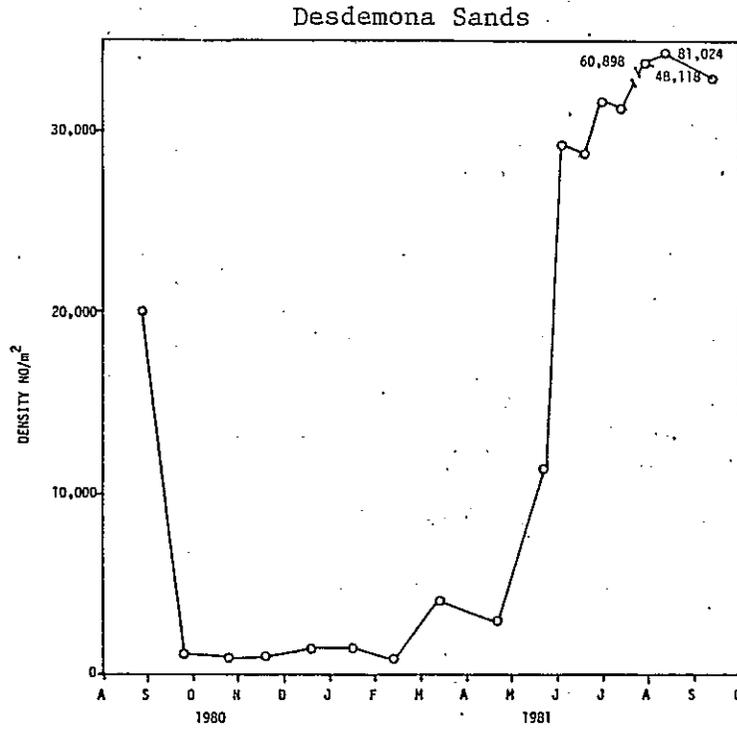


Figure 39. Seasonal Changes in Total Numeric Density of Infauna at the Grays Bay and Desdemona Sands Study Sites

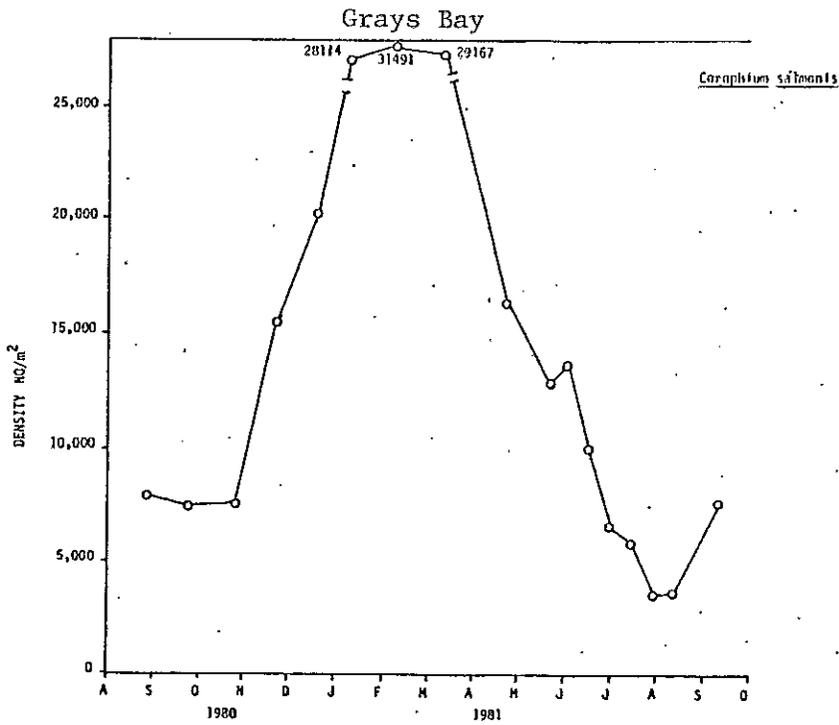
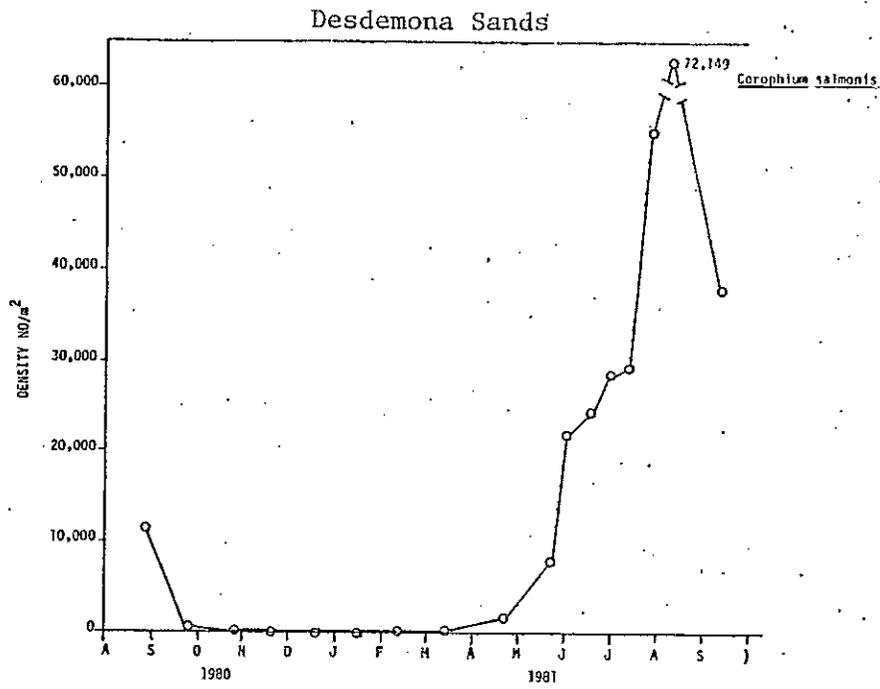


Figure 40. Seasonal Changes in Numeric Density of Dominant Taxa at the Grays Bay and Desdemona Sands Study Sites

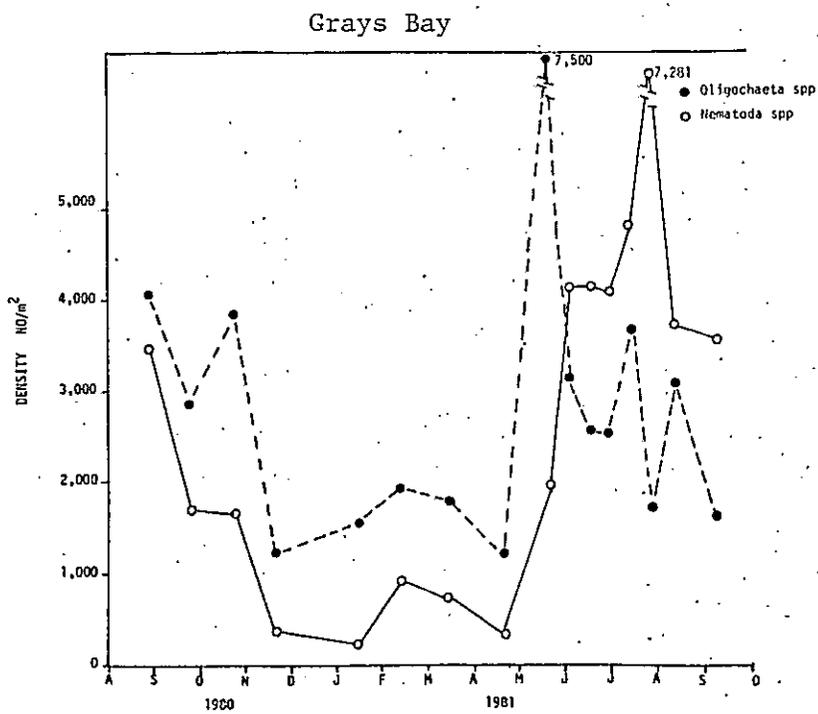
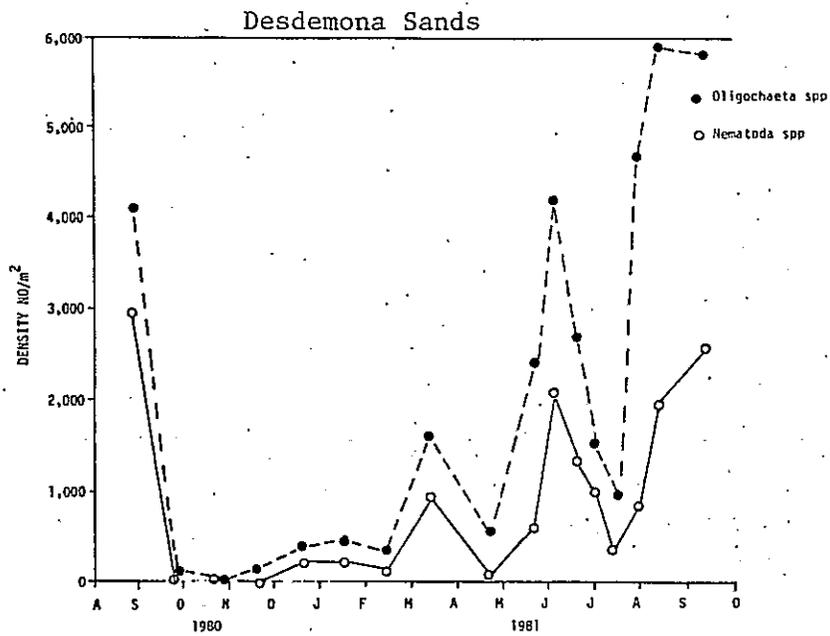
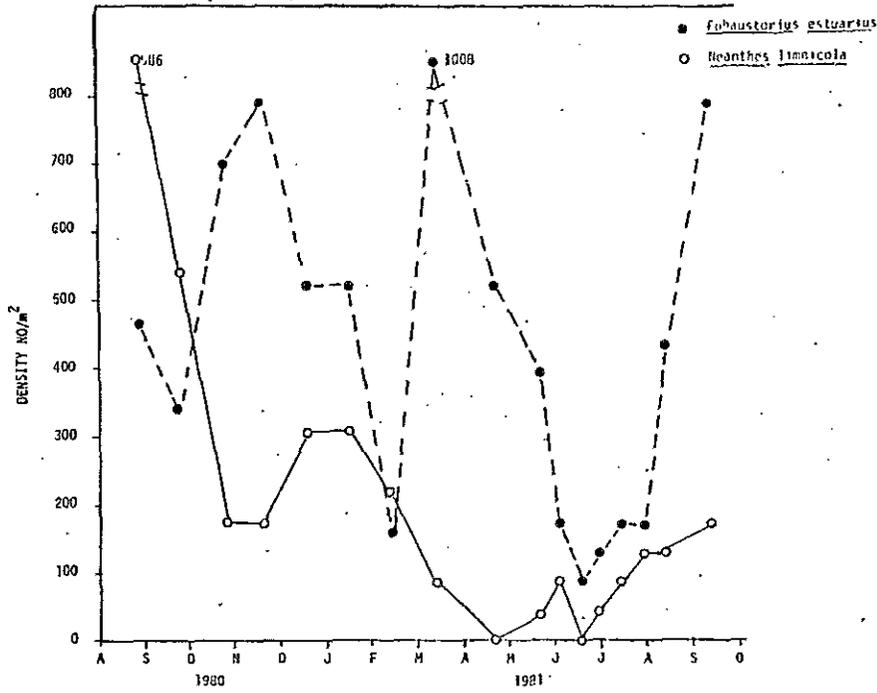


Figure 40. (cont.)

Desdemona Sands



Grays Bay

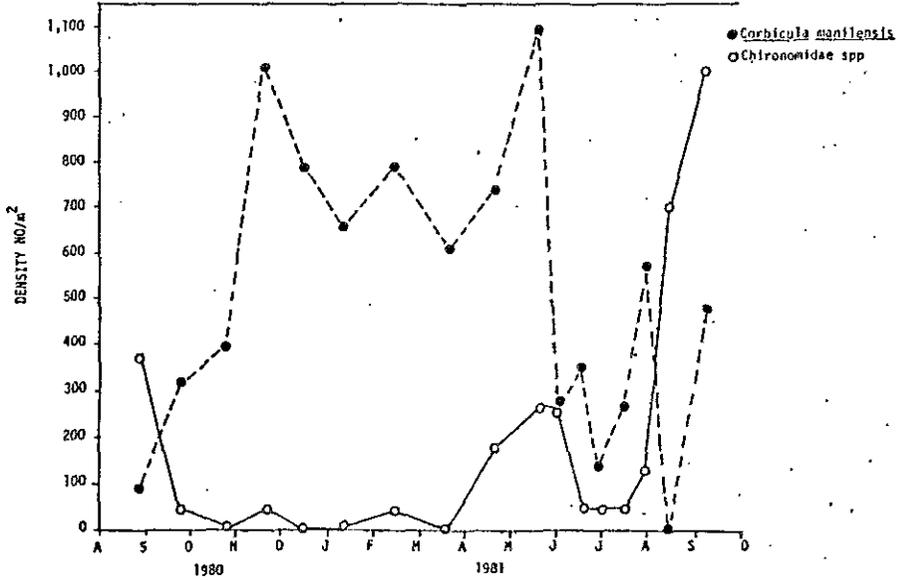


Figure 40. (cont.)

Chironomid larvae, nearly absent from the Grays Bay site during the winter, developed obvious reproductive peaks in the spring and summer.

At Desdemona Sands, Neanthes limnicola density decreased in the fall and winter, and increased again in the summer (Figure 40). This pattern was followed also at the Baker Bay site (Section 3.2), and presumably resulted from winter mortality and summer reproduction events. Eohaustorius estuarias densities, on the other hand, were highly variable, as has been found at other sites in the estuary (authors' data). Probably, this amphipod's density changes arose more from its high mobility than from life history events.

#### 3.4.2 Corophium salmonis Production and Biomass

Weight-length analyses for C. salmonis are summarized in Figure 41. The four regression lines (based on log transformed data) show that animals of a given length appeared heavier in the spring and summer than in than fall and winter. This was probably caused by the greater frequency of egg and young bearing by females during the warmer months. A test of equality according to the procedure of Neter and Wasserman (1974) showed the regression lines to differ at the 0.05 level (Table 30). The reduced model was therefore rejected in favor of the four separate equations, which were applied on seasonal basis in making length to weight conversions.

Results of regression of live weight on length are also presented in Figure 41 and Table 30. For a 4 mm animal, preserved weight (in January 1981) was about 60% of the live weight. Since slopes differed between the two regression lines, the percentage difference varied somewhat with length, smaller animals apparently losing more weight and larger animals less weight than indicated by the 60% value.

Length-frequency histograms (Figures 34 and 35) illustrate the alternation of spring and fall broods described in Section 3.3, although it is also apparent that considerable reproductive overlap occurred in the intervening summer period. The spring and fall broods therefore represent peaks of reproductive activity and were not entirely distinct cohorts.

The clearest example of a cohort was the appearance of the spring brood on May 20, 1981 at both Grays Bay and Desdemona Sands (Figures 34 and 35). It will be noted that C. salmonis was absent from the Desdemona Sands site during the winter months, and that the appearance there of the spring brood was preceded by the immigration of maturing adults. The spring broods at both sites were tracked in terms of median animal length, and the resulting length changes converted to relative growth rates by weight for the period May 20, 1981 to August 3, 1981 (Grays Bay) and the period May 20, 1981 to July 13, 1981 (Desdemona Sands). This procedure provided growth rates for a series of animal sizes. These rates are plotted in Figure 42, and separate curves have been fitted by eye for each site. Because the calculated growth rates do not provide information about very small animals, it was necessary to estimate these rates based on data for C. insidiosum and C. volutator provided in Birklund (1977), who measured growth in natural populations and in artificial

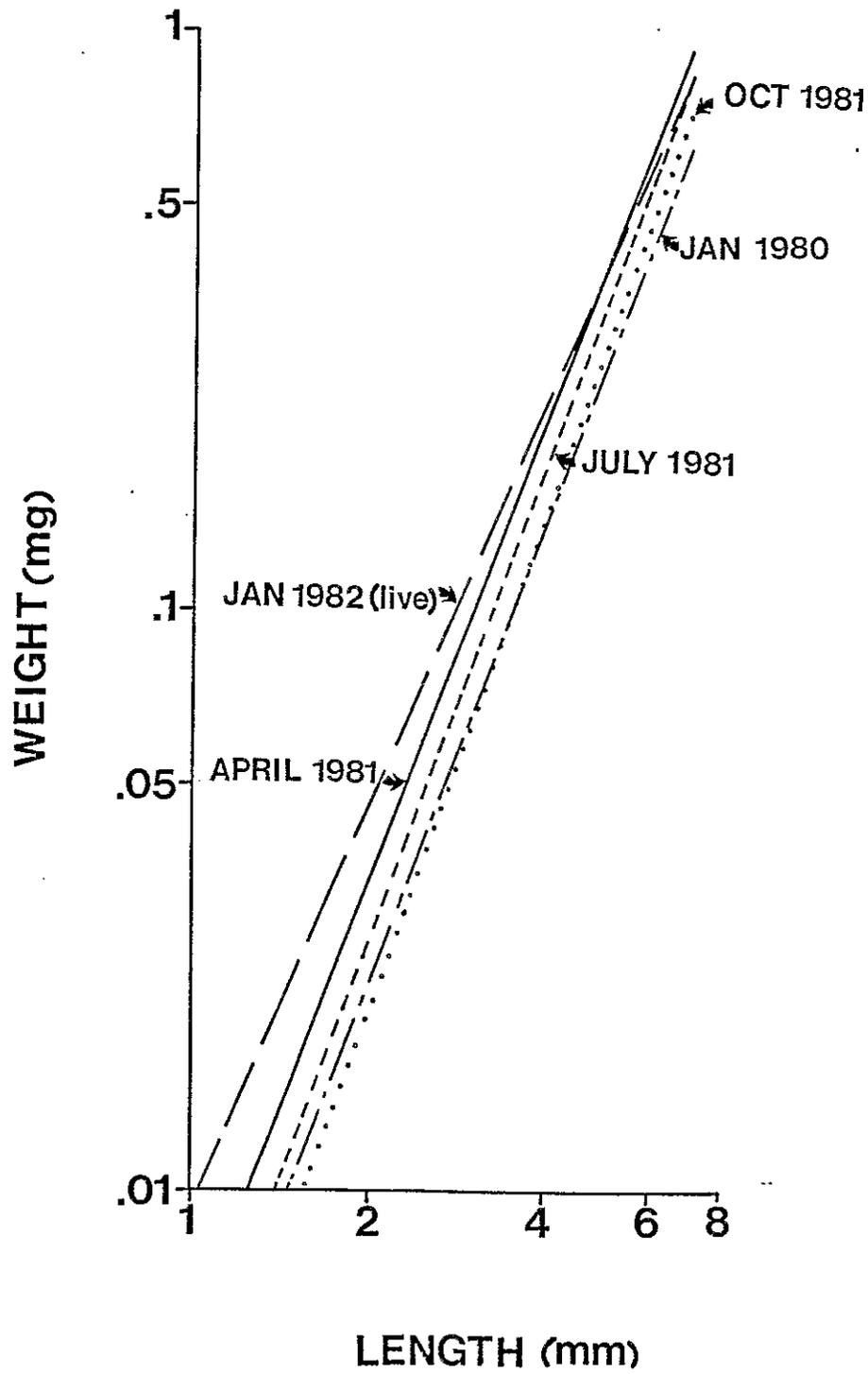


Figure 41. Length-Weight (mg AFDW) Relationships for Preserved and Live Corophium salmonis

Table 30. Regression Equations Relating Length to Weight in Preserved and Live Corophium salmonis. X = Log<sub>10</sub> Length (mm); Y = Log<sub>10</sub> Weight (mg AFDW). Statistical Analysis of the Four Preserved Weight Regressions is Included.

<u>Date</u>	<u>Regression equation</u>	<u>R<sup>2</sup></u>	<u>n</u>
1) October 1980	y = 2.834 x -2.533	0.970	13
2) January 1981	y = 2.658 x -2.463	0.964	13
3) April 1981	y = 2.693 x -2.285	0.980	18
4) July 1981	y = 2.783 x -2.427	0.902	18
5) Reduced model (all dates)	y = 2.289 x -2.495	0.939	62
6) January 1982 (live)	y = 2.315 x -2.037	0.863	15

Statistical analysis of preserved weight regressions:

<u>SSE (reduced model)</u>	<u>SSE (full model)</u>	<u>d.f.</u>	<u>F</u>	<u>Significance</u>
1.119	1.435	4,54	2.586	Differs at 0.05 level

Table 31. Mean Biomass (mg AFDW/m<sup>2</sup>), Production (mg AFDW/m<sup>2</sup>/yr) and Production:Biomass Ratios for Corophium salmonis at the Grays Bay and Desdemona Sands Study Sites.

	Annual			April 21, 1981 to September 11, 1981		
	Mean Biomass	Production	P:B Ratio	Mean Biomass	Production	P:B Ratio
Grays Bay	1,498	8,228	5.49	1,555	4,248	2.73
Desdemona Sands	1,070	13,150	12.29	2,566	13,150	5.12

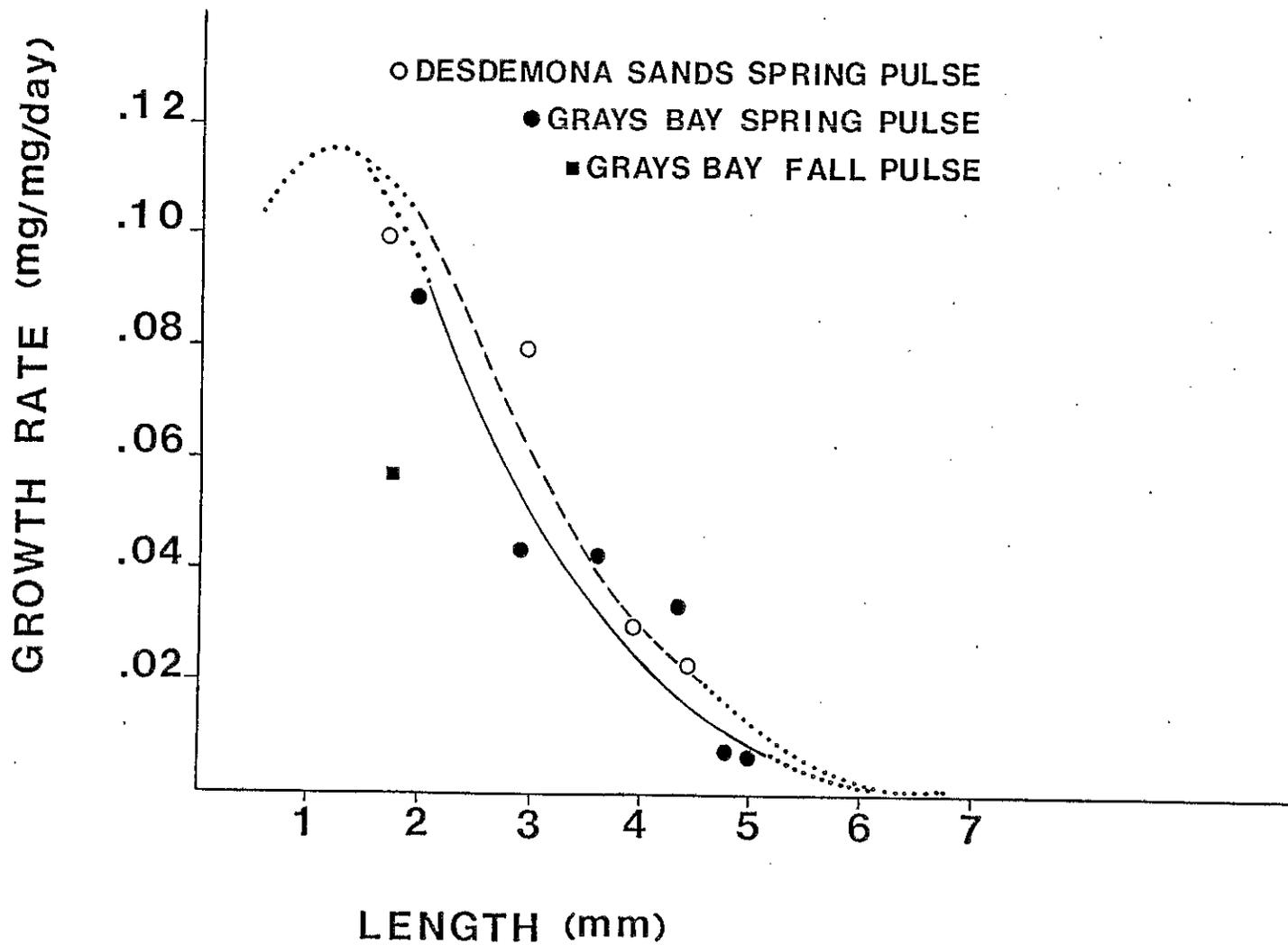


Figure 42. The Relation of Relative Growth Rate to Length of Corophium salmonis. Growth was measured as the Change in Weight of the Median Length Animal Between Successive Sampling Dates.

cohorts isolated in in situ growth cages. His growth curves show relative growth peaking at 1 to 2 mm length, and this was the basis for the extension of the curves in Figure 42 for very small animals. Birklund's growth data, and those of Albright and Armstrong (1982) for C. salmonis in Grays Harbor, show strong similarities to those developed for C. salmonis in the Columbia River Estuary, and lend credibility to the use of the present data in making production estimates.

Size-specific growth rates extracted from the curves in Figure 42 were applied in the calculation of Grays Bay production for the September 25, 1980 to October 14, 1980 interval and for the May 20, 1981 to September 11, 1981 interval. Thus spring brood growth rates were used in calculating portions of both spring and fall production rates. This was justified on the basis that temperatures exceeded 10°C in both periods (Figure 26), and that growth was apparent in the histograms (Figures 34 and 35). However, it is possible that the spring brood growth rates exceeded fall brood growth rates (a single fall brood growth rate was calculated and is plotted in Figure 42), and that this elevated production rates. Spring brood growth rates at Desdemona Sands were used for all production calculations at that site (April 21, 1981 to September 11, 1981). The cohort method of production was utilized for the Grays Bay population from October 24, 1981 to May 29, 1981.

For both sites annual production was considered to be that occurring between September 25, 1980 and September 11, 1981, so that the August 26, 1980 data were omitted from the calculations. Total production by C. salmonis was highest at Desdemona Sands, where 13,150 mg AFDW/m<sup>2</sup> were produced during the year (Table 31). At Grays Bay, 8,228 mg AFDW/m<sup>2</sup> were produced. The temporal distribution of the production varied greatly between the two sites, a large portion occurring before April at Grays Bay, and none occurring before April at Desdemona Sands (Figure 43). This pattern was established by the population density of C. salmonis, which provided a substantial winter time population at the Grays Bay site but was absent at the Desdemona Sands site (Figure 44). The increase of animals at Grays Bay greatly enhanced the overwintering population there, which was largely composed of adults and subadults. Slow growth within this population during winter and early spring resulted in about half of the annual production at this site. Summer production was low due to diminished population density.

At Desdemona Sands, production was necessarily limited to the spring-summer period, following immigration and recruitment. The production pattern (Figure 43) and biomass pattern (Figure 44) for this site are a clear example of colonization and exploitation of a seasonally available habitat.

The differences between the two sites in seasonal production and biomass patterns are reflected in production:mean biomass (P:B) ratios (Table 31). Based on annual values, P:B was 5.49 for Grays Bay and 12.29 for Desdemona Sands. The high Desdemona Sands ratio derived both from low biomass values during much of the year (zero during the winter) and high spring-summer production by the developing C. salmonis colony. If only the period of population residence (April to September) is consid-

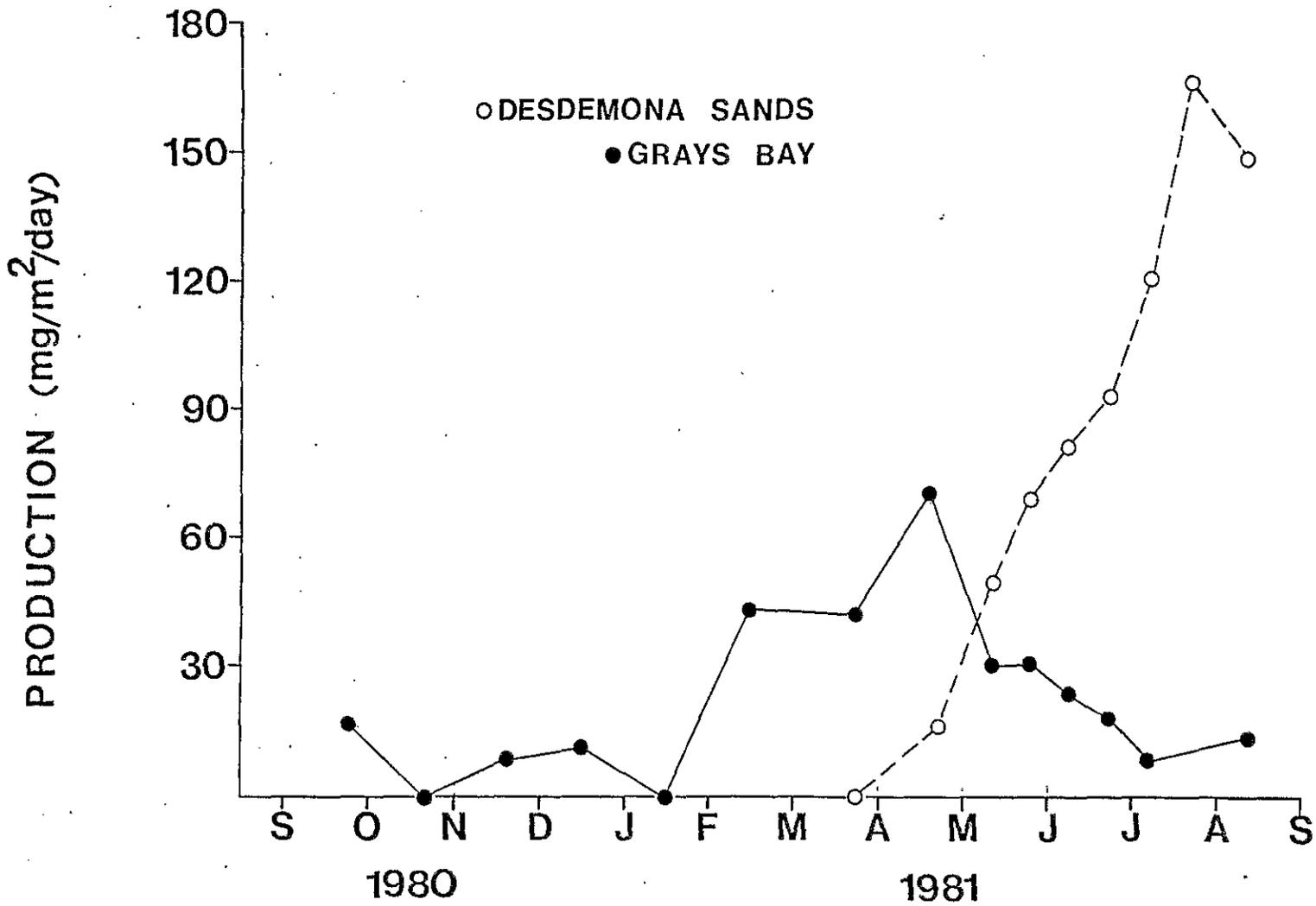


Figure 43. Seasonal Changes in Production Rate of Corophium salmonis

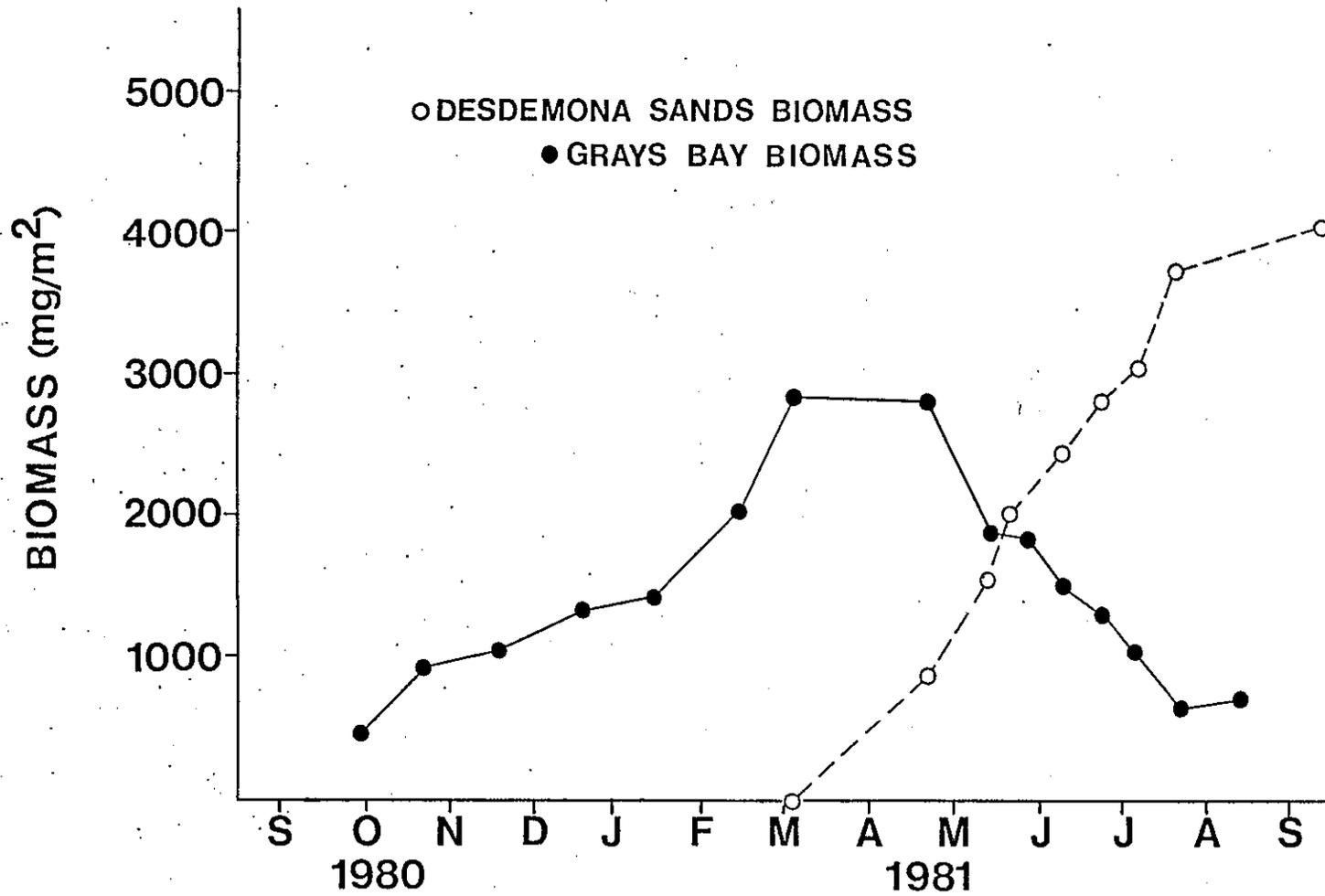


Figure 44. Seasonal Changes in Weight Density of Corophium salmonis

Table 32. Mean Annual Biomass (mg AFDW/m<sup>2</sup>) and Production Rate (mg AFDW/m<sup>2</sup>/yr) for Lesser Taxa at the Grays Bay and Desdemona Sands Study Sites. Production:Biomass Ratios were Taken from Banse and Mosber's (1980) Summary.

Taxon	Grays Bay			Desdemona Sands	
	P:B	Biomass	Production	Biomass	Production
<u>Turbellaria</u>		*		*	
<u>Rhynchozoela</u>	4	1	4	*	
<u>Eteone spp.</u>				*	
<u>Neanthes limnicola</u>	4	1	4	36	144
<u>Oligochaeta</u>	4	171	684	25	100
<u>Fluminicola virens</u>	4	7	28		
<u>Gonoibasis plicifera</u>	4	9	36		
<u>Corbicula manilensis</u>	1	90	90	10	10
<u>Macoma balthica</u>				*	
<u>Neomysis mercedis</u>				*	
<u>Saduria entomon</u>	5			3	15
<u>Corophium spinicorne</u>		*		*	
<u>Eogammarus confervicolus</u>		*		*	
<u>Eohaustorius estuarius</u>	5			37	185
<u>Monoculodes spinipes</u>		*		*	
<u>Pontoporeia affinis</u>		*			
<u>Crangon franciscorum</u>				*	
<u>Chironomidae</u>	2	3	6	*	
<u>Heleidae</u>		*		*	
Total		282	852	111	454

\* < 1 mg

ered, the P:B ratio drops to 5.12, very near that of the year-round Grays Bay population.

### 3.4.3 Lesser Taxa Production and Biomass

The production values for the lesser taxa (Table 32) were based on literature derived P:B ratios. An initial attempt was made to determine P:B according to the equations of Banse and Mosher (1980) which relate P:B exponentially to body size at maturity. The body size values used were maximum mean weights among the four seasonal measurements. However, the resulting P:B estimates appeared unrealistic in comparison to actual literature values for related taxa, and it was concluded that the weights employed were not accurate measures of size at maturity. Therefore, approximate P:B values were assigned, as shown in Table 32, according to the range of literature values summarized in Banse and Mosher (1980) for related taxa. The P:B values used were 4 for various worm taxa and for gastropods, 1 for bivalves, 5 for small crustaceans and 2 for dipterous larvae.

Few of the lesser taxa contributed significant amounts to either biomass or production at the two study sites. At Grays Bay, the lesser taxa together averaged about 282 mg AFDW/m<sup>2</sup> biomass and produced about 852 mg AFDW/m<sup>2</sup>/yr (Table 32). At Desdemona Sands, comparable values were 111 mg AFDW/m<sup>2</sup> and 454 mg AFDW/m<sup>2</sup>/yr. Principal contributors at Grays Bay were *Oligochaeta* and *Corbicula manilensis*, and at Desdemona Sands *Neanthes limnicola*, *Oligochaeta* and *Eohaustorius estuarius*. The greatest single contribution at 171 mg AFDW/m<sup>2</sup> biomass and 684 mg AFDW/m<sup>2</sup>/yr production were by *Oligochaeta* at Grays Bay.

## 3.5 ESTUARY-WIDE DISTRIBUTION STUDY

### 3.5.1 Sediment Properties

In the stratified random survey, the physical features of the sampling strata were represented by sediment texture and organic content. In Figure 45, means and 95% confidence limits for the silt and clay fraction (fines) are presented for each stratum. Some expected patterns appear in Figure 45, although it is clear that variation within strata was often high and that in general it would be difficult to distinguish among the means within the statistical limits commonly used.

The Unprotected Flat habitat (shoals) appeared uniform at about .7 to 10% in its fines content across the three salinity zones. The Protected Flat habitats (bays and in lee of upstream islands) contained 34 to 45% fines in the Marine and Transition Zones, but only about 8% in the Fresh Water Zone. Samples in the Fresh Water Zone were collected primarily in Grays Bay and in the island system, localities which apparently experienced stronger current regimes than expected.

The sediment character of the Minor Channel habitat was extremely variable, as expressed both in differences across zones and in the size of stratum confidence limits. The extreme condition was the Marine Zone Minor Channel habitat, which averaged the finest sediment texture sub-strata (67% fines) for strata of all types, but appeared extremely varia-

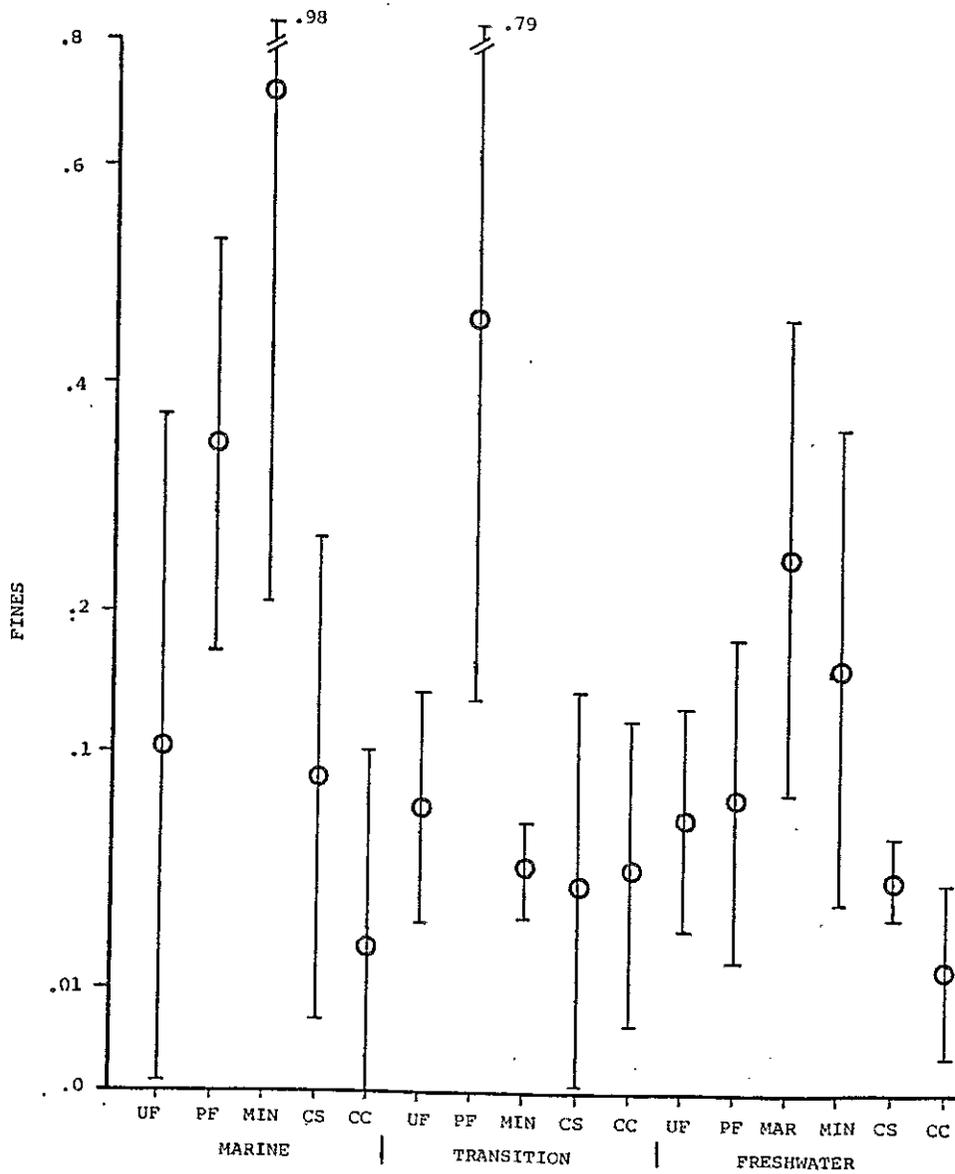


Figure 45. Means and 95% Confidence Intervals for the Fine Sediment Fraction (<0.063 mm) in the 16 Sampling Strata. Stratum Codes are: UF = Unprotected Flat, PF = Protected Flat, MAR = Marsh Channel, MIN = Minor Channel, CS = Main Channel Side, CC = Main Channel Center.

ble. This variability derived primarily from a single very low value, the remaining five values exceeding 40% fines. This habitat included small shipping channels within Baker Bay (Figure 7), and may have accumulated fine sediments following channel dredging work. The Minor Channels of the Transition Zone included both large mid-river channels and smaller channels in Youngs Bay, and averaged only 4% fines. The Fresh Water Zone Minor Channels included a variety of shallow natural channels scattered among the islands and unprotected flats, and averaged 16% fines. This habitat, then, was quite variable in its substrate character across zones.

The Main Channel Sides habitat was more uniform, averaging 4% (Fresh Water and Transition Zones) to 9% (Marine Zone) fines. This habitat included the 5.5 to 9.1-m (18 to 30-foot) depth zone bordering both the main shipping channel and the deeper portions of the down-river section of the North Channel, near Baker Bay.

Fines content of the Main Channel Center habitats generally was the lowest of all the habitats. The mean values were 2% for the Marine Zone, 4% for the Transition Zone and 1% for the Fresh Water Zone. The very low Fresh Water Zone value expresses the high velocity of water moving through the major channels of this zone due to flow confinement created by islands and narrow river width. Fines content was relatively low both in the main shipping channel and in the channel running along the Oregon side of the river through the island system.

The Marsh Channel habitat, restricted to the Fresh Water Zone, averaged 24% fines. This value would likely have been higher but for the fact that the small inner marsh channels were unaccessible by boat and were not sampled. The mean value therefore represents larger marsh channels and the entrances to small ones.

Organic content of substrate samples, measured by a combustion method, was low over most of the estuary (Figure 46). Mean stratum values ranged from 0.7 to 8.6%, although the latter figure greatly exceeded most other values. The Unprotected Flat habitat overall had the lowest organic content, averages in all three zones being 0.8 to 0.9%. The Protected Flat habitat had relatively high values in the Marine and Transition Zones (2.3%) and a moderate level in the Fresh Water Zone (1.1%). The Minor Channel habitat had the greatest range of average values, from 1.0% for the Fresh Water and Transition Zone habitats to 8.6% in the Marine Zone. As with the silt and clay fraction, organic content was quite variable but averaged very high in the Marine Zone Minor Channel habitat.

In both the Main Channel Side and Main Channel Center habitats, organic content was low, means ranging from 0.5 to 1.4%. In both habitat types, the Fresh Water Zone was represented by lower values than the two down-river zones (about 0.6% to 1.2%). This relationship and the low values generally agree with fines content data for these habitats in supporting the expected result that strong river currents remove light sediments from the main river channels. The Unprotected Flat habitats also exhibited this influence in their low fines and organics levels.

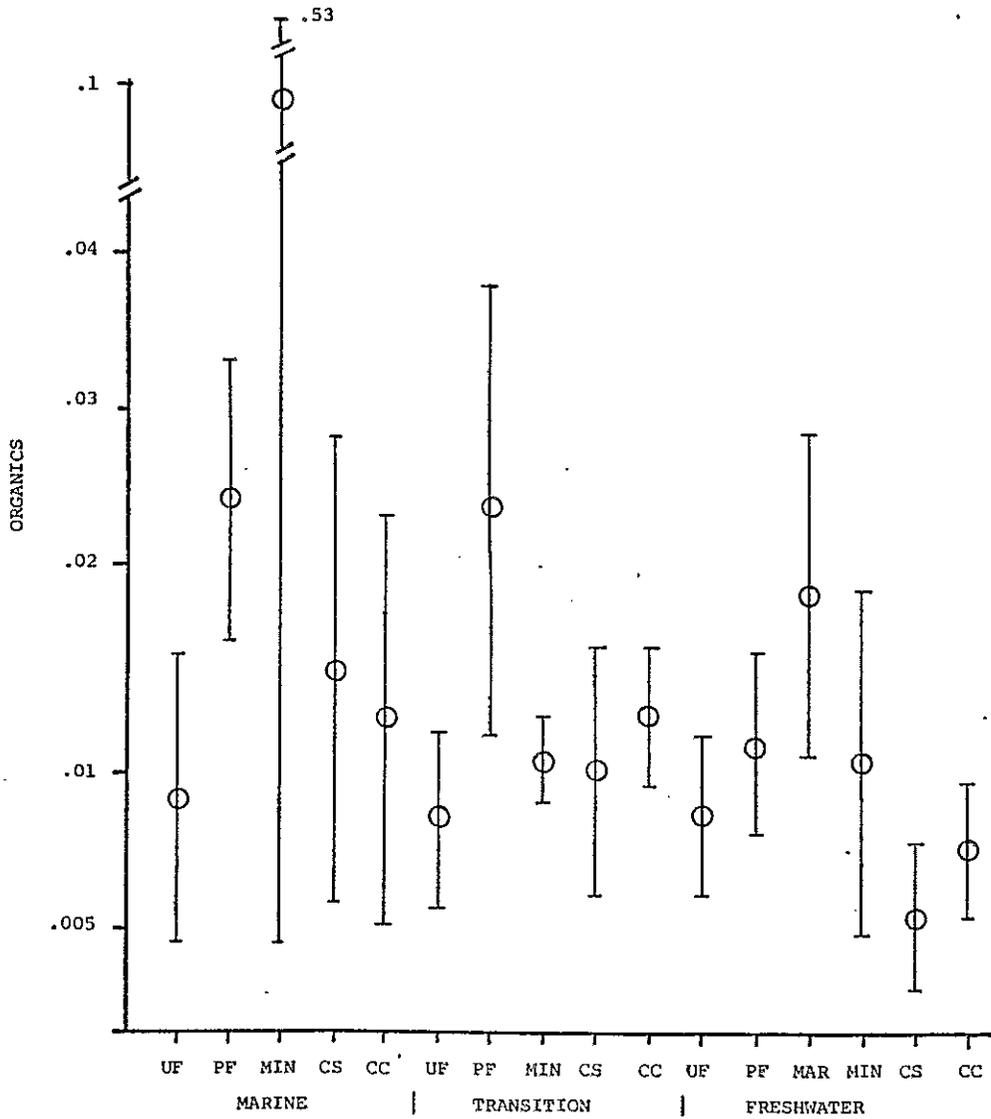


Figure 46. Means and 95% Confidence Intervals for the Organic Content of Sediment in the 16 Sampling Strata. Organic Matter was Measured as Proportion Lost During Combustion. Stratum Codes as in Figure 45.

Consistent with its fines content, organic content of the Marsh Channel habitat was of moderate level, about 1.8%.

The stratum means for fines and organics appeared to have a positive correlation. This relationship is better expressed in Figure 47, which plots fraction fines against fraction organics for all samples. The relationship appears approximately linear for the transformed versions of the two variables, but has considerable scatter ( $r^2 = 0.55$ ). Given the small amounts of sediment which could be allocated to these two analyses and the inherent variability of such measurements, the relationship appears reasonably well developed and suggests the values may have utility in the analysis of the biological data.

### 3.5.2 Distribution of Taxa

The distribution of the 60 most common taxa are summarized on a mean weight by stratum basis in Table 33. These results are described in taxonomic order below.

**Rhynchocoela:** This taxon was found in all salinity zones and in nearly every stratum, but appeared to be most abundant in more marine areas. The taxon may be composed of several species with differing salinity tolerances.

**Nematoda:** The taxon appeared in every stratum, but was most abundant in brackish and freshwater zones. The group most likely is also composed of several species, and many of these are probably too small to be sampled representatively by the methods used.

**Turbellaria:** This taxon was abundant in most Marine and Transition Zone habitats except the Main Channel Center habitat, but was scarce or absent from habitats of the Fresh Water Zone.

**Polychaeta:** This was the most diverse of the taxa for which species level identification was accomplished. Table 33 illustrates the general marine orientation of the taxon, with few of its species extending beyond the Marine Zone. Species which exhibited a relatively wide up-estuary distribution were Eteone spp. (low densities in several Transition Zone habitats), Hobsonia florida (very abundant in the Transition Zone Protected Flat habitat), Neanthes limnicola (captured in every stratum, but most abundant in the Marine and Transition Zones), Paraonella platybranchia (captured in Unprotected Flat and Channel habitats of the Marine and Transition Zone, but not in the Fresh Water Zone), and unidentified juveniles of the genus Spio (occasional specimens in both the Transition and Fresh Water Zones). Of these species, Neanthes limnicola inhabited the least saline area of the estuary. Its up-river distribution was not clearly established in this study.

Some polychaete species appeared to favor fine sediment habitats. These included Neanthes limnicola (although it occurred in other habitats), Hobsonia florida and Pseudopolydora kemp. Species more prevalent in coarse substrates were Nephtys californiensis, Paraonella platybranchia and Spio butleri. In many incidences, however, species were not captured frequently enough to establish trends of this sort.

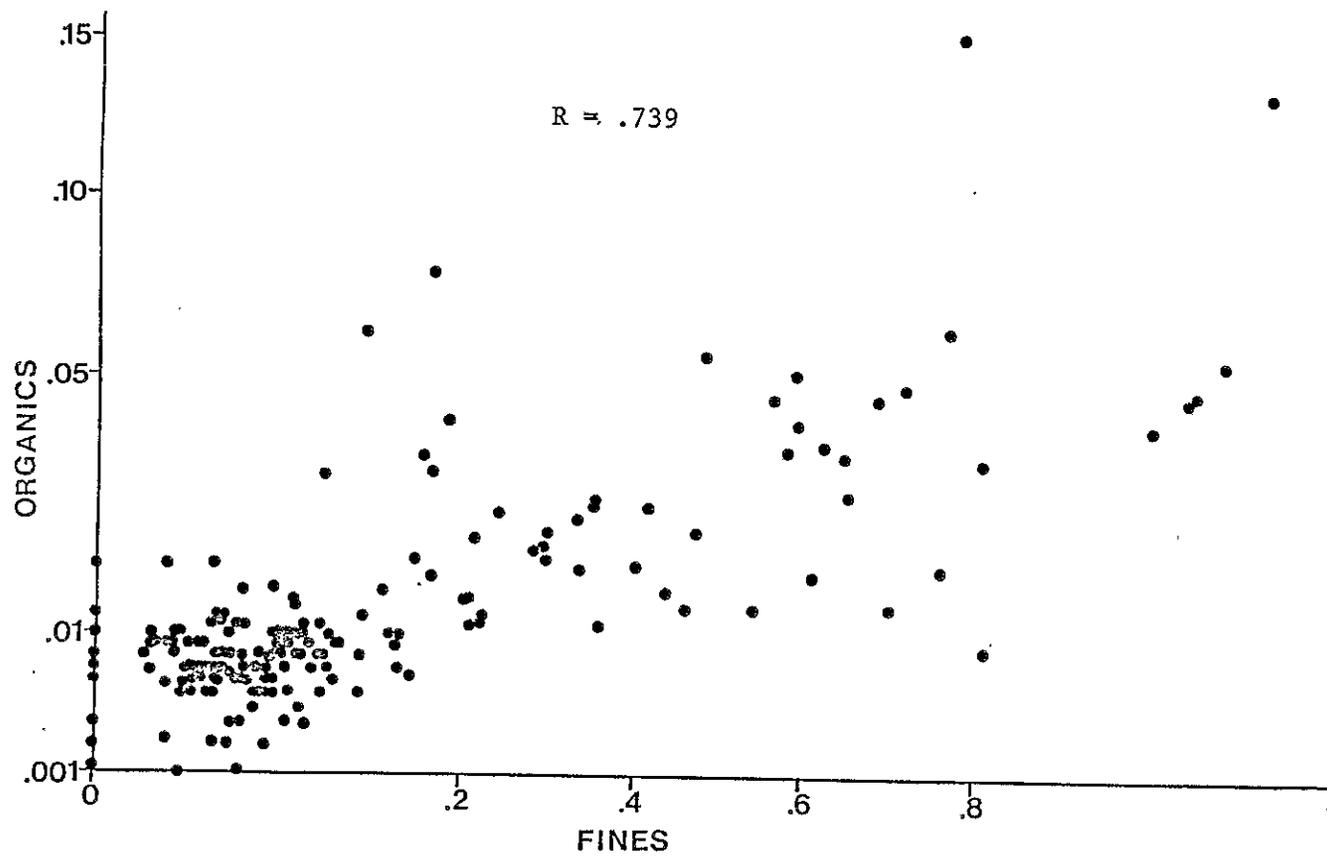


Figure 47. Scatterplot of Sediment Organic Content and Fines Fraction For all Stations

Table 33. Distribution of Taxa by Salinity Zone and Habitat. Salinity Zone codes are M = Marine, T = Transition, F = Fresh Water. Habitat codes are U - Unprotected Flat, P = Protected Flat, M = Marsh Channel, m = Minor Channel, S = Main channel Side, C = Main Channel Center. Densities are in mg AFDW/.05 m<sup>2</sup>, and are Represented as Blank = Less Than .001, 1 = .001 to .01, 2 = .01 to .1, 3 = .1 to 1, 4 = 1-10, 5 = 10-100, 6 = 100-1000.

Taxon	Zone	Habitat					
		U	P	M	m	S	C
RHYNCHOCOELA	M	3	3	-	3	4	3
	T	3	3	-	3	3	3
	F	2	2			1	2
NEMATODA	M	1	2	-	1	1	1
	T	2	3	-	2	2	2
	F	2	2	3	2	2	3
TURBELLARIA	M	3	4	-	3	2	
	T	2	4	-		2	
	F	1	2	1			
POLYCHAETA	M	2	-	3	2		
	T						
	F						
<u>Armandia bioculata</u>	M	3	-				
	T						
	F						
<u>Barantolla americana</u>	M	2	-		2		
	T						
	F						
<u>Capitella capitata</u>	M	3	4	-	3	3	2
	T	1	1	-		2	2
	F						
<u>Eteone</u> spp.	M	3	-		3		
	T						
	F						
<u>Glycera convoluta</u>	M	3	-		3		
	T						
	F						

Taxon	Zone	Habitat					
		U	P	M	m	S	C
POLYCHAETA (cont.)	M	1	-	2	2		
	T						
	F						
<u>Glycide armigera</u>	M	2	-	2	3		
	T						
	F						
<u>Glycide picta</u>	M	3	-	2	2		
	T						
	F						
<u>Heteronastus</u> spp.	M	3	4	-	3		
	T	4	-		1		
	F						
<u>Hobsonia florida</u>	M	2	-		3		
	T						
	F						
<u>Magelona saculata</u>	M	2	-		3		
	T						
	F						
<u>Malacoceros fuliginosus</u>	M	2	-				
	T						
	F						
<u>Mansyunkia aestuarina</u>	M	1	2	-			
	T						
	F						
<u>Medionastus</u> spp.	M	1	3	-	2	2	
	T						
	F						

Taxon	Zone	Habitat					
		U	P	M	m	S	C
POLYCHAETA (cont.)	M	3	4	-	3	2	1
	T	3	5	-	3	2	3
	F	1	1	2	3	1	1
<u>Nephtys californiensis</u>	M	3	-		3	3	
	T						
	F						
<u>Owenia fusiformis</u>	M	1	-	1	1		
	T						
	F						
<u>Paracnella platybranchia</u>	M	3	-		2	3	
	T	2	-	1	2	2	
	F						
<u>Polydora ligni</u>	M	2	2	-	3	2	2
	T						
	F						
<u>Pseudopolydora kempi</u>	M	2	4	-	2		
	T						
	F						
<u>Pyrosopio californica</u>	M	1	-				
	T						
	F						
<u>Scolelepis squamata</u>	M	2	-		3		
	T						
	F						

Table 33. (cont.)

Taxon	Zone	Habitat					
		U	P	M	m	S	C
POLYCHAETA (cont.)	M	2	-	2			
<u>Scaloplos</u> <u>araizer</u>	T	-					
	F						
	M	-		1			
<u>Spiohanes</u> <u>berkeleyi</u>	T	-					
	F						
	M	2	-	2	2		
<u>Spio</u> <u>busleri</u>	T	-					
	F						
	M	1	-	2	2	3	
<u>Spio</u> <u>filicornis</u>	T	-					
	F						
	M	3	-				
<u>Spio</u> spp.	T	1	-				
	F					1	
OLIGOCHAETA	M	3	4	-	4	3	1
	T	3	4	-	3	2	2
	F	3	3	4	3	3	3
GASTROPODA	M	-					
Ancylidae	T	-					
	F	3					
	M	-					
<u>Flumicola</u> <u>virens</u>	T	-					
	F	3	3	4	3	3	2

Taxon	Zone	Habitat					
		U	P	M	m	S	C
GASTROPODA (cont.)	M	-					
<u>Coniobasis</u> <u>pliocifera</u>	T	-					
	F	3	3	3			2
BIVALVIA	M	-					
<u>Corbicula</u> <u>eaniensis</u>	T	-	3	2	3		
	F	4	4	4	5	4	4
	M	3	6	-	5	3	
<u>Macoma</u> <u>baltica</u>	T	3	4	-	2	3	
	F						
	M	2	2	-	2		
<u>Mya</u> <u>arenaria</u>	T	-					
	F						
Mydidae	M	2	3	-	2	3	
	T	-					
	F						
	M	2	-				
<u>Siliqua</u> <u>patula</u>	T	-					
	F						
	M	2	-				
Sphaeriidae	T	-					
	F						
OSTRACODA	M	-					
	T	-					
	F	2	2	2	2		

Taxon	Zone	Habitat					
		U	P	M	m	S	C
MYSIDACEA	M	3	2	-	2	3	3
<u>Archaeomysis</u> <u>grebinitzki</u>	T	2	-		2	3	
	F						
	M	-		3			
<u>Neomysis</u> <u>mercedis</u>	T	1	2	-	1	2	2
	F	2	3	3	2	2	
CUMACEA	M	-				2	
<u>Diastylopsis</u> <u>dawsoni</u>	T	-					
	F						
	M	2	3	-	3	2	
<u>Hemileucon</u> spp.	T	1	3	-	2	2	
	F						
	M	-				1	
<u>Lamprops</u> sp. A	T	-					
	F						
ISOPODA	M	1	-	2	1	1	
<u>Gnoringosphaerona</u> <u>oregonensis</u>	T	-					
	F						
	M	-				2	
<u>Saduria</u> <u>entomon</u>	T	3	-	3	3		
	F			3		3	
AMPHIPODA	M	-				2	
<u>Corophium</u> <u>brevis</u>	T	-					
	F						

Table 33. (cont.)

Taxon	Zone	Habitat					
		U	P	M	m	S	C
AMPHIPODA (cont.)	M	2	3	-		1	
<u>Corophium</u> <u>salmonis</u>	T	3	4	-	4	3	2
	F	4	4	4	4	4	4
	H	2	-			1	
<u>Corophium</u> <u>spinicoorne</u>	T		3	-	2	2	
	F		1	2			2
	H	3	2	-	3	3	2
<u>Corammarus</u> <u>confervicoides</u>	T	3	2	-	3	3	3
	F		1	3	1		2
	M	2	3	-			
<u>Eohaustorius</u> <u>estuaris</u>	T	3	3	-	3	3	2
	F	2	2				2
	H			-		2	2
<u>Eohaustorius</u> <u>washingtonianus</u>	T			-			
	F						
	M			-			
<u>Mandibuloxus</u> <u>uncirostratus</u>	T			-		2	
	F						
	H	2		-		2	2
<u>Monoculodes</u> <u>spiniipes</u>	T			-			
	F						
	M	3	2	-	3	4	4
<u>Paraphoxus</u> <u>milleri</u>	T	3		-	3	3	4
	F						

Taxon	Zone	Habitat					
		U	P	M	m	S	C
AMPHIPODA (cont.)	M		2	-			
<u>Pontoporeia</u> <u>affinis</u>	T			-			
	F						
TRICHOPTERA	M			-			
Limnephilidae	T			-			
	F				2		
DIPTERA	M			-			
Chironomidae	T			2	-		1
	F	3	3	4	3	3	3
	M			-			
Heleidae	T			-			
	F	2	1	2	2	3	3

Oligochaeta: This taxon occurred in all habitats in each salinity zone. Highest abundance was in the finest sediments, as occurred in Protected Flat habitats of the Marine and Transition Zones, in the Minor Channel habitat of the Marine Zone, and in the Marsh Channels. The lack of a more definitive distributional pattern was probably due to the lack of species level identification; there may be several oligochaete species present with different distributional patterns.

Gastropods: Three snail taxa were collected. Of these, unidentified specimens of the family Ancyclidae (limpets) were collected only in Marsh Channels, while Fluminicola virens and Goniobasis plicifera were widely distributed throughout the Fresh Water Zone but were absent from the more saline zones. These species are of fresh water origin, and appeared to exist at their most oceanward distribution in this zone.

Bivalvia: Of four clam species identified, Macoma balthica and Mya arenaria were clearly marine oriented while Corbicula manilensis was fresh water oriented. The fourth species, the razor clam Silqua patula, was collected only once. This is an open-coast species, and the specimen was likely washed in by tidal currents. Mya arenaria (and unidentified juveniles of its family Myidae) were collected only in Marine Zone habitats, principally in the Baker Bay region. Macoma balthica was widely distributed, occurring in both the Marine and Transition Zones. Its greatest abundance was in Baker Bay Protected Flats and Minor Channels, but it was also abundant in Youngs Bay Protected Flats. Corbicula manilensis, the Asiatic clam, is an introduced freshwater species that apparently finds its distributional limit at the lower edge of the Fresh Water Zone. Occasional mature specimens were found in the Transition Zone, but most occurrences there involved newly settled juveniles, which apparently were washed downstream. The final bivalve taxon collected was Sphaeriidae, a family of very small freshwater clams. Some of the specimens have been identified as Pisidium spp. In the present study they were found only in the Fresh Water Protected Flat stratum, but have been collected in Main Channel habitats in a previous study (Higley et al. 1976).

Ostracoda: These small crustaceans were collected only in the Fresh Water Zone, and primarily in shallow habitats. However, most species were small and would be poorly represented by the screening methods used. Marine species are known to occur.

Mysidacea: Two species of mysids were collected, Archaeomysis grebnitzkii and Neomysis mercedis. These species appeared to have complementary distributions, since A. grebnitzkii was captured in Marine and Transition Zones, and N. mercedis was captured in Transition and Fresh Water Zones.

Cumacea: Hemileucon spp. was the most common cumacean captured, occurring in most of the Marine and Transition zone habitats. The other two species, Diastylopsis dawsoni and Leucon sp. A, were represented by only a few specimens in the Main Channel Side habitat of the Marine Zone.

Isopoda: The small isopod Gnorimosphaeroma oregonensis was collected only in Marine Zone habitats. This was apparently an artifact of its preference for shoreline vegetation and rocky substrates. The species may occur in dense populations in these habitats of Youngs Bay (Higley and Holton 1975). The other isopod species captured, Saduria entomon, occurred primarily in channel habitats of all three salinity zones, appearing to favor sandy environments.

Amphipoda: Ten amphipod species were collected in the survey, including three members of the genus Corophium: C. brevis, C. salmonis, and C. spinicorne. C. brevis was represented by a few specimens collected in the Marine Zone Main Channel Center stratum, and did not appear to be a factor in the estuary's infaunal communities. C. salmonis was widely distributed and often extremely abundant in a variety of strata, although its abundance diminished near the ocean. C. spinicorne was consistently present in Protected Flat habitats, but occurred in channel habitats as well. According to Higley and Holton (1975), in Youngs Bay this species was most abundant encrusting on vegetation and rocks; therefore, its major populations were probably not sampled effectively in the present survey.

Two widely distributed amphipod species were Eogammaraus confervicolus and Paraphoxus milleri, which occurred in nearly all habitats of the Marine and Transition Zones. P. milleri, however, was absent from the Fresh Water Zone while E. confervicolus extended into this zone. Two species of Eohaustorius, E. estuarius and E. washingtonianus formed mostly complementary distributions. E. estuarius appeared most abundantly in all habitats of the Transition Zone, while E. washingtonianus was restricted to Main Channel habitats of the Marine Zone. Mandibulophoxus uncirostratus and Monoculodes spinipes also appeared primarily in Marine Zone channel habitats. The final amphipod species, Pontoporeia affinis, is known only from a few specimens collected in Grays Bay. These may have washed down from tributary streams.

Trichoptera: A few specimens of the caddis fly family Limnephilidae were collected in marsh channel samples. A more diverse insect fauna may be present in this habitat and is as yet unsampled.

Diptera: Larvae of the two midge families, Chironomidae and Heleidae were consistently represented in all habitats of the Fresh Water Zone, but were mostly absent from more saline areas. The exception was the occurrence of Chironomidae in Protected Flat and Main Channel Center habitats of the Transition Zone.

### 3.5.3 Distribution of Total Density

Total numeric and weight densities are summarized by stratum in Table 34. Numeric density varied from 26 to 614/.05 m<sup>2</sup> (520 to 12,280/m<sup>2</sup>) over the 16 strata. Both extreme values were for Marine Zone habitats: very low density occurred in the Main Channel Center, and high density in the Protected Flat. Unprotected Flat and Main Channel Side densities were also low, while Minor Channel habitat densities were intermediate. A very similar density pattern was evident among Transition Zone habitats, with the highest density also occurring in the Protected

Table 34. Mean Total Numeric Density (No/.05 m<sup>2</sup>) and Mean Total Weight Density (mg AFDW/.05 m<sup>2</sup>) of Infauna According to Sampling Stratum

	<u>Marine</u>		<u>Transition</u>		<u>Fresh Water</u>	
	Number	Weight	Number	Weight	Number	Weight
Unprotected Flat	60	7.5	50	5.7	188	15.4
Protected Flat	614	230.3	589	102.9	267	14.4
Marsh Channel	---	---	---	---	341	28.3
Minor Channel	159	82.3	85	6.8	99	139.2
Main Channel Side	41	10.7	43	4.9	120	13.8
Main Channel Center	26	3.6	39	5.1	131	11.5

Flat habitat and nearly equal to that of the Marine Zone highest density. Fresh Water habitats, however, all supported moderate animal densities which ranged from 99 to  $341/.05 \text{ m}^2$  (1,980 to  $6,820/\text{m}^2$ ).

Biomass density was highest at  $230 \text{ mg AFDW}/.05 \text{ m}^2$  ( $4.6 \text{ g AFDW}/\text{m}^2$ ) in the Marine Zone Protected Flat. As with numeric density, biomass density of the Marine Zone mostly increased going from the least to the most protected habitats. In large part, these increases reflected the increased prevalence of the clam Macoma balthica in shallower habitats.

In the Transition Zone, highest biomass density was  $103 \text{ mg AFDW}/.05 \text{ m}^2$  ( $2.1 \text{ g AFDW}/\text{m}^2$ ) in the Protected Flat habitat. All other habitats varied around  $5 \text{ mg AFDW}/.05 \text{ m}^2$  ( $.1 \text{ g AFDW}/\text{m}^2$ ). Fresh Water Zone habitats were about 10 to  $30 \text{ mg AFDW}/.05 \text{ m}^2$  ( $.2$  to  $.6 \text{ g AFDW}/\text{m}^2$ ) except for the high value of  $139 \text{ mg AFDW}/.05 \text{ m}^2$  ( $2.8 \text{ g AFDW}/\text{m}^2$ ) of the minor channels. Except for the Protected Flat habitat, the Transition Zone weight densities were consistently lower than those of corresponding habitats in both the Marine and Fresh Water Zone habitats. This relationship is illustrated in Figure 48, which exhibits both means and confidence limits for the strata.

A relationship between animal density and substrate character is suggested by the mean values summarized in Figures 45, 46 and 48. This relationship is examined through plots of weight density against the sediment fines fraction (Figure 49) and against the sediment organic fraction (Figure 50). Both relations show considerable scatter, but it is clear that the fines fraction is a better predictor of animal density. The regression coefficient (1.0074) is significantly different from 0 ( $p < .0001$ ), although correlation is low ( $r^2 = .258$ ).

#### 3.5.4 Station Classification According to Community Structure

Canonical analysis of discrimination was utilized to determine the frequency with which samples collected from individual strata could be classified according to their animal densities as belonging to that stratum. This test employed the numeric density data for 49 common taxa, with a separate test being conducted on each salinity zone. Overall, 56 of 60 samples or 93% of the samples were correctly classified into their habitat of origin in the Marine Zone, but only 74% (45 of 61) and 63% (46 of 73) were correctly classified in the Transition Zone and Fresh Water Zone, respectively (Table 35). For the Marine Zone, errors occurred only between Protected and Unprotected Flat habitats, and between Main Channel Side and Main Channel Center habitats. Classification errors in the other two zones, as well as being more frequent, were more dispersed, forming no strong pattern of habitat association.

These results suggest that community structure was most varied and habitat distinct in the Marine Zone, and that the original definition of habitats on the basis of physical characteristics provided a closer fit to animal distribution patterns in that zone than in the other two zones.

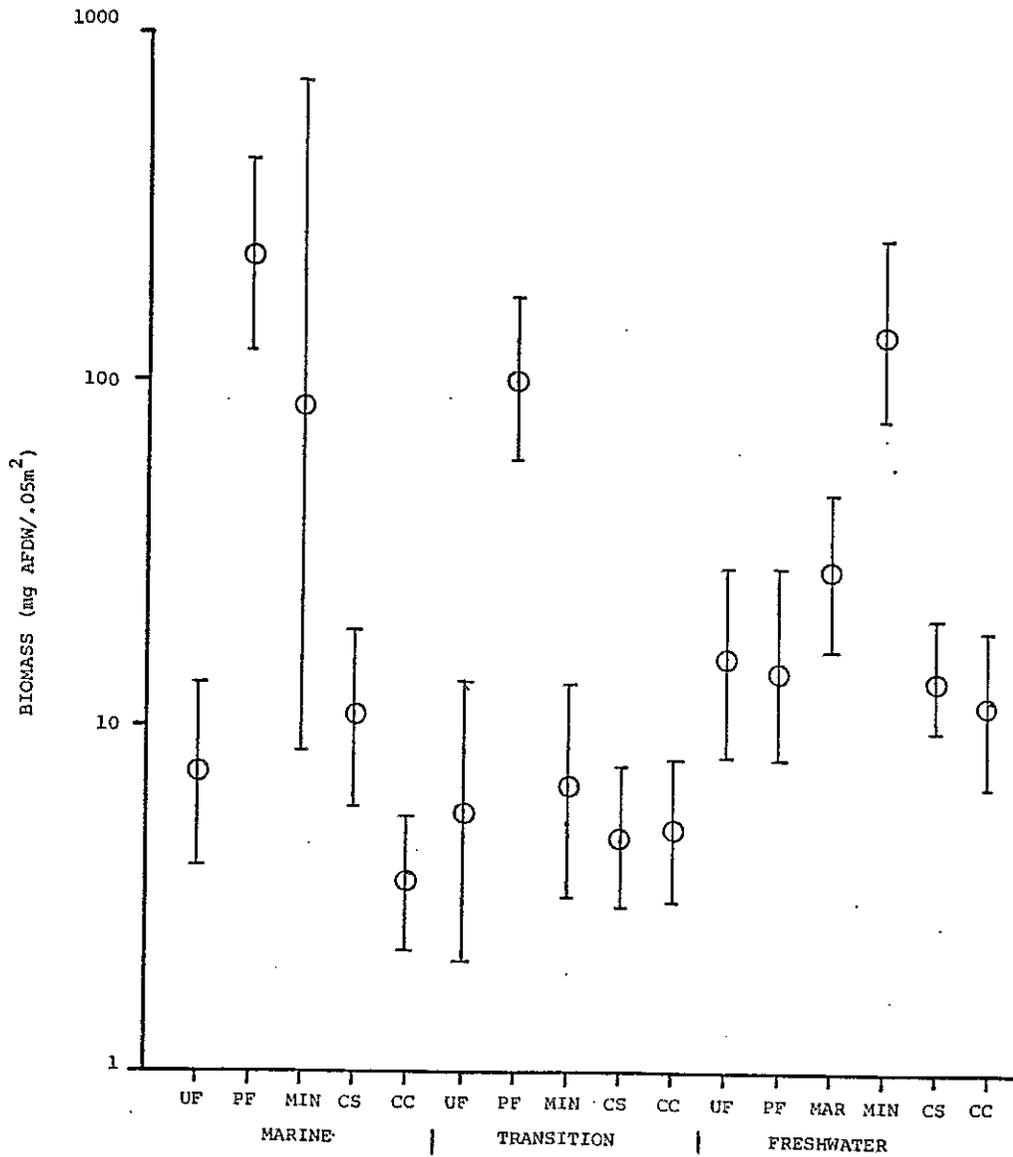


Figure 48. Means and 95% Confidence Intervals for Total Biomass in the 16 Sampling Strata. Stratum Codes as in Figure 45.

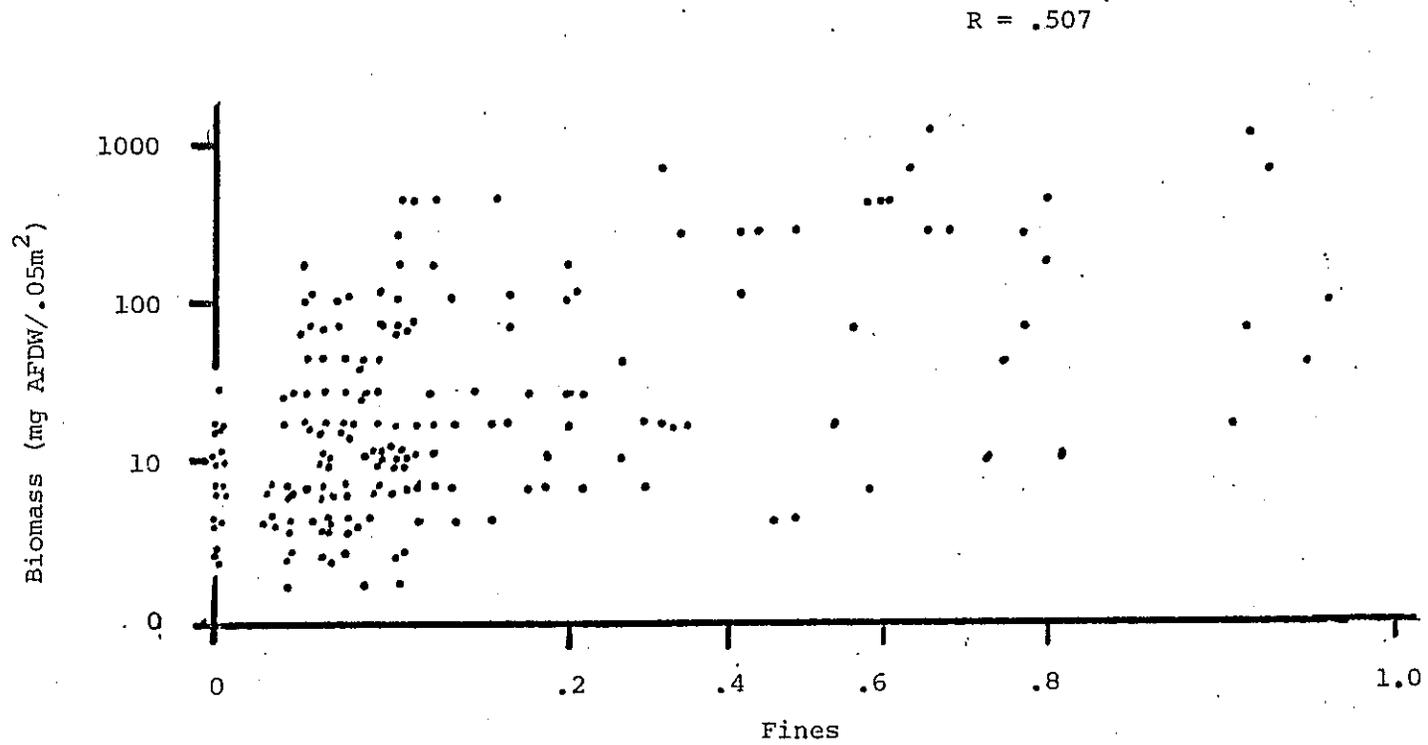


Figure 49. Scatterplot of Total Biomass and Sediment Fines Fraction For all Stations

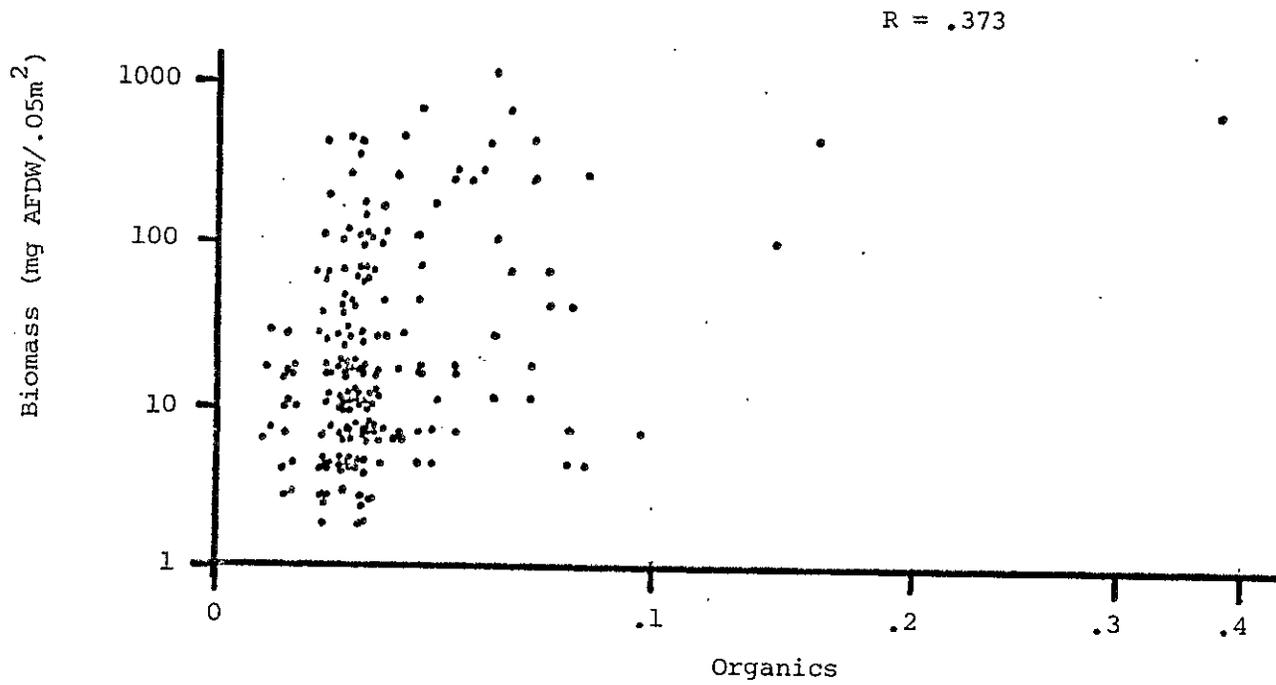


Figure 50. Scatterplot of Total Biomass and Sediment Organic Fraction For all Stations

Table 35. Classification of Stations According to Taxon Densities Using Canonical Analysis of Discriminance. The Analysis Defined a Centroid for Each Stratum According to the Animal Content of its Member Stations, and then Determined the Most Probable Stratum Membership for Each Station. The Accuracy of this Classification Indicates How Closely Stratum Boundaries Match Animal Distribution Patterns.

Assigned Habitat							
<u>MARINE ZONE</u>							
Original Habitat	No. of Stations	Unprotected Flat	Protected Flat	Marsh Channel	Minor Channel	Main Channel Side	Main Channel Center
Unprotected Flat	12	91.7	8.3	--	0	0	0
Protected Flat	18	5.6	94.4	--	0	0	0
Minor Channel	6	0	0	--	100.0	0	0
Main Channel Side	12	0	0	--	0	91.7	8.3
Main Channel Center	12	0	0	--	0	8.3	91.7
						overall: 93.3	
<u>TRANSITION ZONE</u>							
Unprotected Flat	13	53.8	7.7	--	30.8	0	7.7
Protected Flat	12	8.3	83.3	--	8.3	0	0
Minor Channel	12	16.7	0	--	83.3	0	0
Main Channel Side	12	8.3	0	--	8.3	75.0	8.3
Main Channel Center	12	8.3	0	--	8.3	8.3	75.0
						overall: 73.8	
<u>FRESH WATER ZONE</u>							
Unprotected Flat	15	66.7	0	6.7	6.7	20.0	0
Protected Flat	12	16.7	66.7	0	8.3	8.3	0
Marsh Channel	10	0	0	70.0	20.0	0	10.0
Minor Channel	12	0	16.7	0	66.7	16.7	0
Main Channel Side	12	33.3	0	0	8.3	58.3	0
Main Channel Center	12	0	0	0	16.7	33.3	50.0
						overall: 63.0	

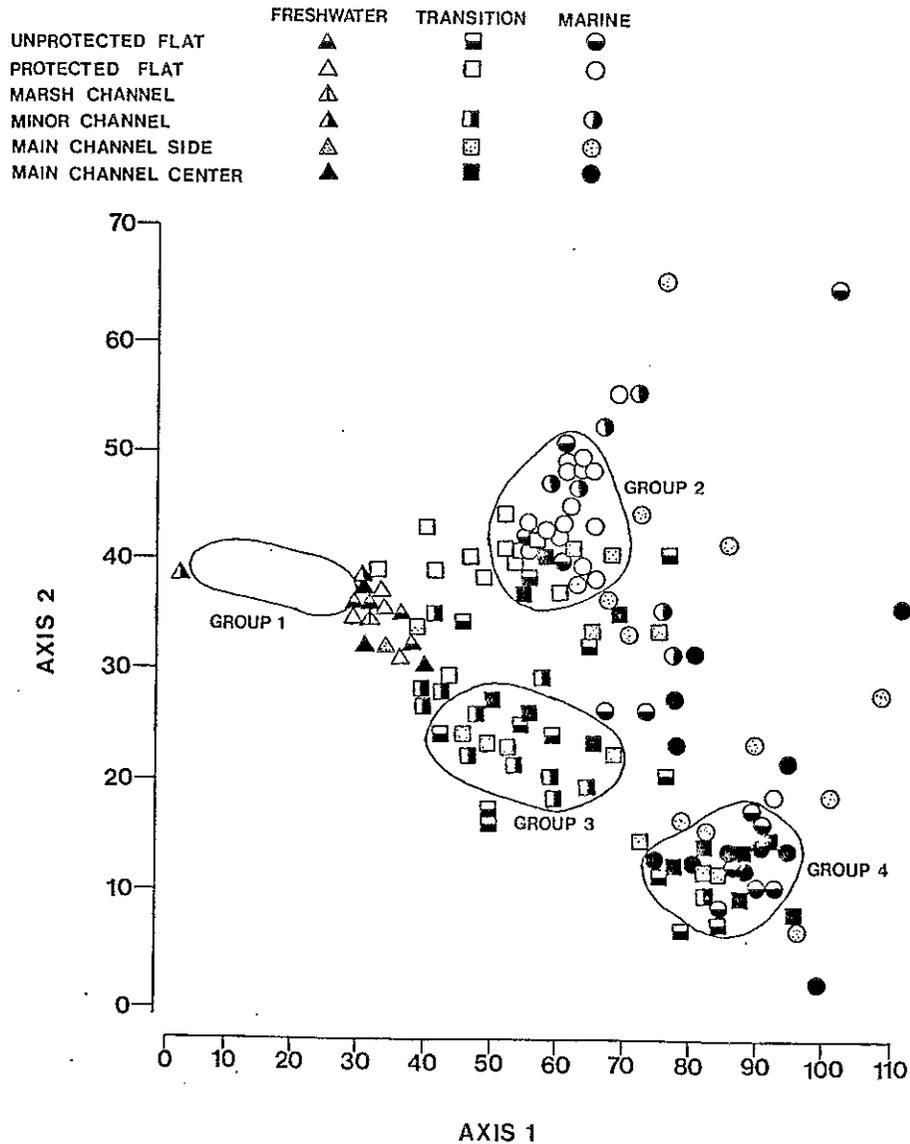


Figure 51. Results of Reciprocal Averaging Ordination, Expressed As a Plot of Station Scores for the First Two Axes. Group Designations are Arbitrary, and are Used to Define Probable Animal Assemblages. Group 1 is Too Densely Packed for Depiction of Individual Station Points, but is Composed Entirely of Fresh Water Zone Stations. There are no Obvious Habitat Groupings Within Group 1.

### 3.5.5 Analysis of Community Distribution

Reciprocal averaging ordination of the numeric data illustrated patterns of animal distribution which can be related to environmental gradients. Figure 51, in which station scores for the first two axes are plotted, shows a distinct pattern of change from freshwater to marine stations. The most striking feature of Figure 51 is the highly condensed placement of most of freshwater stations. That is, compared to stations in the lower estuary, freshwater stations were barely separated from each other by the generation of these two ordination axes, which captured most of the variation in community structure. The trend toward station separation appears to be progressive along Axis 1, producing a wedge-shaped pattern. Along both the upper and lower edges of the wedge, the change is clearly from Fresh Water to Transition to Marine Zone habitats. The change upward along Axis 2 is mostly from Main Channel to Protected Flat habitats.

These two trends suggest that Axes 1 and 2 represent patterns of change in community structure associated with salinity and sediment texture, respectively. These and other possible axis:environmental-gradient relationships possibilities were investigated by plotting station scores against the environmental variables measured (station location, station depth, sediment fines fraction and sediment organic fraction). Of all the possible plots (four ordination axes and four environmental variables), the strongest relations were Axis 1-station location and Axis 2-fines fraction, which are displayed in Figure 52 and 53.

The relation between Axis 1 and station location (Figure 52) is very well developed, and presumably shows that the first (and strongest) ordination axis captured the progressive changes in community structure occurring along the up-river salinity gradient. It can be seen that slope is greatest in the intermediate portion of the graph, emphasizing the high rates of community change which occurred in the Transition Zone.

The relationship between Axis 2 and fines (Figure 53) is less well developed. One possible interpretation of the plot is that the influence of fines was felt primarily in the <20% interval. Some of the scatter in this plot may arise from the homogeneous freshwater community which appears across many substrate types (see Group 1 of Figure 51).

One interesting feature of Figure 51 is the close agreement of the Fresh Water Zone to Transition Zone boundary with actual sample placement in the plot. That is, community structure apparently diversified at about the point where the Fresh Water Zone to Transition Zone change was defined, which was near the upper limits of salinity intrusion. A similar relationship is not apparent for the Transition Zone to Marine Zone boundary.

Reciprocal averaging ordination also provided an interpretation of individual taxa distribution. As described earlier, ordination axes for taxa corresponded to those for stations, so that taxa and stations with similar axis scores were associated. This relationship (the taxon plots are not reproduced here) were utilized to help identify taxon groupings which might correspond to community types. Four station groups were thus

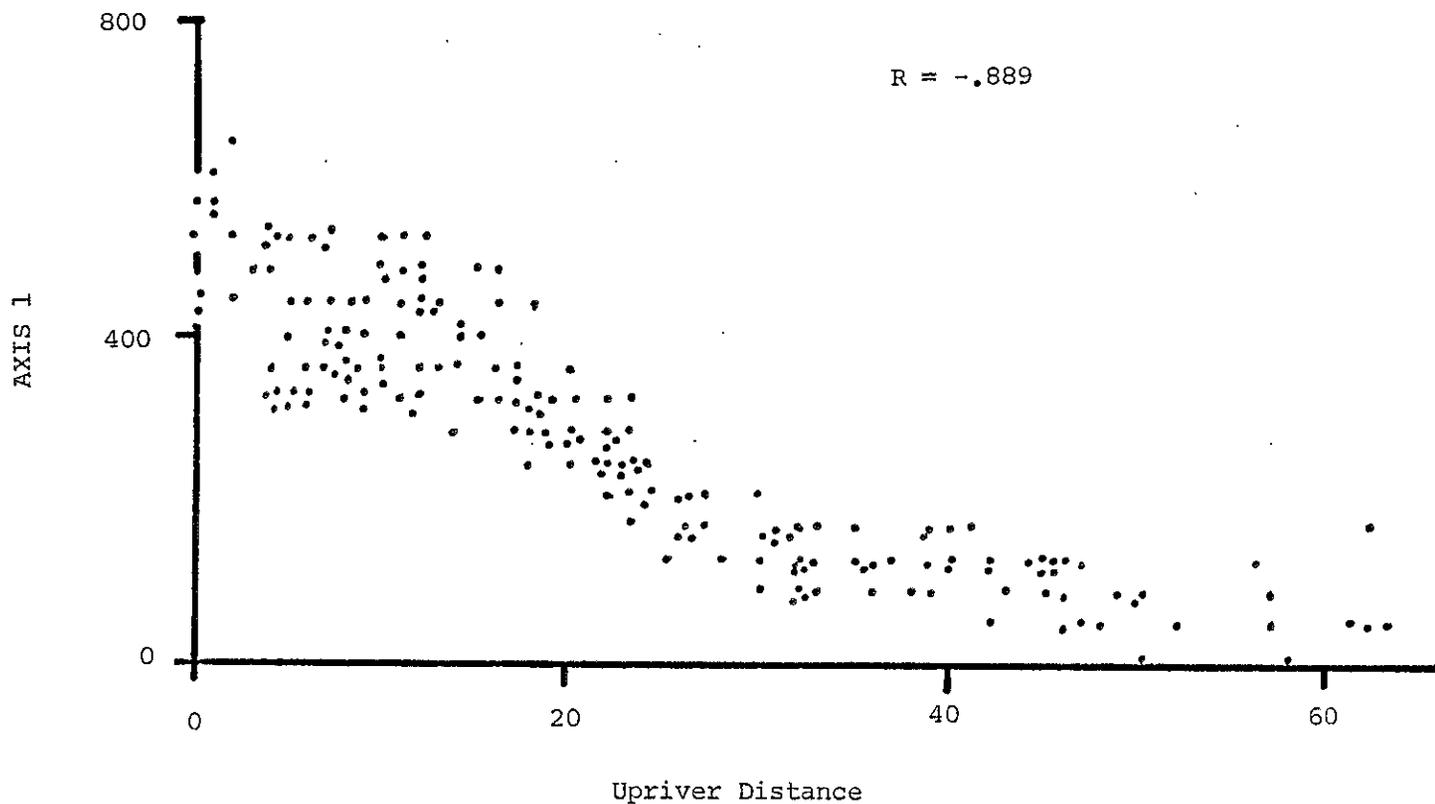


Figure 52. Scatterplot of Ordination Station Scores of Axis 1 Against Location in Estuary. The Scores Decrease with Distance From the Ocean, Suggesting that this Axis, Which Represents Much of the Variation in Community Structure, Measures Community Response to Decreasing Salinity.

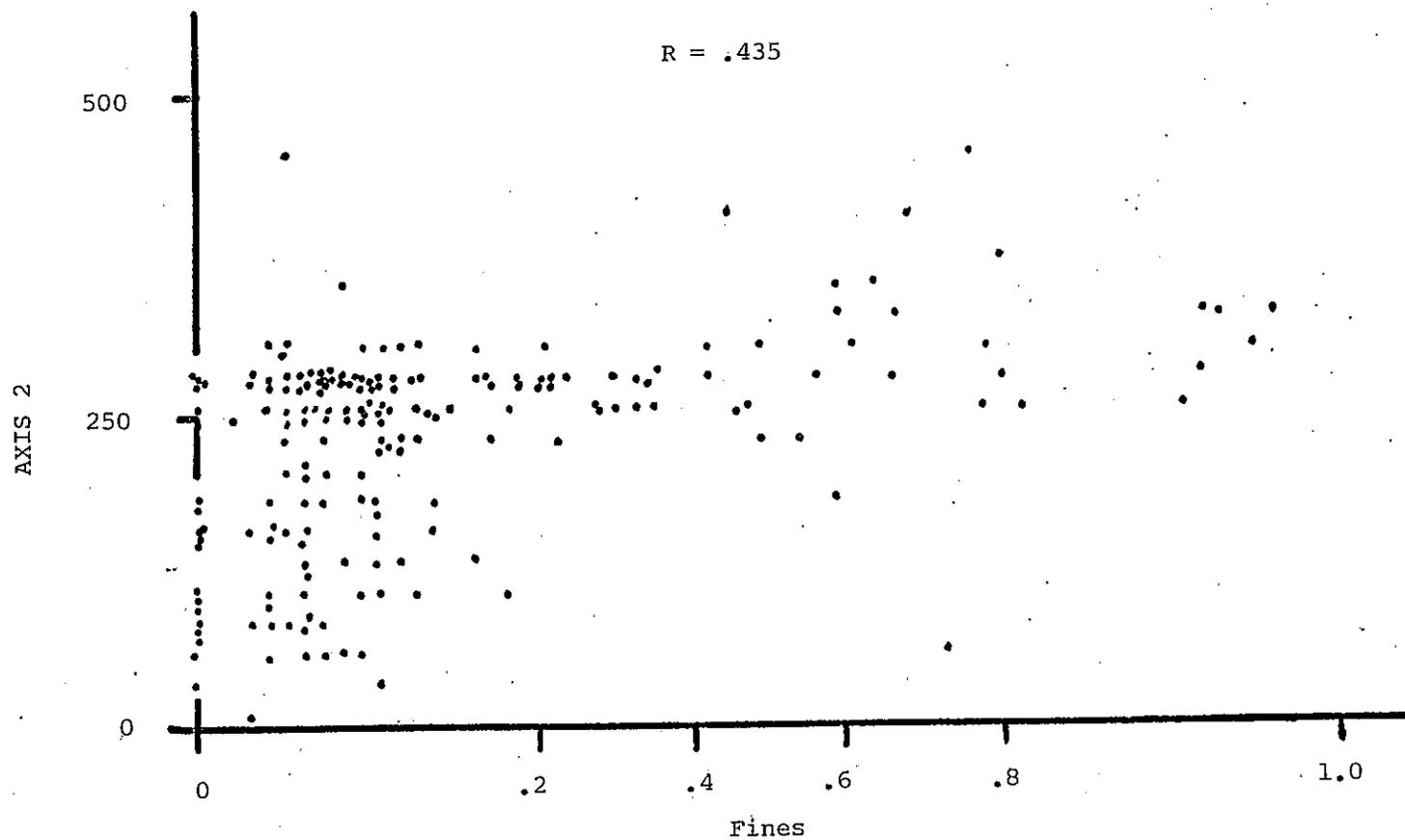


Figure 53. Scatterplot of Ordination Station Scores for Axis 2 Against Sediment Fines Fraction. While Not as Clear as the Axis 1 Response to Salinity, the Gradient Captured by Axis 2 Appears Related to Sediment Composition.

outlined in Figure 51 to identify possible community types. It is emphasized that although the groups are reasonably compact, definition of these groups was largely subjective and is provided only for descriptive purposes.

Group 1 included 53 of the 73 Fresh Water Zone samples, but no samples from the other two salinity zones. Based on the taxon ordination scores and inspection of the data, taxa characteristic of this group were Corophium salmonis, Corbicula manilensis, Heleidae, Chironomidae, and Oligochaeta. Minor contributors were Fluminicola virens, Goniobasis plicifera, and Neanthes limnicola. It should be noted that although C. manilensis contributed rather strongly to the definition of this group, most of the individuals captured were juveniles and should not be interpreted as indicating an actively reproducing adult population.

Thirty-three samples contributed to Group 2, and of these 16 were from Baker Bay (Marine Zone Protected Flat). Other samples included were six from Youngs Bay (Transition Zone Protected Flat) and a scatter of samples from other Marine and Transition Zone habitats. Several widely distributed species connected these sites. These species included Hobsonia florida, Macoma balthica, and Neanthes limnicola. Oligochaeta, Turbellaria and Corophium salmonis also helped define Group 2. These common taxa were the dominant forms in Baker Bay and comprised essentially the whole fauna of Youngs Bay. This relationship was sufficient to cause close alignment of Baker Bay and Youngs Bay samples in the reciprocal averaging sample plot, despite the presence of several other mostly less common polychaete species exclusive to Baker Bay. One of these polychaetes which was especially abundant was Pseudopolydora kempii.

The Group 3 sample assemblage included only Transition Zone samples from Channel and Unprotected Flat habitats. Most (12 of 16) were from Minor Channel and Main Channel Side habitats. The dominant taxa of these samples were Eogammarus confervicolus, Eohaustorius estuarius, Neanthes limnicola, and Rhynchocoela.

Group 4 comprised samples from a variety of strata in both the Marine and Transition Zones. Of 23 samples in this group, 8 came from Unprotected Flats, 11 from Main Channel Center, 3 from Main Channel Side and 1 from Minor Channel habitats. Characteristic taxa were Rhynchocoela, Paraphoxus milleri, Archaeomysis grebenitzkii and, to a lesser extent, Paraonella platybranchia and Spio filicornis.

## 4. DISCUSSION

### 4.1 VERTICAL DISTRIBUTION STUDY

The vertical distribution of animals and sediments was analyzed from three cores collected in intertidal sand flats of three different salinity zones in the Columbia River Estuary. The Grays Bay site was fresh water dominated and was composed primarily of fine sand, with 10 to 20% silt and clay. The site supported a dense population of the amphipod Corophium salmonis as well as several other taxa. The Desdemona Sands site, located on a water-swept sandy shoal in the salt/fresh water mixing region of the estuary, was composed of medium sands having almost no silt or clay. The Desdemona Sands core contained very few animals. The marine influenced Baker Bay site supported a predominantly polychaete and bivalve community. Sediments there were composed largely of fine sand in the upper 12 to 14 cm, but was muddy below this depth.

Based on this study, the highly abundant amphipod Corophium salmonis appeared to be confined to the top 15 cm in Grays Bay. Juveniles appeared concentrated in the top 2 cm. Corophium species are surface feeders and tube-builders, and thus have a strong surface orientation.

The ampharetid polychaete Hobsonia florida is also a surface feeder and tube-dweller. In the Grays Bay core, it appeared limited to the top 15 cm, although too few specimens were collected to make this certain. Other surface-oriented taxa captured in Grays Bay were insect larvae, the bivalve Corbicula manilensis and a few unidentified gastropods. Burrowing taxa found below 15 cm were nematodes and oligochaetes.

In Baker Bay, the polychaetes, amphipods, bivalves and oligochaetes were mostly confined to the upper 10 cm. The main exception was Mya arenaria, a deep-burrowing clam that lives at least 30 cm deep. Amphipod genera captured in the Baker Bay core (Ampelisca, Eogammarus and Paraphoxus) are apparently epibenthic and/or shallow burrowers, as opposed to the deeper dwelling Corophium of Grays Bay. The bivalve Macoma balthica was probably limited in depth distribution by the length of its siphons, with larger animals occurring in deeper sediments. Hobsonia florida is a tube-builder while the spinoid polychaetes are burrowers. However, both of these polychaete taxa are surface deposit feeders, which explains their concentration near the surface.

The nereid polychaete, Neanthes limnicola was found nearer the surface in the Baker Bay core than in the Grays Bay core (which included very few specimens). Habitat characteristics which might cause this difference were not apparent. Neither core showed evidence of an anoxic layer that would limit depth penetration.

Other surface dwellers in the Baker Bay core were the carnivorous polychaete Eteone spp. and juvenile bivalves (probably Macoma balthica). Free-burrowing taxa having wider depth ranges included Nematoda, capitellid polychaetes and oligochaetes. All of these taxa were likely composed of several species, each following its own depth patterns, which taken together created the wide depth bands illustrated in Figure 10.

Putting the information together for the Grays Bay and Baker Bay cores, it may be concluded that a sampling depth of 15 cm is suitable for the Grays Bay small macrofauna, and a depth of 10 cm for the small macrofauna of Baker Bay. The following limitations must be added however: (1) The data apply to the taxa specifically studied; (2) certain elements of the deeper burrowing worm fauna will be missed; (3) deep-dwelling bivalves will be missed; and (4) C. salmonis should be sampled to a depth of 15 cm wherever it occurs.

Unfortunately, the lack of sufficient data for the Desdemona Sands site prevents development of similar criteria for that habitat. It may be reasonably assumed, however, that the Grays Bay data provide useful guidelines.

With the exception of the Baker Bay core, there were no distinct changes in sediment texture with depth. In the Baker Bay core, fine sediments increased but this occurred too deep in the soil to be related to the distribution of most of the animals. Thus for none of the cores could a relationship between sediment texture and animal distribution be established. Other sediment properties (e.g., interstitial salinity, organic content, oxygen level and nitrogen content) which might have helped explain some of the vertical density patterns were not measured. An obvious and important restriction on many animals' depth distribution is the presence of reduced, anaerobic sediments lying below an oxygenated layer. This condition was not apparent in any of the three cores of this study, and would very likely have produced different distributions for some taxa from those depicted here.

The meiofauna of Grays Bay, like the macrofauna, roughly separated into two distributional groups: Those largely confined to the top 15 cm (Rhynchoecoela, bivalve juveniles, Ostracoda, copepod nauplii, Corophium salmonis and Tardigrada), and those with an apparently wide vertical distribution (Nematoda, Oligochaeta, Harpacticoida and insect larvae). Literature on specific meiofaunal taxa suggests that they respond to subsurface physical, chemical, or biological factors within the sediment. McLachlan et al. (1977) related nematode abundance to nitrogen concentration in the sand, and densities of interstitial harpacticoids to median particle size. Hogue and Miller (1981) also reported that nematodes responded to environmental heterogeneity on a scale of centimeters. These latter authors suggested that nematodes were attracted to local concentrations of buried organic matter. The Grays Bay meiofaunal data were too limited to adequately address the causes of distribution of nematodes and some other mobile subsurface feeders. It is quite possible that these organisms and some macrofauna as well would achieve different vertical distributions on other dates or at other nearby sites according to the vertical distribution of their primary food resources.

The sieve retention data showed that some juvenile macrofauna (amphipods and bivalves) from Grays Bay passed through a 0.5 mm screen, but were retained on a 0.25 mm screen. It is also possible that many juvenile polychaetes in Baker Bay passed through the 0.5 mm screen. The proportions of the macrofauna retained on specific screens must fluctuate with changes in the size distribution of specific populations as seasonal peaks of juveniles enter the populations. In addition, the character of

the sediments being sieved has a large effect on screening efficiency, since large amounts of either organic debris or mineral sediments inhibit passage of small animals through the screen. Overall, however, the use of a 0.5 mm mesh screen appears adequate to document patterns of abundance in macrofaunal surveys in the estuary. That is, loss of juveniles does not appear to present serious problems for defining community composition and relative density levels. This view is tempered by the fact that several taxa commonly included in the macrofauna (e.g., Nematoda, Oligochaeta, Rhynchocoela) were predominantly captured on meiofaunal size screens in the Grays Bay core. Therefore, analysis of the estuary-wide survey data gave precedence to larger animals such as amphipods and polychaetes.

The size-retention and vertical distribution information was also utilized in the development of the life history studies conducted in Grays Bay, Desdemona Sands and Baker Bay. Core samples taken to study the life history of Corophium salmonis were set at 15 cm deep and a screen size of 0.125 mm was used to insure collection of the youngest life stages. Life history studies of the polychaete and bivalve community of the Baker Bay mudflat used cores 8 cm deep and a 0.25 mm minimum screen size. In this case, a black anaerobic layer beginning at 4 to 5 cm effectively restricted infaunal depth penetration to 6 cm, which was shallower than that found in the predominantly aerobic sandy core collected in the present study. The 8 cm depth therefore was a more practical sampling depth. A 0.25 mm screen was used because additional studies of size retention indicated that juveniles of bivalves and polychaetes to be studied would be retained on this mesh size.

To conclude, the vertical distribution study demonstrated that in both marine-influenced and nearly freshwater bays within the Columbia River Estuary, infaunal communities were composed of both surface oriented and deep-living species. Studies of this kind emphasize the importance of understanding the basic life history properties of organisms which may be subjected to severe changes in environmental conditions, as might be caused by dredged materials deposition. For species which are active burrowers and which frequent deeper sediment zones, burial presumably is less of a problem than for species having limited vertical mobility. Tube dwellers requiring access to overlying water, and surface lying filter feeders appear more susceptible than burrowers. Resource managers need to take into account the species structure of individual infaunal communities in assessing the probable impact of severe changes in benthic habitats.

#### 4.2 BAKER BAY MUDFLAT COMMUNITY INTENSIVE STUDY

Community structure on the Baker Bay mudflat was viewed in terms of diversity, evenness, richness, and feeding strategies. In these terms the community appeared quite stable. The only significant change in community composition index values occurred during the Hobsonia florida recruitment in June and July, when the evenness and diversity indices decreased.

Although community structure remained mostly stable, densities of individual taxa changed seasonally as a result of recruitment and mortal-

ity. Of the environmental variables measured, surface salinity and temperature changed seasonally, but sediment composition did not change. However the changes in salinity and water temperature could not be consistently related to spawning or recruitment activities. Variability in salinity and temperature due to tidal changes, precipitation and similar influences on mudflat conditions may have contributed to this lack of correspondence. Interstitial salinities and temperatures (not measured) might relate more clearly to the infaunal density patterns, especially for taxa which are not surface oriented (e.g., Oligochaeta and Capitellidae). Benthic recruitment patterns were probably also influenced by changes in benthic primary production, which were in turn affected by temperature, salinity and day length changes.

Benthic primary productivity in the vicinity of the study site was relatively high, and river water and the surrounding marshes provided a good supply of detrital material. Gross benthic primary production reached a high of 81 mg C/m<sup>2</sup>/hr and sediment organics averaged approximately 200 mg AFDW/m<sup>2</sup> (McIntire and Amspoker 1984). These food sources supported a predominantly surface deposit-feeding population of benthic infauna through the year.

Oligochaetes, although not dominant in terms of biomass (contributing 1.8% of the community biomass), were numerically dominant. This taxon was probably composed of several species, which may help explain both their abundance and the lack of seasonal density change, assuming different species followed different reproductive cycles. Also, oligochaetes were not quantitatively sampled with the 0.5 mm screen used. The proportion of oligochaetes lost through this screen was indicated by the Grays Bay vertical distribution study, where only 3% of the oligochaete population was captured on a 0.5 mm mesh screen (Section 3.1.3). The rest were retained on screen sizes ranging down to 0.063 mm, which means that small species and juveniles were largely missed in the present study. The apparent decrease in oligochaete density during the study may have been due to progressive increases in sieving efficiency (more oligochaetes passing through the screen).

Based on the gonad index, the Macoma balthica population had one major spawning period (June and July) during this study, and possibly a much smaller spawning period in late September. This agrees with Bachelete (1980) who determined that the species often has two or more spawning periods. The June and July spawning period was reflected in a large number of spat settling in the fall (the planktonic larval stage lasts 2 to 3 months, according to Henriksson [1969]). It is likely that some spat settled later than the spawning period at the study site would indicate, assuming populations living in deeper water had a late fall spawning period and contributed to the intertidal spat fall. That is, the relatively young population in Baker Bay (<4 years old) may not have the same reproductive patterns as older populations which may occur in deeper waters. This thesis is supported by the work of Nichols and Thompson (1982) who reported that M. balthica populations in the high intertidal areas of San Francisco Bay spawned once per year, while lower intertidal populations spawned twice per year.

Growth by members of the Baker Bay M. balthica population was rapid from May until September, as would be expected on the basis of warmer temperatures and increased primary production rates. However, wide fluctuations during both winter and summer months in measured temperatures (and salinities) at this exposed intertidal site apparently obscured this relationship. In other studies (e.g., Bachelet 1980; Nichols and Thompson 1982), growth and spawning by M. balthica appeared to be directly temperature dependent. More complete data, expressed perhaps as degree-days, would likely demonstrate a similar relationship for the Baker Bay population.

Annual production by M. balthica at the Baker Bay site was 13.56 AFDW/m<sup>2</sup>/yr, and average biomass was 9.32 AFDW/m<sup>2</sup>. These values put average yearly turnover (P:B) at 1.45, which falls within the range of M. balthica P:B values listed for other areas:

<u>Location</u>	<u>P:B</u>	<u>Reference</u>	14/^\
Tvaren Bay, Baltic Sea	0.388:1	Bergh 1974	
Ythan Estuary, Scotland	2.07:1	Chambers and Milne 1975	
Lynher Estuary, England	0.9:1	Warwick and Price 1975	
Gravelingen Estuary, Netherlands	0.30 to 1.95:1	Wolff and deWolff 1977	
Petpeswick Inlet (estuary), Nova Scotia.	1.9:1	Burke and Mann 1974	

The M. balthica population in Baker Bay was young, considering that individuals may live up to 35 years in the ocean at the 50 m depth (Bergh 1974). Baker Bay probably provides a healthful environment for M. balthica to grow, but not to grow old, for several reasons. (1) It is a favorable place for spat to settle, since spat tend to settle in areas that are sheltered, silty, and high in the intertidal region (Beukema 1973). (2) M. balthica grows faster at shallower depths (Bergh 1974; Bachelet 1980). Baker Bay supports a productive benthic diatom population and has a steady supply of detritus. (3) The older segment of the M. balthica population may prefer the cooler and more stable environment of deeper portions of the estuary. The species is capable of migrating (Brafeld and Newell 1961), and it is possible that maturing individuals move out of the shallow intertidal mudflats. Beukema (1973) found that juvenile M. balthica leave the high level mudflats during the first winter and migrate to the lower intertidal and subtidal areas. (4) Birds may feed selectively on the large individuals in the intertidal regions.

Pseudoploydora kemp appears to undergo strong yearly fluctuations in abundance. In the Baker Bay population, a single recruitment occurred in the late summer of both 1980 and 1981, but was followed by a steady population decline in 1980 and a very rapid decline in 1981.

Fluctuations in recruitment and mortality of the P. kemp population probably were accurately assessed. Although maturity was poorly esti-

mated due to the fragility of gravid females, the appearance of young was adequately documented by increases in catches of small individuals on the 0.250 mm screen. (The adequacy of the 0.250 mm screen was affirmed by checks made for young on a 0.125 mm screen.) The early life history of this species is conducive to a growth and production study, in that the larvae are brooded in the egg capsule until they reach at least 12 setigers in length. When released, they may be planktonic for only several hours to days, or they may remain on the bottom and begin the benthic phases immediately (Blake and Woodwick 1975). Thus mortality between larval release and settlement is probably small.

Production rate by the P. kempi population was estimated at 1.12 g AFDW/m<sup>2</sup>/yr and average biomass at 0.34 g AFDW/m<sup>2</sup> (including all size fractions). This places the annual P:B ratio at 3.29.

The Hobsonia florida life history data appear complete, since as Zottoli (1974) states, eggs of the species (identified as Amphictes floridus in his paper) are fertilized in the tube where the larvae remain until the two-setiger stage. The larvae then leave the tube and continue to grow in the mud. Thus benthic cores effectively sample individuals of all sizes, and except for the first few weeks of development, the young are effectively retained on a 0.250 mm mesh screen (author's data). These life history attributes allowed accurate field analysis of recruitment and growth.

Annual production by H. florida was 1.37 g AFDW/m<sup>2</sup>/yr and average biomass was 0.30 g AFDW/m<sup>2</sup>, indicating an annual P:B value of 4.57.

Another ampharetid polychaete, Ampharete acutifrons, common in the River Lynher, Cornwall, England, has a life history similar to H. florida (Price and Warwick 1980). It also is a sedentary, surface deposit-feeder polychaete with a benthic larval stage. In the River Lynher it is an annual species (lives for only one year). Warwick and George (1980) reported that Ampharete acutifrons had three cohorts present in Swansea Bay, which was similar to the population structure exhibited by Hobsonia florida in Baker Bay. Average P:B ratios reported by Warwick and Price were quite close to the 4.57 value of H. florida. The ratios varied between 4.00 and 5.47, even though production varied over two orders of magnitude (.12 to 12.54 g/m<sup>2</sup>/yr) during the five years of the study.

Estimating secondary production of lesser taxa can be very difficult since these taxa have very different life history patterns and trophic relationships. However, two of the four methods used to calculate production were close in their estimates and were intuitively reasonable in their approach. These were: 1) estimating production as a direct proportion of lesser taxa biomass to H. florida and P. kempi biomass (this gave a value of 2.04 g AFDW/m<sup>2</sup>/yr) and 2) estimating production by using meiofaunal P:B ratios for oligochaetes and P. elegans, and macrofaunal ratios based on the equations of Banse and Mosher (1980) for all other lesser taxa. Estimated production using this later method was 2.50 g AFDW/m<sup>2</sup>/yr. It was more reasonable to use a biomass comparison of lesser taxa with M. balthica excluded since M. balthica is large compared to the other taxa and its P:B ratio was relatively low. When using the regression equation relating maximum organism weight to P:B (Banse and Moser

1980), oligochaetes should be considered as meiofauna since a very small percentage of the population was retained on the 0.5 mm mesh screen. The assumed P:B of oligochaetes using this method (4.3) was close to that calculated for oligochaetes (3.0) by Haka et al. (1974) (Warwick et al. 1977).

Total community production was estimated at 18.32 g AFDW/m<sup>2</sup>/yr (Table 36). This estimate used the average of the two median calculations of lesser taxa production. Community production fell within reasonable bounds for an estuarine mudflat community on the basis of the following two studies. Wolff (1977) estimated total production of a highly productive community in the Grevelingen Estuary in the Netherlands at 57.4 g AFDW/m<sup>2</sup>/yr. Production estimates from an intertidal Macoma community in the Lynher River Estuary, Cornwall, England (Warwick and Price 1975) were also similar to the Baker Bay estimate at 13.31 g dry wt/m<sup>2</sup>/yr, or about 11.31 g AFDW/m<sup>2</sup> using a conversion factor of 0.85 (Winberg 1971).

These two estuarine systems are not similar to the Columbia River Estuary even though all three estuaries support Macoma/polychaete communities in areas of similar substrate. The European estuaries are marine-dominated systems. The most important food sources in these systems are benthic microphytobenthos, water column phytoplankton, and import of organic detritus from the ocean. Baker Bay in the Columbia River Estuary, in contrast, is a river dominated bay with little oceanic input of detritus and very little water column phytoplankton production (Lara-Lara 1983). However, the bay receives a large amount of detritus (probably primarily of river origin) and has a productive benthic diatom flora. It is an estuarine system that is very different from the ocean influenced systems of Europe and from the saltmarsh systems on the east coast of North America. However, the productivity of the benthic infauna at the intertidal mudflat studied in Baker Bay was similar to that of the benthic infauna of the European estuaries described above.

#### 4.3 COROPHIUM SALMONIS LIFE HISTORY STUDY

##### 4.3.1 Life Cycle of Corophium salmonis

The populations of Corophium salmonis at both Grays Bay and Desdemona Sands displayed life cycles based on two generations per year. A fall generation of juveniles was produced during late summer and early fall. The reproducing adults then died during the following winter. The juveniles produced in the fall grew and matured throughout the winter, reproduced the following May and June, and disappeared later in the summer. The spring generation juveniles grew rapidly through the summer and produced the fall generation.

Davis (1978) found that Corophium salmonis in Youngs Bay, located close to the Desdemona Sands site, also had a two generation per year life cycle. Overwintering females produced a spring generation by May with the population dominated by juveniles in the summer. This was similar to that found in the present study at both the Grays Bay and Desdemona Sands study sites. In Davis' study, the proportion of gravid fe-

Table 36. Total Community Production at the Baker Bay Study Site

<u>TAXON</u>	<u>PRODUCTION</u>
<u>Macoma balthica</u>	13.559
<u>Hobsonia florida</u>	1.368
<u>Pseudopolydora kemp</u>	1.122
	<u>16.049</u>
Residual (lesser) taxa	2.271
	<u>18.320</u> gAFDW/m <sup>2</sup> /yr

males in the total population increased to 60% in August. These females then produced the fall generation.

A study of benthic invertebrates in the Sixes River Estuary, Oregon also revealed similar reproductive patterns for C. salmonis, with a recruitment of juveniles occurring in the spring (Reimers et al. 1979). A study of C. salmonis in Grays Harbor, Washington found a population in early spring comprised of overwintering individuals and an increase in reproductive activity in late April and early May (Albright and Armstrong 1982). Brooding of eggs began in late March 1980 and continued to the end of the study in September 1980.

Corophium volutator, a burrowing species of intertidal mudflats along the coasts and estuaries of Europe and eastern North America, also has a two generations per year life cycle. Watkin (1941) found that C. volutator produced an overwintering population made up of older mature individuals and juveniles newly hatched in August. The second generation of the year was produced in February, March and April. Fish and Mills (1979) also observed two generations per year for C. volutator in the Dovey Estuary, North Wales, although spring reproduction commenced in May instead of February. McLusky (1968) found that a C. volutator population in the Ythan Estuary, Scotland had a single breeding season per year extending from May to August. Hart (1930) also observed that C. volutator were annual or semiannual reproducers.

Differences in the onset of spring reproduction and in the number of generations produced per year are probably related to differences in environmental conditions. The onset of spring reproduction was found to be correlated with the increase in temperature in the spring. McLusky (1968) reported that 7°C was the minimum temperature needed for C. volutator reproduction. The site studied by Watkin (1941) may have reached this minimum temperature earlier in the year than the other study sites.

At Grays Bay the lowest temperature (of channel water at low tide) was 6.5°C in December 1980. At Desdemona Sands the lowest temperature was 5°C, in February 1981. Temperatures at both sites exceeded 10°C except during the November to March period, and exceeded 15°C from June to October. The frequency of gravid females rose rapidly in April and May, and juveniles appeared at both sites in May. During the February to May period, water temperature rose from about 6 to 11°C. Thus, it seems probable that temperatures that stimulate reproductive activity in C. salmonis are similar to those for C. volutator.

Other Corophium populations which have two generations per year include C. arenarium from the Dovey Estuary, North Wales, and C. insidiosum from the northeast coast of England (Fish and Mills 1979; Sheader 1978). C. sextoni from Torbay, England, breeds in April and May to produce the spring generation and in July through September to produce the summer-fall generation (Hughes 1978). Another species, C. bonnellii, although parthenogenic, also produces two generations per year (Moore 1980).

Sex ratios of Corophium salmonis populations at Grays Bay and Desdemona Sands significantly differed from 1.0 in few instances during the study. In June and July 1981 females significantly outnumbered males at Grays Bay. This may have been caused by selective predation on males. C. salmonis provides a major food source for many fish species in the Columbia River Estuary. Haertel and Osterberg (1967) found that most of the amphipods consumed by fish in the fresh water areas of the estuary were C. salmonis. Coho salmon and chinook salmon captured at Miller Sands (RM-24) consumed large quantities of C. salmonis, especially from March to July (McConnell et al. 1978). Haertel and Osterberg (1967) found that 50% of the diet of both starry flounder and prickly sculpin in the Columbia River consisted of C. salmonis. Prickly sculpin consumption peaked in the spring but starry flounder consumed most during the summer and fall. According to Higley and Holton (1975) starry flounder is probably the most abundant predator of C. salmonis in Youngs Bay. Both starry flounder and juvenile chinook salmon there heavily utilized C. salmonis during the rapid growth period of June to September.

Higley and Holton (1975) found that some fish guts examined contained only large adult males with well developed second antennae. Similarly, male C. spiniorne were often more abundant in stomachs of juvenile chinook collected in the Sixes River Estuary (Bottom et al. 1982). This pattern was also occasionally observed for C. salmonis in chinook stomachs from the Sixes River Estuary. Since Corophium use their second antennae to forage for food outside the burrow while they remain inside, adult males with larger second antennae maybe more subject to predation (Davis 1978). Males of some species (C. volutator, C. salmonis, and C. spiniorne) are also more active outside the burrow than females which would make them easier targets for predation (Watkin 1941; McCarthy 1973; Bottom et al. 1982; Reimers et al. 1979). During periods of heavy predation such selectivity would reduce the sex ratio so that females outnumber males. Albright and Armstrong (1982) reported that C. salmonis greater than 4.00 mm in length generally had a M/F sex ratio less than 1.0 and that it was due to a higher rate of mortality for mature males, probably from predation. They suggested that the tendency of mature Corophium to wander over the tidal flats in search of females exposed them to the predation.

An alternative explanation was offered by Shearer (1978) and Watkin (1941) who observed that the sex ratio (M/F) of C. volutator declined in June and July, and attributed this change to the die-off of large overwintering males. Die-off again occurred in September and October for males which matured throughout the summer (Watkin 1941). Either die-off or predation could have contributed to the change in the sex ratio observed at Grays Bay.

At the Desdemona Sands site significant departures of the sex ratio from 1.0 occurred in late summer and in early fall and involved males outnumbering females. Males can be identified at a much smaller size than females, approximately 1.5 to 2.0 mm vs. 2.0 to 2.5 mm. This characteristic could have lead to males appearing to outnumber females during periods when the population was dominated by juveniles and immatures, as was the case in August 1980 and July through September 1981. Davis (1978) found that C. salmonis males captured in the water column of

Youngs Bay generally outnumbered females, but that females outnumbered males in the substrate. However, these differences for the most part were not significant.

Mean brood size in the present study was 16.1 at Desdemona Sands and 14.2 at Grays Bay. Davis (1978) calculated a similar brood size (15.3) for the Youngs Bay population. Mean brood size for C. salmonis in Grays Harbor, Washington was lower at 11.4 during the spring 1980, although intactness of the broods was not taken into consideration (Albright and Armstrong 1982).

Both Grays Bay and Desdemona Sands populations had higher mean lengths for mature females than those reported for Youngs Bay. Grays Bay females averaged 5.03 mm and Desdemona Sands 4.90 mm, while Davis (1978) reported that most females in breeding condition at Youngs Bay were between 4.00 and 4.75 mm. The majority of C. salmonis in Grays Harbor became sexually mature by 4.5 mm (Albright and Armstrong 1982). Davis also reported that females could be sexed at a length of 1.5 mm, while in the present study females were not sexed below 2.0 mm. Albright and Armstrong (1982) also found that the sex of C. salmonis could not be determined for individuals less than 2.0 mm in length. These differences in the length at which sex could be determined may have been due to different techniques of measurement.

Davis (1978) found no apparent seasonal trend in mean brood size for the Youngs Bay population over a period of April 1974 through August 1974, January and February 1975 and September, October and December 1975. For both Grays Bay and Desdemona Sands, however, mean brood size differed from spring to fall. At both sites the spring brood size tended to be larger than fall brood size. This difference may be related to seasonal changes in the length of mature females. Mature females in the spring tended to be larger than those in the fall at both Grays Bay and Desdemona Sands. Spring females from the overwintering population had a longer season in which to mature and grow than females maturing during the summer. Hart (1930) observed that growth of the winter stock of C. volutator was slower than that of the summer stock and that the winter stock reached maturity at a larger size. Nair and Anger (1979) also found that the age at which C. insidiosum reached sexual maturity was greatly influenced by temperature. Fish and Mills (1979) observed the C. volutator and C. arenarium both produced larger broods from overwintering females than from summer generation females. They suggested that this was not due solely to the smaller body length of the summer females, but was regulated by the interrelated effects of body length, metabolism, level of food supply and temperature. The larger brood sizes by overwintering females of these two species may have reflected different food levels in each season. It is also possible that high summer temperatures resulted in a reduction of nutrient transfer to the gonads because of increased metabolic utilization.

This same interaction of factors probably regulated adult length in spring and fall female Corophium salmonis of the Columbia River Estuary, and may also explain observed differences in mean brood size between the Desdemona Sands and Grays Bay populations. The Desdemona Sands population had a larger average brood size but smaller average female length

than the Grays Bay population. High summer temperatures found at both sites could have caused more rapid maturation and reduced nutrient transfer to the gonads as described by Fish and Mills (1979) and Nair and Anger (1979), resulting in the smaller fall brood sizes. Differences in animal size and brood size between sites are more difficult to interpret. The younger, more productive animals found at Desdemona Sands may characterize temporary colonies, as compared to the larger and less productive animals of the more stable Grays Bay population.

Differences in brood size within the fall and the spring periods may have been due to the inclusion of broods containing embryos. It was difficult to determine whether or not these broods were intact and as a result inclusion of these broods may have caused estimates of brood size to be low.

#### 4.3.2 Migration of Corophium salmonis

The density fluctuations of Corophium salmonis observed at Grays Bay and Desdemona Sands cannot be explained solely by recruitment of juveniles. Densities at Grays Bay were influenced by adult immigration during the winter and by adult emigration, die-off or predation during the spring. From March to April 1981, density at Grays Bay declined from 29,298/m<sup>2</sup> to 16,447/m<sup>2</sup>. Die-off of large overwintering individuals apparently occurred, but declines in the larger size ranges were not sufficient to explain the population decline. Predation may have contributed to the population decline. Spring brings enhanced predation by such estuarine fish as salmon and starry flounder, and adult Corophium appear to be more susceptible to predation than either juveniles or immatures. Another likely cause of the decline is emigration by some of the adults to uninhabited areas. The spring appearance of adults and subadults at Desdemona Sands, and the winter immigration to Grays Bay both imply that movements of this type are possible. At this point it is not possible to determine the relative roles of die-off, predation and migration in the spring decline at Grays Bay. It seems likely that a combination of these events was at work.

A different density pattern occurred at Desdemona Sands, where the entire population disappeared in the fall and adults reappeared the following spring. As at Grays Bay, die-off, predation and migration may have contributed to the population decline. The role of predation seems less important, since sand shoals are probably not common feeding habitats, and since fall is not a time of high utilization of the estuary by fish. For example, Higley and Holton (1975) found that C. salmonis was consumed by juvenile chinook salmon and starry flounder primarily from June through September. Similarly, feeding by salmon at Miller Sands was concentrated from March to July (McConnell et al. 1978). Although some late summer feeding by fish occurs, it is unlikely that predation alone would have completely removed the population from the Desdemona Sands site. Fall die-off could have removed many older animals, but should have left an overwintering population of young animals.

Another possible cause of depopulation at Desdemona Sands is strong currents sweeping animals off the site. However, fall is not the time of heaviest river flow and there was no evidence of severe scouring at the

site, based on sediment stake measurements. Scouring would be strongest in the spring when runoff is highest due to the melt of winter snow pack in the upper basins. Rather than die-off, predation or scour, it seems most likely that the animal colonies appear and disappear according to variations in a more subtle environmental parameter.

Migration would seem to play an important role in Desdemona Sands density changes. Davis (1978) found C. salmonis to be very active in vertical migration. He suggested that the migrations may interact with tidal currents to achieve distribution throughout a patchy environment. In this way, the C. salmonis may leave habitats that have become crowded or otherwise unsuitable and colonize habitats with more favorable conditions. This type of migration appears to have occurred at Desdemona Sands. The disappearance and reappearance of C. salmonis at the site suggests that conditions there changed from fall to spring.

Among factors that may determine the suitability of a site for Corophium populations are temperature, salinity and sediment characteristics. Temperatures measured at the two sites were very similar, making it unlikely that the more dramatic density changes occurring at Desdemona Sands were caused by temperature patterns. Hart (1930) observed that the nature of the substratum and the salinity of the water were the main factors leading to the localized distribution of Corophium volutator. However, Albright and Armstrong (1982) observed that the distribution and abundance of C. salmonis in Grays Harbor, Washington was largely determined by sediment type and beach slope. In that study, salinity did not appear to be as important as sediment type in controlling C. salmonis distribution and abundance. In the present study, sediment characteristics at Desdemona Sands did not change appreciably during the study; however, salinities at the two sites diverged during the fall (Figures 26 to 28).

The salinity at Desdemona Sands rose in fall 1980 to greater than 10 ppt. This salinity increase coincided with the disappearance of Corophium salmonis from the site. A subsequent decrease in salinity in February 1981 was soon followed by the reappearance of C. salmonis. On this basis, the disappearance and recolonization at Desdemona Sands appear to have been a response to yearly salinity fluctuations at the site.

The fall immigration of adults to the Grays Bay site coincided with the disappearance of the population at Desdemona Sands. Similarly, adults declined during the spring at Grays Bay as the colony reappeared at Desdemona Sands. Low-tide salinity at Grays Bay, where the population was present throughout the year, remained consistently below 7 ppt, even during the fall when freshwater runoff was lowest and salinity intrusion greatest. Populations of C. salmonis appeared to colonize new habitats in the estuary as salinity conditions became suitable, but emigrated when higher salinity water advanced into areas where the salinities had been low. In McConnell's et al. (1978) benthic study at Miller Sands (which is near Grays Bay), salinities never exceeded 1.2 ppt. C. salmonis density patterns at several stations with tidal levels similar to that of the Grays Bay station exhibited peak values during the November to March period. Down-river, near the Desdemona Sands site, a seasonal study

conducted on both intertidal and subtidal populations of C. salmonis showed the species to have density patterns like that of the Desdemona Sands population, with peak densities occurring in May (Higley et al. 1982). The site was located along the northeast shoreline of the outer portion of Youngs Bay and would have been subjected to a wide range of salinities during the year.

McLusky (1968) suggested that migrations of Corophium volutator may have occurred in response to salinity. At a site in the Ythan Estuary he found that C. volutator was absent when salinities were 0.5 to 1.0 ppt, but in July as the salinity increased to above 2 ppt, the species appeared. Based on this observation and laboratory studies, McLusky concluded that salinity was the critical factor controlling the distribution and abundance of C. volutator. Later, McLusky (1970) found that this species had a stable salinity preferendum of 10 to 30 ppt and that the species exhibited a distinct avoidance of low salinities, supporting the migration theory.

Mills and Fish (1980) found that the distributions of C. volutator and C. arenarium in the Dovey Estuary appeared to reflect their individual tolerances to low salinities. Because of its distribution, C. arenarium rarely encountered water less than 10 ppt, while C. volutator inhabited areas with salinities as low as 2 ppt. These authors also determined that optimum breeding success and population growth was apparently restricted to an even narrower salinity range than that at which normal embryonic development occurred. These results contrasted with the work of Boyden and Little (1973), who felt that no evidence existed to suggest that salinity preferences determined the distribution of C. volutator and C. arenarium in the Severn Estuary, UK.

Siegfried et al. (1980) found that the downstream distribution of C. stimpsoni populations within the Sacramento River was regulated by the extent of the salinity intrusion. Hazel and Kelley (1966) observed that both C. stimpsoni and C. spinicorne were limited in their downstream distribution in the San Joaquin Delta by the location of the edge of the salinity gradient. There is evidence, therefore, from studies of other Corophium species to support the idea that C. salmonis adjusts its distribution within the estuary according to seasonal salinity fluctuations.

Vertical migration may play an important role in Corophium movements. Davis (1978) found that C. salmonis were active vertical migrators and concluded that dispersal was the most likely reason for the migrations. He noted that long distances could be traversed throughout the brackish water region of the Columbia River Estuary in a few hours, with distance and direction variable depending on individual activity in relation to current direction. Thus it would be possible for widely distributed habitats to be rapidly colonized or abandoned depending on conditions. Davis observed that in September C. salmonis in the surface and midwater strata were older juveniles between 1.5 mm and 3.0 mm. This reflected the composition of the benthic population at that time in Youngs Bay, and indicated that these older juveniles were the actively moving part of the population in the fall. In the present study the population at Desdemona Sands in August 1980 was also composed almost

entirely of older juveniles and it was this population that disappeared in September. The population which recolonized Desdemona Sands in April consisted of older immatures and adults, which reflected the population structure in Grays Bay at that time.

Morgan (1965) observed that most C. volutator swam on the ebb tide, but that some swam on the flood tide, allowing both downriver and upriver migration and colonization. Davis (1978) found that C. salmonis had no preference for either ebb or flood tide and would also be capable of both upstream and downstream migrations.

The results of the present study and related literature indicate that C. salmonis populations in the Columbia River Estuary may appear and disappear according to the suitability of environmental conditions, and that dispersal is accomplished through vertical migration into tidal currents by animals of various sizes and maturity. The distribution and dynamics of C. salmonis populations must therefore be viewed as highly changable and adaptive to changing conditions.

#### 4.4 COROPHIUM SALMONIS COMMUNITY DYNAMICS STUDY

Combining the production results for Corophium salmonis (Table 31) and lesser taxa (Table 32) at the two study sites, total macrofaunal production amounted to 9.1 g AFDW/m<sup>2</sup>/yr at Grays Bay and 13.7 g AFDW/m<sup>2</sup>/yr at Desdemona Sands. These values may be put in perspective by comparison with those of some other estuarine infaunal communities.

The closest such comparison is with the Macoma balthica community in Baker Bay (Section 4.2). This intertidal mudflat community was dominated by M. balthica in terms of both biomass and production, the bivalve producing 74% of the total 18.3 g AFDW/m<sup>2</sup>/yr. Two polychaetes, Hobsonia florida and Pseudopolydora kempfi, together produced 13%, while 15 lesser taxa produced 12% of the total. Warwick and Price (1975) measured total macrofaunal production at 13.3 g dry weight/m<sup>2</sup>/yr in a Macoma community, in the Lynher River Estuary, England, which was dominated by the carnivorous polychaete Nephtys hombergi. Wolff and DeWolf (1977) found macrofaunal production to vary from 0.1 to 120 g AFDW/m<sup>2</sup>/yr over the Grevelinger Estuary, Netherlands, as they charted different habitats and communities. They estimated production to average about 57 g AFDW/m<sup>2</sup>/yr estuary wide. A Venus (Bivalvia) community of Carmarthen Bay, South Wales, produced about 26 g AFDW/m<sup>2</sup>/yr (Warwick et al. 1978).

These community production values show the 9 to 14 g AFDW/m<sup>2</sup>/yr produced by the C. salmonis communities studied in the Columbia River Estuary to be of a moderate, perhaps low, level for estuarine fine sediment habitats. The similarity of the three production measurements (including the 18.3 g AFDW/m<sup>2</sup>/yr Baker Bay measurement) for the estuary imply that production levels may be moderate throughout the estuary. Not all potentially productive habitats in the estuary have been investigated, of course. It is possible that production rates within Youngs Bay or in the Cathlamet Bay region are substantially higher. However, the similarity of the fauna and their densities in these areas (Section 4.5) to those investigated do not support this conjecture. These comments

apply only to the small macrofauna and do not pertain to communities of large bivalves.

About 90% of the Grays Bay production and 96% of the Desdemona Sands production was contributed by Corophium salmonis. Thus, the overwhelming dominance by this species was expressed in terms of production rate, as well as numbers and biomass. In one sense, these production percentages may be misleading, since C. salmonis was completely censused using fine mesh screens, while counts of the other species were restricted to the 0.5 mm screen. Table 1 shows that only a small proportion, about 3%, of the Grays Bay oligochaete population is retained on a 0.5 mm screen. Meiofaunal elements of this taxon therefore may have achieved a substantial and unmeasured production level. Whether oligochaetes are studied as part of the meiofauna or macrofauna, however, it is still clear that C. salmonis dominated macrofaunal production.

The simplicity of the Grays Bay and Desdemona Sands macrofaunal communities and their dominance by C. salmonis are probably due to environmental instability, especially variable salinity. The Desdemona Sands region of the estuary, and less so the Grays Bay region, experience extreme and sometimes rapid salinity changes through a tidal cycle. At Desdemona Sand, low tide may bring nearly fresh water over a sandflat which a few hours earlier was covered by 15 ppt water. Large tidal exchanges, a relatively simple physical structure to the estuary, high freshwater flow rates and consequent high flushing rates produce a mid-estuary zone of fluctuating brackish conditions. In terms used by Boesch (1977), the system is strongly poikilohaline both seasonally and tidally, and by Smith's (1956) description, the system is a "gradient" estuary, with the middle reaches subject to pronounced salinity changes. (However, the upper and lower reaches probably vary more in salinity than is suggested by Smith's definition.) The estuary's salinity regime is thus very different from the relatively stable gradients seen in the Baltic Sea or Chesapeake Bay, and from the regularly fluctuating salinity pattern of some small estuaries, as described by Sanders et al. (1965).

These salinity conditions, and perhaps sedimentary ones associated with them, provide for a rather simple infaunal community in the middle and upper portions of the estuary. This fauna is composed of a few euryhaline marine and freshwater derived salt tolerant forms. Local fish feeding patterns appear to reflect this simplicity in their strong emphasis on C. salmonis, according to such studies as Haertel and Osterberg (1967) and Higley and Holton (1975). It is possible that the dominance by C. salmonis of mid-estuary habitats makes trophic relations of this zone more susceptible to disturbance than zones having more diverse infaunal communities.

Highest relative growth rate by C. salmonis was 0.10 mg/mg/day, measured at Grays Bay for 1.75 mm animals, according to analysis of the spring cohort. This is very near the maxima recorded by Birklund (1977) for C. insidiosum and C. volutator, but somewhat lower than the 0.15 mg/mg/day measured by Albright and Armstrong (1982) for C. salmonis males in Grays Harbor. In all these studies, growth rate generally decreased with size for animals exceeding 2 mm. Although Albright and Armstrong interpreted a slight peak at 5 mm, this peak was not evident either in Birk-

lund's data or in the Columbia River data. The otherwise close similarity of the Grays Harbor and Columbia River data suggest that growth in these populations was either regulated by similar seasonal phenomena or was not resource limited. The fact that growth at the newly colonized Desdemona Sands site approximated that at the Grays Bay site also supports this view. Were growth not restricted, production would mostly reflect population structure and density, which are in turn influenced by migration and predation. However, Birklund indicates that inter-specific competition affected growth rates in his study, and that a sewage outfall may have increased production at one of his sites. Therefore higher individual growth rates by C. salmonis may be achieved under other conditions not yet studied.

Annual production rates have been measured in few amphipod populations. Birklund's (1977) C. insidiosum populations produced from 0.2 to 8 g dry weight/m<sup>2</sup>/yr, and the C. volutator populations 2 to 4 g dry weight/m<sup>2</sup>/yr. Klein et al. (1975) measured production by Ampelisca brevicornis in Helgoland Bight of the North Sea. The values varied from 0.4 to 0.7 g dry weight/m<sup>2</sup>/yr according to site and estimation procedure. The A. brevicornis population studied by Hastings (1981) produced 1.31 to 1.68 g dry weight/m<sup>2</sup>/yr, while an A. tenuicornis population studied by Shearer (1979) produced only 0.103 g AFDW/m<sup>2</sup>/yr. This last value represented just 3.6% of total macrofaunal production, and illustrates the variability to be expected from single population production studies.

Corophium spp. often are major macrofaunal contributors to community production. This is especially so where, as in the case of C. salmonis, the species occupies estuarine zones characterized by highly variable salinities that limit community diversity and thus interspecific competition. At Grays Bay C. salmonis production was 8.2 g AFDW/m<sup>2</sup>/yr and at Desdemona Sands it was 13.1 g AFDW/m<sup>2</sup>/yr. Based on the live to preserved tissue conversion factor of 60% presented earlier, live tissue production rates were 13.7 and 21.8 g/m<sup>2</sup>/yr. The ash-free dry weights correspond to dry weight values of about 9.7 and 15.4 g/m<sup>2</sup> using Winberg's (1971) conversion factor of 0.85. These production values are considerably higher than those for C. insidiosum and C. volutator in Denmark (Birklund 1977), and are higher than the 3.6 to 10.7 g dry weight/m<sup>2</sup>/yr measured for C. salmonis in Grays Harbor (Albright and Armstrong 1982). While no community information is given by Albright and Armstrong, the community likely resembled that of the present study, based on the salinity regimes. Their sites were predominantly silt in texture, and retained the characteristically high volatile solid content (5 to 10%) of fine estuarine sediments. The sediments of the present study sites were more sandy in texture. While organic content data are not available for the study sites, the survey data (Section 3.5.1) provide useful information. The Unprotected Flat habitat of the Transition zone (which includes the Desdemona Sands site) averaged just .8% combustible solids, while the Protected Flat habitat of the Fresh Water Zone (including the Grays Bay site) averaged 1.1%. Despite the finer sediments and higher organic content of the Grays Harbor habitat, it was the mid-river shoal habitat of Desdemona Sands in the Columbia River that supported the highest C. salmonis production rate.

It is possible that the estimation procedure inflated the Desdemona Sands production value. This would occur if immigration favored large animals or if small animals were selectively preyed upon. Either would cause the cohort's median animal length to increase beyond that caused by individual growth. The evidence to date, however, is that migration roughly reflects the source population size structure, or if anything favors smaller animals (Section 4.3.2; Davis 1978). Predation, on the other hand, likely concentrates more on large males which, in C. volutator at least, wander over the substrate in search of females (Watkin 1941) and are made visible by their very large second antennae. These animals are presumably available to both fish and shorebird predators. Shorebirds are frequently seen on the exposed Desdemona Sands tidal flats (personal observation), and in England one species (the red-shank, Tringa totanus) is known to concentrate its feeding in areas of high C. volutator densities (Goss-Custard 1970). Supporting the view of higher predation on males is Albright and Armstrong's (1982) observation that the male:female ration of C. salmonis in Grays Harbor decreased with animal size.

Usually, errors of estimating relative growth rates and biomass result in minimum estimates of production (Birklund 1977). Given this fact and the information above on migration and predation, production was likely under, rather than over estimated for the Columbia River sites. Estimation procedures and growth rates being similar among the three Corophium studies (Birklund 1977; Albright and Armstrong 1982; this study), it would seem that the relatively high Desdemona Sands production value is not anomolous, but rather represents special conditions at that site. These include the seasonal colonization and rapid growth by C. salmonis in a habitat having limited inter-specific competition due to environmental conditions. The population was strongly weighted to young individuals achieving high growth rates, and attained very high summer numeric densities (nearly 100,000/m<sup>2</sup>) before declining in the fall. It is possible, but not certain, that similar production rates also occur in other C. salmonis colonies over the mid-estuary shoals. Although these colonies are probably patchily distributed (Section 4.5), their trophic effect may be substantial due to their relatively high production rates. However, the fate of this production, whether it is lost downstream, consumed by fish and other predators, or transported upstream by tidal currents, is not known.

At Grays Bay annual production at 8.2 g AFDW/m<sup>2</sup>/yr was lower than at Desdemona Sands, but still equivalent to the highest rates of Grays Harbor. The Grays Bay production was achieved by a numerically declining population, in contrast to the increasing population of Desdemona Sands, and more than half of this production occurred in the overwintering brood during the February to May period preceding the spring brood. That is, production was dominated by maturing animals at Grays Bay, and by young animals at Desdemona Sands.

In the Grays Harbor study C. salmonis densities followed a winter low, summer high pattern similar to the Desdemona Sands population, although the Grays Harbor population apparently persisted through the winter. This seasonal pattern would be expected from reproduction events, but is in contrast to that occurring in the Grays Bay population. The

contrasting patterns illustrate the variety in population dynamics possible for an opportunistic species like C. salmonis having strong migratorial tendencies. The Grays Bay site with its enhanced overwintering population and consequentially high early spring production level may represent a less common pattern that is caused by immigration of adults and subadults.

P:B was 5.5 for Grays Bay and 12.3 for Desdemona Sands, based on mean annual biomass. These values reduce to 2.7 and 5.1, respectively, if only the late April to early September period is considered (as suggested by time of residence at Desdemona Sands). Birklund (1977) estimated P:B at 2 to 5 for C. insidiosum and 3 to 4 for C. volutator in a Danish fjord for the May to early September period. In Grays Harbor, the C. salmonis populations studied by Albright and Armstrong (1982) had P:B ratios of 7.2 to 8.6 for April through September. It is clear from these studies that P:B will vary according to which portion of the year is represented, since production and biomass are usually both highest in the spring and summer. Presumably an annual based P:B is the most reliable index, since it integrates a complete seasonal cycle of population change, although the term of a single cohort could be chosen as well.

A conservative estimate may be made of the annual P:B ratio for Grays Harbor populations by assuming moderate winter biomasses and lower winter production. For this study's station 1.8 MC, a winter biomass of 1 g dry weight/m<sup>2</sup> implies an annual P:B of 8.3, while a perhaps a more realistic winter biomass of 0.5 g/m<sup>2</sup> indicates an 11.2 annual P:B. It may be presumed then that C. salmonis populations undergoing spring pulses as did station 1.8 MC and in more drastic form at the Desdemona Sands site, will have annual P:B ratios in the vicinity of 10. Where other factors intervene, such as winter immigration, strong interspecific competition, or consideration of a different time span, P:B may be considerably less than 10.

Figure 44 shows that biomass standing crop at Grays Bay underwent a winter increase to a maximum of about 2,800 mg AFDW/m<sup>2</sup> and then a spring and summer decrease to the original fall level of about 600 mg AFDW/m<sup>2</sup>. During this period, a minimum of 1,000 mg AFDW/m<sup>2</sup> (20,000 individuals/m<sup>2</sup> at 0.05 mg, based on a median length of 2.75 mm) was added to the population by immigration, and about 600 mg AFDW/m<sup>2</sup> by production. These inputs plus the remainder of the 8,228 mg AFDW/m<sup>2</sup> of production were subsequently exported or lost to predation, most of this loss occurring during the spring and summer when rates of juvenile recruitment and individual growth were high.

At Desdemona Sands, biomass standing crop increased steadily through the spring and summer to about 4,000 mg AFDW/m<sup>2</sup>. Total production, all of which occurred in this period, was 13,150 mg AFDW/m<sup>2</sup>, more than sufficient to account for the standing crop increase (in contrast to the winter increase at Grays Bay). Therefore a minimum of 9,000 mg AFDW/m<sup>2</sup> was exported from the site during the spring and summer, assuming import was negligible. More production, possibly considerably more, could have occurred shortly after the study was terminated, since population density, although declining, was still high and temperatures were warm. The

site appeared depopulated again in fall 1981, based on cursory examination (Section 4.3).

In the spring, the Desdemona Sands population maintained high population growth while the Grays Bay population declined. If enhanced spring-time predation controlled the population at Grays Bay, then such an influence was not dominant at Desdemona Sands. It is possible that the more protected nature of the Grays Bay site, or other habitat features, encouraged greater predator activity there than on the river-swept shoal at Desdemona Sands. The fact that the male:female ratio declined in the summer at Grays Bay but not at Desdemona Sands (Section 4.3) offers support for greater predator impact at Grays Bay.

Muus (1967) observed that a spring-summer succession of predators invaded the brackish Danish bay he studied. These included a flounder (Platichthys flexus), a goby (Pomatoschistus micropus), and two decapods (Crangon crangon and Carcinides maenas). He found that each predator, growing through its bay residence, initially exploited the meiofauna and later consumed larger infauna, including Corophium spp. He concluded that this predation pressure reduced or restricted standing stocks of harpacticoids, Corophium spp. and other species with high reproductive potential.

In the Columbia River Estuary, similar predator influxes may be seen in the spring and summer immigrations of Crangon franciscorum and newly metamorphosed starry flounder (Platichthys stellatus), and in the reproductive pulse of the mysid Neomysis mercedis (Higley and Holton 1975). According to Orcutt (1950), the smallest starry flounder feed on harpacticoids and later utilize Gammarus spp. and Corophium spp. in Monterey Bay, California. Several studies in the Columbia River Estuary (e.g., Haertel and Osterberg 1967; Higley and Holton 1975) have shown that both large and small starry flounder as well as several other fish species heavily utilize Corophium populations in the low salinity zone of the estuary. We have observed very small (<3 cm) flounder swimming in shallow depressions on the exposed sand flats of Grays Bay. When water-covered these intertidal habitats may be the site of strong predation pressure on harpacticoids, juvenile C. salmonis, and other meiofaunal size animals by small predators. Such strong effects on the meiofauna are not clearly established, and in fact have been argued against by several authors, especially Banse and Mosher (1980). However, there is reason to believe that predation may exert a controlling influence, in local situations at least, on C. salmonis populations in the Columbia River Estuary. In the absence of quantitative feeding data it is not possible to determine the magnitude of this influence.

## 4.5 ESTUARY-WIDE DISTRIBUTION STUDY

### 4.5.1 Relationship of Biomass Levels and Sediment Composition

Results of the stratified random survey showed that low levels of the silt and clay (fines) fraction prevailed over most of the estuary. This agrees with prior observations by Hubbell and Glenn (1973) that sand was the predominant textural grade in the flats, slopes and channels of their study. The highest levels of the fines fraction occurred in protected areas and the lowest in current-swept shoals and deep channels. Minor Channels of Baker Bay were surprisingly high in fines (and organics as well), probably because these channel included dredged ship channels that act as still-water sinks for fine sediments.

Mean sediment organic content varied from .5 to 8.6% over the 16 strata. By comparison, Sanders (1960) estimated surface organic content to be about 6 to 7% in muddy sediments of Buzzards Bay, Massachusetts, and Tenore (1972) found levels of about 4 to 6% in mud and .6% in sand of the Pamlico River Estuary, North Carolina. The range of values measured for the Columbia River Estuary appear similar to these other estuaries. Like the fines fraction, the organic content of Columbia River Estuary sediments was generally low over the estuary.

The total infaunal biomass level was loosely correlated with the fines fraction. As reviewed by Gray (1974) and Wolff (1983), various species and trophic groups respond differently to the silt and clay content and to the organic content of the sediment, according to their life history characteristics. Sanders (1958) generalized that the deposit feeders of Buzzards Bay were most abundant in muddy areas while suspension feeders favored sandy areas. While the trophic structure of the Columbia River Estuary benthos was not determined, the prevalence of deposit feeding is apparent in the dominance of such species as *Corophium salmonis*, *Macoma balthica* and *Hobsonia florida* and in the general absence of major beds of large bivalve suspension feeders. Since deposit-feeding is best supported by the rich organic deposits of protected habitats, highest biomass levels would be expected in these areas, as was observed in the Columbia River Estuary.

Mean biomass levels in the Columbia River Estuary varied between .1 g AFDW/m<sup>2</sup> (Transition Zone Main Channel Side) and 4.6 g AFDW/m<sup>2</sup> (Marine Zone Protected Flat). Most of the estuary fell into the .1 to .4 g AFDW/m<sup>2</sup> range, representing the major expanses of sandy habitats. Wolff's (1983) summary indicates that in temperate estuaries individual species often average less than 1 g AFDW/m<sup>2</sup>. In the Grevelingen Estuary (Netherlands), considerable variation in total biomass occurred seasonally (Wolff and deWolf 1977). Highest levels were 120 g AFDW/m<sup>2</sup>, which occurred in a mixed filter feeder/deposit feeder/grazer community. Deposit feeders and grazers alone, however, never exceeded 40 g AFDW/m<sup>2</sup>. A similarly mixed community in Carmarthen Bay, South Wales, studied by Warwick et al. (1978) had a mean annual biomass of 46 g AFDW/m<sup>2</sup>, most of this appearing as bivalves. Lie (1974) estimated that biomass levels averaged 13.7 g AFDW/m<sup>2</sup>, and ranged from 0.5 to 54 g AFDW/m<sup>2</sup> across 48 stations widely distributed over Puget Sound, Washington. Molluscs contributed 35% and polychaetes 5% of the station average. Wolff's (1983)

summary emphasizes the dominant contribution made by large filter feeders to the highest estuarine biomasses. He reports values near 1,000 g AFDW/m<sup>2</sup> for both mussel (Mytilus edulis) and oyster (Crassostrea virginica) beds.

In the Columbia River Estuary most of the main-stem region from Tongue Point to Baker Bay lacks major beds of filter-feeding bivalves. Mya arenaria occurs in Baker Bay and Anodonta spp. occurs in the Fresh Water Zone, but their biomass levels are not known. Neither species has been observed to occur in large dense colonies, however, and large portions of the estuary thus lack high biomasses of long-lived filter-feeders which would exploit water-borne foods. Existing species, mostly deposit feeders, apparently achieve modest biomass levels according to habitat type.

The baseline study by Richardson et al. (1977) of benthic assemblages at the mouth of the Columbia River Estuary found both biomass and numeric densities to increase with depth. The depth gradient also included increasingly fine sediment content. Biomass varied from .5 to 118 g AFDW/m<sup>2</sup> in their seasonal study. Many stations averaged less than 5 g AFDW/m<sup>2</sup>. Station 11 near the river mouth varied between 0.8 and 7.2 g AFDW/m<sup>2</sup>. This location was in 11 to 13 m of water and had about 1 to 5% fines, which is similar to the mean fines for the Marine Zone Main Channel Center inside the estuary. At .07 g AFDW/m<sup>2</sup>, however, mean biomass level of this estuarine habitat was considerably lower than that at their Station 11. Of the other estuarine habitats, the Protected Flat habitats were in the biomass range of Station 11, but sandier habitats were lower.

Part of the difference between the biomass levels of Richardson et al. (1977) and the present study may be due to their use of a larger and heavier grab sampler, which was capable of collecting deeper samples and larger animals. However, dominant species at Station 11 were small crustacea, polychaetes and a surface crawling gastropod. All of these were effectively sampled by the sampler used in the present study. It seems likely therefore that biomasses determined by this study reflect a generally lower inner estuary density level than occurs over the continental shelf in the path of the Columbia River plume.

Wide stratum confidence intervals for sediment properities did not allow rigorous comparison of stratum means. However, some patterns appear that suggest relationships which could be investigated in the future.

For the fines fraction and the organics fraction, Protected Flat habitats always exceeded Unprotected Flat habitats as well as the Main Channel Center and Main Channel Side habitats. This relation was expected on the basis of current strength effects. Among the latter three habitats, relationships among the stratum means varied. In all three salinity zones, fines of the Unprotected Flat habitats exceeded those of the two channel habitats. However, for the Marine and Transition Zones (but not the Fresh Water Zone), organics was higher in the two channel habitats than in the Unprotected Flat habitat. Thus, the two channel habitats appear to have accumulated more organics in the Marine and Tran-

sition Zone than would be expected by their fines content. Another comparison is also suggestive: the organics fraction of the Marine and Transitions Zone exceeded that of the Fresh Water Zone for both channel habitats. Taken together, these relationships suggest that organic materials may be accumulating in or associated with substrates of these deep channel habitats of the Marine and Transition Zones, an event which could be explained by particle flocculation associated with marine and fresh water mixing.

In a similar analysis of biomass means, the pattern mostly favored the Unprotected Flat habitat and the Fresh Water Zone. That is, biomass means did not follow the organics trend of suggesting trophic enrichment for the deep channel habitats.

Organics might accumulate in the deeper habitats in response to mixing events and to reverse tidal flows of saltwater along the bottom, processes which would occur less strongly in the current-swept shallower habitats. The apparent lack of response by infaunal biomass levels may indicate that such organic enhancement in deeper habitats actually does not occur, or that the single survey is not representative of the enrichment process. It may also be that the higher organics measured in the deep zones are associated primarily with the sediment water interface, and due to occasional strong currents, are not incorporated into the sediments. In this case, epifaunal organisms might benefit more than infaunal ones from the flocculation process.

#### 4.5.2 Distinctiveness of Infaunal Communities in the Columbia River Estuary

Discriminant analysis differentiated among the a priori habitats with 93% accuracy in the Marine Zone, 73% in the Transition Zone and 63% in the Fresh Water Zone. Thus habitat distinctiveness as measured in terms of community composition was good (about 75% of the stations overall were correctly classified), but diminished substantially from Marine Zone to Fresh Water Zone. The high rate of accurate classification in the Marine Zone indicates that habitat boundaries there enclosed reasonably well defined animal assemblages. Mean sediment fines in the Marine Zone exhibited the strongest differences among habitats of the three zones, also indicating better habitat definition in that zone. It is apparent, however, that accuracy of habitat classification was not dependent only on the careful choosing of a priori boundaries. A very strong influence in the classification process was oceanward trends in the composition and diversity of the animal communities. This trend involved development of progressively more complex communities toward the ocean due to the incorporation of marine-derived species which apparently were more habitat specific than those upstream. This trend was expressed in the station plot of the reciprocal averaging ordination, which showed a wedge-shaped pattern opening toward the Marine Zone. The high dispersion among Marine Zone stations in this plot as compared to the very tight grouping of Fresh Water Zone stations was created by the trend toward simpler Fresh Water Zone communities.

The greater complexity of near-ocean communities derived primarily from the polychaete and amphipod faunas. Echinoderms, coelenterates and

some other groups typical of ocean environment were not captured in the estuary. The polychaete and amphipod faunas themselves were not richly represented, even at the most marine stations, and diminished dramatically before RM-12 near Youngs Bay. Thus, a total of just 70 taxa were identified in the survey, 28 being polychaete species and 10 being amphipod species. By way of comparison, Richardson et al. (1977) identified some 425 species in their survey of the benthos outside the mouth of the Columbia River Estuary.

Dramatic changes in species richness are the rule along estuarine salinity gradients. Maximum richness typically occurs at both ends of the gradient, and only a few species, primarily of marine origin, invade the brackish water environment. Wolff (1983) summarized a line of argument to explain this paucity of estuarine species. Briefly, the argument states that speciation is less likely and extinction more likely in unstable environments, and that in any case estuaries rarely persist long enough to evolve established faunas. These factors, and the difficulty of invading the unpredictable brackish estuarine environment, have limited faunal diversity there. In the Columbia River Estuary, the strength and irregularity of the freshwater flow appears to have allowed very few species to succeed beyond the Marine Zone.

Dominant species of the Columbia River Estuary were those which occur elsewhere along the Pacific Northwest coast. Corophium salmonis, Eogammarus confervicolus, Hobsonia florida, Neanthes limnicola and Macoma balthica are common members of brackish water faunas. C. salmonis is member of a world-wide genus, several members of which inhabit west coast estuaries (Shoemaker 1949). C. salmonis is one of several Corophium species capable of entering entirely freshwater habitats (although most species require brackish to saline water), and together with C. spinicorne is found upriver to the Portland area (Blahm et al. 1979; McConnell et al. 1973; Sanborn 1973).

Bousfield (1958) described Anisogammarus spp. (=Eogammarus), C. spinicorne, Haustorius (=Eohaustorius) washingtonianus, Exosphaeroma (=Gnorimosphaeroma) oregonensis and Neomysis mercedis as members of a relatively rich euryhaline marine fauna that invades coastal streams and pools along the Pacific coast. Neanthes limnicola is also a widely distributed euryhaline species, which at times invades freshwater habitats (Stephens 1972). Hobsonia florida is introduced from Atlantic coast (North America) estuaries, perhaps rather recently. The species is now distributed widely in Pacific Northwest estuaries (Banse 1979). Macoma balthica is widely distributed in brackish water habitats (e.g., Mulscher 1973; Newell 1965; Muus 1967).

This brackish water fauna characteristic of the Transition and Fresh Water Zones of the Columbia River Estuary graded into a richer and more marine fauna at the river mouth. Beyond this zone, however, the fauna continues to change down the continental shelf under the diminishing influence of powerful Columbia River flows. Continuity of the estuary and shelf faunas is apparent in the similarity of Richardson's et al. (1978) inshore communities to the down-river estuary communities defined in the present study. Common species were Spio filicornis, Nephtys californiensis, Eogammarus confervicolus, Monoculodes spinipes and

Diastylopsis dawsoni. Continuing down the shelf, sediments are finer and the fauna denser and richer (Richardson et al. 1977). A contrast of Richardson's et al. species list with that for the estuary indicates how dramatically species richness increases with depth. For example, instead of one Tellinid clam (Macoma balthica) as found in the estuary, there were 12 species on the shelf. In addition, the shelf fauna contained over 80 polychaete species, 28 gastropod species, 55 bivalve species and 100 amphipod species. These shelf species were grouped by Richardson et al. into several animal assemblages that varied in composition and density according to season and to shifts in sediment texture created by winter storms. The assemblages were apparently distinct from other benthic assemblages studied along the Oregon-Washington continental shelf. This is in contrast to the fauna of the estuary, which includes assemblages found in other estuaries of the Pacific Northwest.

Four species groups or community types in the estuary were identified through reciprocal averaging ordination. Group 1 (Corophium salmonis, Corbicula manilensis, Heleidae, Chrionomidae, Oligochaeta, Fluminicola virens, Goniobsis plicifera and Neanthes limnicola) was oligohaline-freshwater oriented. Group members apparently invaded all Fresh Water Zone habitats. Group 2 (Oligochaeta, Hobsonia florida, Macoma balthica, Turbellaria, Neanthes limnicola and Corophium salmonis) characterized fine sediment habitats of the Transition and Marine Zones. Group 3 (Eogammarus confervicolus, Echaustorius estuarius, Neanthes limnicola, Rhynchocoela, Paraphoxus milleri, Corophium salmonis and Oligochaeta) was abundant in sandy habitats of the Transition Zone. Group 4 (Rhynchocoela, Paraphoxus milleri, Archaeomysis grebnitzkii, Paraonella platybranchia and Spio spp.) was abundant in sandy habitats of the Marine and lower Transition Zones. These groups were not defined in a strict functional or trophic relation sense. Rather, they are descriptive and follow the intent of Mills' (1969) definition of a community as a group of co-occurring organisms, presumably interacting with each other and the environment, and separable by means of ecological survey.

Although these ordination groups suggest a commonality of community structure across some habitat boundaries, discriminant analysis found that habitats in the Marine Zone, and to a lesser extent in the other two salinity zones, contained mostly differing community structures. Different results according to analytic procedure are due to contributions made by minor taxa and to differences in density levels, which more strongly affected the results of discriminant analysis than those of ordination analysis, since ordination double standardizes the data (by species and by station) before computing the axis scores. Thus, where proportional relations among densities were similar, the axes scores were similar, and stations with similar faunas but different density levels were grouped together. This result was especially apparent in the Fresh Water Zone. The value of the species groups obtained from the ordination plot is that they focus on differences in species content and not on overall density level.

Carriker (1967) provides a model of estuary segmentation along the salinity gradient based on the Venice system and that of Day (1951; 1964). This model classified successively fresher portions of the estuary as polyhaline (18-30 ppt), mesohaline (5-18 ppt), oligohaline (0.5-5

ppt) and limnetic (<.5 ppt). These divisions apply most usefully to homiohaline estuaries where gradients in salinity (and animal communities) are mostly stable. Other (poikilohaline) estuaries exhibit tidally and seasonally variable salinity gradients, and provide different problems to the estuarine community (Boesch 1977). According to Boesch (1977), large-scale seasonal salinity changes produced little response by the benthos of the Brisbane Estuary (Australia), but has caused major community changes in some other estuaries.

Sanders et al. (1965) define three types of estuaries in terms of the pattern of salinity change. Stable estuaries are those with low flushing rates and stable salinity gradients. Very large systems tend to be stable. Fluctuating estuaries are small systems having regular (tidal) cycles of salinity change throughout their length. Gradient estuaries, intermediate in size, exhibit variable salinity patterns along their length: the upper region tends to be constantly low in salinity and the lower region constantly high in salinity, while in the middle regions salinities vary sharply. The observation of these authors is that changes in interstitial salinities follow those of overlying water more closely in gradient estuaries than in fluctuating estuaries, the reason being that the regular pattern of short-term salinity changes in the fluctuating estuary creates an integrative response by the interstitial salinity. The result of these differences in interstitial salinity fluctuation is that infaunal animals are confronted by more difficult osmoregulatory problems in sediments of a gradient estuary than in sediments of a fluctuating estuary. There is therefore a greater species reduction in the gradient than in the fluctuating (or stable) estuary. A second factor which influences the interstitial salinity response is sediment texture. Muddy substrates allow less exchange than do loose sand substrates, and therefore have more stable interstitial salinities.

The Columbia River Estuary is quite large but has a high flushing rate and experiences strong salinity changes due to winter and spring freshets and to large tidal exchanges. This estuary is thus gradient in nature, and probably has greater salinity changes than indicated by the descriptions of Sanders et al. (1965). Strong currents create a predominantly sandy environment throughout the estuary. Thus both salinity patterns in the estuary and the character of its substrates create osmoregulatory problems for infaunal species. It appears then that the estuary offers a difficult environment, especially in its middle reaches. These observations provide some insight into the patchy distribution and low diversity of infaunal communities in Transition and Fresh Water Zones of the estuary.

The Columbia River Estuary, like most other estuaries, is by nature an unstable environment. As reviewed by Boesch (1974) and Tenore (1972), unpredictable systems are characterized by low species diversity. Such systems have been thought to be more susceptible to disturbance since loss of one or a few species implies greater impact on simplified food chains than on complicated ones. This argument ignores the nature of the species composing communities of high vs. low diversity. In an unstable environment such as an estuary, many species exhibit opportunistic life history characteristics which allow them to adjust rapidly to changing conditions. These characteristics include high reproductive potential,

rapid dispersal, large populations and high mortality rates. More stable environments have more species with the opposite characteristics. It is probable that opportunistic species respond better to stress and comprise more resilient, if simpler, communities. Thus, communities in more saline, stable regions along the salinity gradient might suffer more from a given stress than those in a less saline, more fluctuating environment.

This argument could be carried to the Columbia River Estuary with its few widely distributed species to imply that its species might withstand severe stresses, assuming the species have sufficiently opportunistic life history characteristics. However, it is obvious that the argument is mute if the stress is such that the range or density of one of these few species is severely reduced. There appears, for example, no obvious replacement, given the physical attributes of the estuary, for the amphipod Corophium salmonis, which figures so strongly in the estuary's food chains. It is important therefore to recognize that the estuary's physical characteristics have formed a relatively simple and perhaps sensitive trophic system.

#### 4.5.3 Utility of the Stratified Random Survey Technique

The stratified-random design used in this survey provided an efficient means of data reduction, while necessarily generalizing about habitat and faunal distributions. Salinity zone boundaries were perhaps the most arbitrary divisions assumed, since large-scale salinity changes occur over the estuary. Location of the Fresh Water Zone to Transition Zone boundary appears to have been supported, in this survey at least, by observed changes in community structure. The Transition Zone to Marine Zone relationship was more diffuse, and probably can be improved in future work by giving consideration to the greater salinity intrusions which occur along deeper contours. This would likely create better definition of stratum communities (i.e., stratum means would be more accurate and have lower variances), although the zone boundaries would still impose sharp divisions on gradational changes in community structure. The zone names are of course not literal descriptions. The Marine Zone is mostly brackish and occasionally freshwater, while low salinity water periodically invades portions of the Fresh Water Zone.

Both sediment and biological properties exhibited high variability within individual strata. Much of this variability probably derived from local current and depositional patterns generating patchily distributed habitat conditions. The episodic nature of population increases and decreases by some of the estuary's dominant infaunal species must also have contributed to the high variances. Such within-stratum variation mostly cannot be removed by refining stratum definitions, and can only be handled by increased sampling effort.

The habitats as defined generated mostly expected patterns in sediment properties and density, with Protected Flat habitats having higher levels of sediment fines and biomass than the Unprotected Flats, Main Channel Center and Main Channel Side habitats. The Minor Channel habitat, with its unexpectedly high fines and biomass levels in the Marine and Fresh Water Zones probably deserves re-definition. The Marine and Fresh Water Zone Minor Channel samples were collected in small channels

of the bays and among islands, while the Transition Zone samples were collected in portions of the north channel and represent a deeper and a more heavily scoured habitat which could be combined with other deep channel habitats.

Habitat definition is most difficult to achieve in the Freshwater Zone due to the complexities created by the island system. However, the survey has shown that in the areas studied, community structure was both simple and similar across Fresh Water Zone habitats. Confidence intervals of means for this zone were not particularly wider than those of the other zones. Therefore there may be little need for more sophisticated boundary definition in future studies, depending on the goals of the research.

Until substantiated by further investigations on an estuary-wide basis, the results of this survey should be considered as preliminary and not definitive, since the survey provides only a single view of a dynamic fauna whose density and distributional patterns may be presumed to change on seasonal and annual bases. This concern was strongly stated by Boesch (1973) in describing the results of benthic studies conducted near the mouth of the James River, Virginia. Boesch states:

The gross nature of seasonal changes in these macrobenthic assemblages indicates that 'one-time' surveys of temperate estuarine benthos may be of limited value. The associations in the Hampton Roads areas are not static entities, but are very dynamic, loosely cohesive, and variable.

The September timing of the Columbia River Estuary survey means that many populations had achieved their highest density levels and were declining due to predation and seasonal factors. Marine species were probably distributed near their upstream limits due to reduced late summer freshwater river flow. Winter freshets and spring snow melt likely push the distributions of many species downstream and limit upstream juvenile recruitment. An understanding of these possibly oscillatory changes in distributional pattern requires seasonal information not developed in the CREDDP studies.

Stratified-random surveys of estuarine benthos are presently few in number, but are recommended by their ability to generate unbiased means and variances for testing differences among strata (Cuff and Coleman 1979). McIntyre (1971) specified that the three objectives of marine benthos surveys are to make valid statements about the number of species present, the distribution of the fauna, and the density of the fauna. Species accumulation curves have often been used to establish the adequacy of survey designs, emphasizing the first objective and frequently leading to excessive sampling effort at individual stations. Recent studies by Coleman et al. (1978) and Cuff and Coleman (1979) have shown that sampling effort need not be as large as originally supposed for a stratified random survey and that where regional density comparisons are the objective, a single replicate per station is the optimal sample allocation under most conditions. Saila et al. (1976) in determining optimal sample size for stations and strata, concluded that from 1 to 3 samples per station and from 7 to 34 per stratum would allow valid conclusions

about density differences for the benthos he studied. The stratified design also accomplishes the other two objectives of McIntyre, since species accumulation curves may be developed for strata as well as for stations (Cuff and Coleman 1979), and distributional patterns are established where, as in the present study, stations are broadly distributed over the estuary into all known habitats by the stratum allocation procedure.

Future benthic studies in the Columbia River Estuary could profitably employ stratified-random designs, either in estuary-wide studies or in investigating local community variation along natural or man-caused environmental gradients. These studies should seek to define relatively homogenous strata and establish suitable sample size levels. Saila et al. (1976) provide some equations which may serve as guidelines for this; they based their estimates on the criteria of defining a stratum within 50% of the transformed mean with 90% confidence. This is less rigorous than implied by the 95% confidence limits computed in the present survey, but is perhaps more realistic in view of the high variance levels common to environmental studies.

#### 4.5.4 Recommendations for Further Study

While determining broad patterns of animal distribution and estimates of density levels, the present survey left several areas uninvestigated. Important topics requiring further study include seasonal and annual changes in distributional patterns in relation to environmental changes, and life history properties of dominant species. In addition, the character of the invertebrate fauna of the freshwater marsh drainage channels requires study, especially as this fauna contributes to fish production. Studies of other estuarine marsh systems, for example the Fraser River of British Columbia (Dunford 1975), have established that juvenile salmonids and other fish species regularly invade these dendritic systems and consume both aquatic and terrestrial invertebrates. The marsh fauna and the extent of their utilization in the Columbia River Estuary are as yet uninvestigated. The invertebrate fauna and population dynamics for the marshes fringing Youngs Bay and Baker Bay are also relatively unknown. A single survey of Youngs Bay marshes by Higley et al. (1979) found high densities of Corophium spinicorne, Gnorimosphaeroma oregonensis and Eogammarus confervicolus, among other species.

Several infaunal taxa require taxonomic study. These are Turbellaria, Nematoda, Rhynchococla, Oligochaeta, Chironomidae and Heleidae. Species identification for these groups would clarify distributional patterns and analysis of community structure.

The survey also left the large bivalves (Anodonta spp., Mya arenaria, Clinocardium nuttallii) and mud shrimp (Callinassa californica) largely unstudied, since these species require entirely different study techniques from those of the smaller macrofauna. Anodonta spp. appears to be localized in the Fresh Water Zone, and Mya arenaria, Clinocardium nuttallii and Callinassa californica in the Marine Zone (presumably most are in Baker Bay). Production levels, habitat relations, and trophic relations are presently unknown for Columbia River Estuary populations of these species.

It is important to recognize both the simplified character of the Freshwater and Transition Zone communities, and the dominating role of a very few species. Comparisons among these simple communities may not lend themselves to such common methods of community structure analysis as the computation of diversity indices. Rather, more can probably be learned from the study of the population dynamics of the major species in relation to each other and to habitat variation. Such work would involve study of species behavior, physiology and reproduction in response to environmental variation, and controlled field studies of factors inducing species colonization and departure. Certainly, because of its very wide distribution (from Baker Bay to at least RM-100), its contribution to estuarine food chains, and its dominance of the simple estuarine infauna, Corophium salmonis should become as well studied as any estuarine species.

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APPENDIX A

Summary of life history properties  
of the benthic infauna of the Columbia River Estuary

This section summarizes the life history characteristics of the benthic infauna taxa collected in the distributional survey (Section 3.5). The information is presented in chart form in Figure 54. Literature on which the characterizations are based is numerically coded in Figure 54; Table 37 interprets these codes, and Table 38 lists the references.

In Figure 54, each taxon is classified into one or more types within the following categories: salinity range, substrate preference, life style, feeding type, reproduction/dispersal mode and season of reproduction. Especially for Pacific Northwest species, literature on these topics is sparse. It was therefore necessary to base some of the classification on data from temperate zone estuaries outside the Pacific Northwest. Where even this type of information was unavailable, information for related taxa was incorporated; this information is indicated by "R" entries in Figure 54. Usually, "R" entries were based on data for other members of the genus, but in some instances they were based on general family characteristics suggested by the author. Several taxa (e.g., Nematoda, Eteone spp.) were not identified to species in the present study and classifications for these taxa were all necessarily of the "R" type.

Many of the species vary in their life history patterns according to regional conditions, so that, for example, reproductive activity by a species may be more seasonally restricted in this region than in an area with consistently higher temperatures.

A particular species may, of course, occur in more than one salinity zone or more than one substrate. It is also true that some species can switch feeding modes (e.g., from surface deposit feeding at low tide to suspension feeding at high tide, as in Macoma balthica), and can vary their reproductive strategies (e.g., from benthic larvae to pelagic larvae according to nutritional resources, as occurs in Capitella capitata). This flexibility is characteristic of the opportunistic life histories adopted by many estuarine species. The result is that classification within each life history category is not according to mutually exclusive types.

Based on the qualifications discussed above, especially the paucity of suitable literature information, it is obvious that Figure 54 cannot be viewed as a definitive life history classification. Instead it represents an initial summary and serves as a rough guide, and is certainly open to revision.

The classification categories are described below.

- (1) Salinity Range: The ranges utilized are those of the Venice system of classification of brackish waters (Symposium on the Classification of Brackish Waters 1959). This classification is best suited to estuaries having relatively stable salinity gradients. In an estuary such as the Columbia River Estuary where salinity intrusion varies greatly on both tidal and seasonal scales, a species' distributional pattern is probably determined more by its tolerance to salinity extremes than by

(text continued on pg. A-16)



	SALINITY RANGE				SUBSTRATE	LIFE STYLE				FEEDING TYPE				REPRODUCTION DISPERSAL				SEASON OF REPRODUCTION				LITERATURE							
	TIDAL FRESH < 0.5 ppt	OLIGOHALINE 0.5-5 ppt	MESOHALINE 5-18 ppt	POLYHALINE 18-30 ppt		MUD	MUDDY-SAND	SAND	SUBMERGED OBJECTS	EPIBENTHIC MOBILE	EPIBENTHIC NON-MOBILE	EPIFAUNA TUBE-DWELLER	INFAUNA TUBE-DWELLER	MOBILE BURROWER	NON-MOBILE BURROWER	SUSPENSION	SURFACE DEPOSIT	SUB-SURFACE DEPOSIT	PREDATOR	SCAVENGER	ADULT/JOV. MIGRATION		PLANKTONIC LARVAE	BENTHIC LARVAE	BENTHIC YOUNG	BROODED LARVAE/YOUNG	WINTER	SPRING	SUMMER
<i>Halaceroes fuliginosus</i>									R						R														14
<i>Manayunkia aestuarina</i>		■								■					■	■					■								10,14,15,19
<i>Mediomastus</i> spp			R	R	R	R					R				R														10,14,24,46
<i>Neanthes limicola</i>	□	■	■	■	■	■	■	■		■																			31,38-42
<i>Nephtys californiensis</i>			□	□	□	□	□	□		□								■			R								1,6,7,14,18,23-25,43,113
<i>Ovantia fusiformes</i>			■	■	■	■	■	■		■																			7,10,14,23,24,113
<i>Paranella platybranchia</i>			□	□	□	□	□	□			?																		24
<i>Polydora ligni</i>		■	■	■	■	■	■	■		■																			10,11,14,15,27,44,45
<i>Pseudopolydora kempii</i>		■	■	■	■	■	■	■		■								□											19,36,47,48,113
<i>Pygospio californica</i>		R	R								R	R	R	R	R	R					R	R							1,10,14
<i>Pygospio elegans</i>		■	□								R	R	R	R	R	R													6,7,14,15,19,36,113
<i>Scolecotele squamata</i>										R	□				R						R	R							1,14,24,49,50,113
<i>Scoloplos armiger</i>		R	■	■	■	■	■	■			□				■														1,6,7,14,15,21,24,28,113
<i>Spio butleri</i>			□								R	□			R						R	R							14,113
<i>Spio filicornis</i>			■	■	■	■	■	■		■					R	■					■	■							1,7,10,14,24,50,51,113
<i>Spiophanes berkeleyorum</i>			■	■	■	■	■	■					R	R	□						R	R							7,10,14,21,23,24,113
OLIGOCHAETA																													
Oligochaeta spp									R			R				R	R					R							5,24
GASTROPODA																													
Ancylidae spp	■	■								■	■	■	■	■	■	■													5,110
<i>Fluminicola virens</i>	■																												5,110
<i>Goniobasis plicifera</i>	■				□	■	■	■		■																			5,52,53,110

■ PROMINENT CHARACTERISTIC OF SPECIES

□ OCCASIONAL CHARACTERISTIC OF SPECIES

R CHARACTERISTIC FOUND IN RELATED TAXON

? POSSIBLE CHARACTERISTIC OF SPECIES  
(INFORMATION INCOMPLETE)

Figure 54. (cont.)

	SALINITY RANGE				SUBSTRATE				LIFE STYLE				FEEDING TYPE			REPRODUCTION DISPERSAL			SEASON OF REPRODUCTION			LITERATURE							
	TIDAL FRESH < 0.5 ppt	OLIGOHALINE 0.5-5 ppt	MESHALINE 5-18 ppt	POLYHALINE 18-30 ppt	ASD	MUDDY-SAND	SAND	SUBMERGED OBJECTS	EPIBENTHIC MOBILE	EPIBENTHIC NON-MOBILE	EPIFAUNA TUBE-DWELLER	INFAUNA TUBE-DWELLER	MOBILE BURROWER	NON-MOBILE BURROWER	SUSPENSION	SURFACE DEPOSIT	SUB-SURFACE DEPOSIT	PREDATOR	SCAVENGER	ADULT/ADV. MIGRATION	PLANKTONIC LARVAE		BENTHIC LARVAE	BENTHIC YOUNG	SCORDED LARVAE/YOUNG	WINTER	SPRING	SUMMER	FALL
<b>BIVALVIA</b>																													
<i>Clinocardium nuttallii</i>			□	■	□	■	■		■				■	■							■						■		24,27,68,109
<i>Corbicula manilensis</i>	■	□			□	□	■		■			■	■	■	□							■			■	■	■	■	54-60,110
<i>Macoma balthica</i>			?	■	■	■		□				■	■	■	■						■					■	■	■	15,36,61-67
<i>Mya arenaria</i>		?	■	■	□	■	■					■	■	■	■									?		■	■	■	20,24,27,29,68-70,109
<i>Siliqua patula</i>			■	■		■	■					■	■	■	■											■	■	■	68,109
Sphaeriidae spp	■			■		□						■	■	□									■		■	■	■	■	71,110
<b>OSTRACODA</b>																													
Ostracoda spp					R	R	R	R			?				R		R	R			R					?	?		5,6
<b>MYSIDACEA</b>																													
<i>Archaeomysis grebnitzkii</i>				■		■						■	□	■								■		■	■	■	■	■	1,93,116
<i>Neomysis mercedis</i>	■	■	■	?				■									■	■	■			■	□	■	■	□	■	■	1,73-76
<b>CUMACEA</b>																													
<i>Diastylopsis dawsoni</i>						R	■	?			?	?		?	?	?	?						■						2,4,24,32
<i>Hemileuon</i> spp								?			?	?		?	?	?	?						■						4,32
<i>Lamprose</i> Sp A						R		?			?			?	?	?	?						■						4,24,32
<b>ISOPODA</b>																													
<i>Gnathasphaeroma oregonensis</i>	■	■	■	■	■	■	■	■				■	■						R	■			■						24,27,77-82
<i>Saduria entomon</i>	■	?	?	?	■	□		■				■	■									■							82,83,111

■ PROMINENT CHARACTERISTIC OF SPECIES

□ OCCASIONAL CHARACTERISTIC OF SPECIES

R CHARACTERISTIC FOUND IN RELATED TAXON

? POSSIBLE CHARACTERISTIC OF SPECIES  
(INFORMATION INCOMPLETE)

Figure 54. (cont.)



Table 37. Interpretation of Literature Codes Used in Figure 54.  
Table 38 lists the References.

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| 31. Higley, D.L.; Jones, K.K.;<br>Wilson, S.L.; Holton, R.L.<br>1982       | 70. Pfitzenmeyer, H.T. 1962                | 114. Eliason, A. 1962                                  |
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its response to average salinity as suggested by the set boundaries provided by Venice classification. However, the classification is the one most often referred to in the literature, and is useful within the limitations stated. Note that a species need not occur throughout a salinity zone in order to be recorded for that zone. The ranges are approximate in any case, and are not to be taken as definitive.

- (2) Substrate: The primary subject of the summary chart is the infauna, which precludes some taxa that are exclusively pelagic or attached to hard substrates. However, many taxa regularly move between rock or vegetation shelters and soft substrates, and are therefore at least temporarily part of the infauna. Other species may build tubes either in soft substrates or on solid surfaces. These variations are provided for by including "submerged objects" along with the three soft substrate types.
- (3) Life Style: Six life styles are utilized to characterize each species' relation to the substrate. As might be expected, some animals do not fit the types well, and the classification must therefore be somewhat arbitrary. As used here, the meaning of each type is as follows:
  - Epibenthic mobile - moves freely over the substrate surface.
  - Epibenthic non-mobile - mobility slight in relation to its body size.
  - Epifaunal tube dweller - builds tubes on substrate surface.
  - Infaunal tube dweller - builds tubes within soft substrates.
  - Mobile burrower - moves freely within soft substrates.
  - Non-mobile burrower - horizontal mobility within the substrate is slight or infrequent in relation to animal size.
- (4) Feeding Type: Animals are classified according to their predominant activity. Overlap may occur, as for example when deposit feeders consume small organisms and are therefore technically predators. The manipulative and selective processes of deposit feeding by burrowing crustaceans presumably differ from those executed by most burrowing worms. However, these and similar distinctions are not made here.
- (5) Reproduction/Dispersal: Divisions within this category suggest a species' dispersal ability, which is an important determinant of success in a physically dynamic environment such as an estuary. Planktonic larval stages and adult migration along the bottom or vertically into tidal currents are principal mechanisms of dispersal. Dispersal also involves the danger of loss to the open sea.

(6) Season of Reproduction: The seasons are defined as follows:

Winter: December-January-February

Spring: March-April-May

Summer: June-July-August

Fall: September-October-November.

APPENDIX B

Quality assurance procedures

The procedures followed to assure the proper level of gear performance and data accuracy are reviewed in this section. Those procedures concern such activities as gear maintenance, sample collection, preservation and processing, and data analysis.

1. Record Keeping and Sample Labeling: Standardized record sheets were developed for both field and laboratory data. These sheets utilized a hierarchical organization of data records based on type of study, location and type of data. Data recording was either directly on computer coding forms or required only a single transcription to these forms. Errors of transcription were thereby minimized. Sample labeling followed the same hierarchical system and utilized a double labeling system (inside and outside of sample container), which was extended to the smallest subsamples (e.g., vials of identified animals). Errors due to lost or misidentified samples were thereby reduced to zero levels. A log of sample collection and analysis was kept for each sample set.

2. Gear Performance: The principal pieces of gear utilized were grab samples, coring devices and a portable salinometer. Sampling gear was regularly inspected and observed during and between sampling trips. This gear is not complicated, and mal-adjustments were readily observed. Portable salinometer readings were corrected by reference to a standardization curve relating its readings to those of laboratory instruments. Field performance was regularly checked using resistors that produced known conductivity readings. Where the accuracy of the salinometer was in doubt, water samples were obtained and analyzed by hydrometer in the laboratory.

3. Sample Collection: In sample collection, several criteria were observed to prevent retention of incomplete samples. For grab samples, an even penetration of both jaws was required, as judged by equal amounts of sediment on both sides of the sample; any sample which evidenced leakage was discarded. All core samples were collected by hand, allowing accurate control of sample depth and retention. Sample contamination was avoided by thoroughly washing the samplers, stands and containers prior to use. Sediment samples were chilled and later frozen for storage to stabilize the organic fraction.

4. Sample Processing: Formalin preserved samples were washed, screened, labelled and stored in alcohol according to an established set of procedures. These procedures insured that the damage and loss of animals was minimal and that cross-sample contamination was unlikely. A vibrator-motor type shaker device was employed to gently and efficiently screen the samples. Use of the motor-driven device reduced variability among workers in screening efficiency. Screens were carefully scrubbed and rinsed between samples. Screen sizes were adjusted to the goal of the particular study. A 0.5 mm screen was employed for distributional studies, and either 0.25 or 0.125 mm screens, depending on the species investigated, were used in life history studies to assure capture of juveniles. Each sample was sieved twice on the appropriate screen: once upon transfer to alcohol, and again prior to sorting. Subsequent handling employed very fine mesh screens. Efficiency of animal picking and sorting was checked by repicking of about 5% of the samples. This was sufficient to identify and correct inconsistencies among workers. Deter-

mination of animal ash-free dry weights was based on a twostage drying and ashing procedure. Separate containers were constructed to hold the animals for each weight determination, and these were handled with forceps and stored in dessicators between weighings. The Cahn electrobalance model G used was calibrated on each use.

5. Data Coding and Analysis: Computer coding and punching was validated by double-punching or by back-reading computer data listings to raw data forms. Accuracy of computer run outputs was rarely in question, since commercial statistical packages or well-established in-house programs were generally employed. These runs, which employed complex statistical routines, were verified by checking data input and program control statements. Some newly written data management programs were checked against sets of test data before they were put to regular use.